MASARYK UNIVERSITY

Faculty of science

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INTERDISCIPLINARY INVESTIGATIONS INTO THE NATURE OF ECOLOGY AND EVOLUTION

Postcards from along the road
during my first quarter century of research

Habilitation thesis

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JEFFREY CLARK NEKOLA.
Interdisciplinary investigations into nature of ecology and evolution.

ABSTRACT

Why are there so many species of life on Earth? Why are they found where they are? How do they live together? How have they evolved? Why do they look the way they do? What do they tell us of the past and what do they suggest about the future? And how can they and humanity coexist in this finite world? These questions - and others - underlie my research. My primary focus is to understand the mechanisms which have given rise to our diverse world and the things we need to do to protect it. This thesis represents a current state of play across my interdisciplinary foray into the nature of ecology, accumulated during the first 25 years of research. This work begins with an overview of why I have been active in so many ecological fields, prefaced on the ancient Indian parable of the Blind Men and the Elephant. Following this, I have broken my working into seven major categories, ranging from Taxonomy, Faunistics, and Floristics through Population and Community Ecology, Spatio-temporal Ecology, Biogeography and Macroecology, Ecological Theory and Modeling, Conservation Biology, and Human Macroecology and Sustainability. The document ends with a concluding set of synthetic ideas that have emerged from this intergrated multi-scale series of analyses.

ACKNOWLEDGEMENTS

There have been innumerable people who has assisted my research efforts over the last quarter century – too many to individually name here. But among them a few rise to the surface. First, my PhD advisor Peter White has encouraged me from the start of my career to think broadly and holistically about ecological questions. I am grateful for the encouragement that Robert Cameron, Douglas Larson, Clifford Kraft, James Brown, and Brian McGill have provided over the years. I would likely not have stayed in the field without their efforts. I also greatly appreciate those over the last decade who have financially helped me keep the lights on in my lab and home, in particular Charles Drost, Ken Hotopp and Ben Hutchens. Lastly, I deeply thank Michal Horsák, Milan Chytrý and everyone else in the Department of Botany and Zoology at Masaryk University for offering me a career lifeline and opportunity to continue my research within the field.

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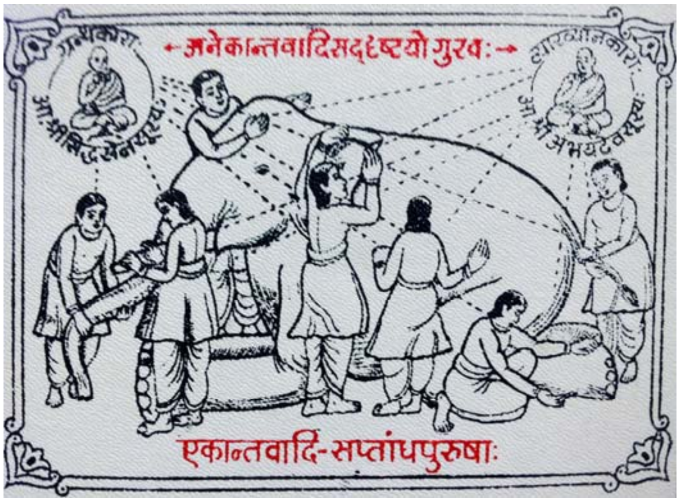

A group of blind men heard that a strange animal, called an elephant, had been brought to the town, but none of them were aware of its shape and form. Out of curiosity, they said: "We must inspect and know it by touch, of which we are capable". So, they sought it out, and when they found it they groped about it. In the case of the first person, whose hand landed on the trunk, said "This being is like a thick snake". For another one whose hand reached its ear, it seemed like a kind of fan. As for another person, whose hand was upon its leg, said, the elephant is a pillar like a tree-trunk. The blind man who placed his hand upon its side said, "an elephant is a wall". Another who felt its tail described it as a rope. The last felt its tusk, and stated an elephant is hard and smooth and like a spear. – **Buddhist Udana 6.4**

Six blind elephants were discussing what men were like. After arguing they decided to find one and determine it by direct experience. The first felt the man and declared, 'Men are flat.' After the other blind elephants felt the man, they agreed. – **Mark Hartman**

We have to remember that what we observe is not nature in itself, but nature exposed to our method of questioning. – **Werner Heisenberg**

INTRODUCTION

Why are there so many species of life on Earth? Why are they found where they are? How do they live together? How have they evolved? Why do they look the way they do? What do they tell us of the past and what do they suggest about the future? And how can they and humanity coexist in this finite world? These questions - and others - underlie my research. My primary focus is to understand the mechanisms which have given rise to our diverse world and the things we need to do to protect it.

As intimated by the ancient Indian parable of the Blind Men and the Elephant, the ability to accurately interpret large-scale pattern – and identify potential underlying mechanism – is greatly enhanced by viewing systems through multiple lenses, preferably at different observational scales. This is especially important for ecological systems which range from sub-cellular to global scales and include multiple potential focal entities ranging from molecules to biomes. They are arranged into nested hierarchies of components, ranging from organic molecules and cells through populations, species, guilds, and trophic levels. They require the continual input of energy, material, and information to maintain their highly organized, far-from-equilibrium thermodynamic states. Even the simplest ecological system contains thousands to billions of individuals of tens to thousands of different species, ranging from unicellular prokaryotes, protists, and fungi to multicellular plants and animals. These individuals and species interact with each other and their extrinsic abiotic environment in inherently non-linear ways. Such relationships are neither entirely deterministic nor stochastic, include positive and negative feedbacks, and often possess long-lasting contingent effects across both space and time.

Discovering general processes supporting and maintaining diversification thus by necessity requires an interdisciplinary focus. While this can certainly be accomplished via collaboration – and I have participated in many such projects – I have also found it useful to be interdisciplinary within my own brain. In this way I maintain hands-on, real-word experience across the full range of biodiversity topics, and can use this knowledge to identify common threads and understand potential analytical pitfalls. Often this leads to novel insights. While the specialization of research programs can lead to fundamental discoveries, it is important to remember that for almost a century biological and ecological research was conducted by investigators who held expertise across a wide breadth of the natural sciences. 19th Century field naturalists like Charles Darwin and Alfred Russell Wallace made lasting and often radical impacts on the field, not the least of which was the development of evolutionary theory. Given the complexity of ecological systems, some advances may only be possible via the inductive, holistic, and non-experimental techniques pioneered by these scientists. In combination with the modern tools of contemporary ecology, the field naturalist model can thus serve as an avenue for important future advances in ecological theory.

Inspired by the astonishing breadth of knowledge accumulated by investigators such as Iowa's Bohumil Shimek, who became a national authority in botany, malacology, ecology, paleoecology, and glacial geology (as well as being a close personal friend of Tomáš Masaryk and champion for Czechoslovakian independence), I have organized my research program upon the field naturalist model to address fundamental issues in the diversification and organization of ecological communities. As a result, I have vertically integrated my research activities to range from organism taxonomy through population, community, and spatiotemporal ecology to biogeography, macroecology, and ecological theory and modeling. To ensure that my outlook does not become myopic, I have also horizontally integrated this program across three divergent taxa groups: vascular plants (sessile autotrophs), lepidoptera (mobile heterotrophs), and terrestrial gastropods (functionally sessile heterotrophs). In addition, I have maintained an active field research program which spans thousands of study sites on three continents. I am particularly interested in documenting findings that challenge current paradigms, as it is through such observations that scientific revolutions are based.

The essential component of such an eclectic research program is to do what the blind men in the above parable did not: integrate their findings to allow documentation of large-scale, cross-system reality. Accomplishing this task requires not only the ability to be expert within multiple frames of reference, but also the ability to take a cross-system philosophic perspective to identify potential correspondences and synergies. And like the elephants in the second parable, it is essential that the limitations of given observational approaches and deductive / inductive strategies be understood. Thus, as intimated by Heisenberg, by observing nature and biodiversity through multiple methods of questioning, it may be possible to glimpse the true nature of nature.

Over the course of the last quarter century I have published 75 peer-reviewed works. As of October 27, 2017 these have generated 5266 citations with an H-index=26, a G-index=72, and an Age-Weighted Citation Rate=443.2. My research activities can be roughly grouped into seven categories: (1) Taxonomy, Floristics and Faunistics; (2) Population and Community Ecology; (3) Spatio-Temporal Ecology; (4) Biogeography and Macroecology; (5) Ecological Theory and Modeling; (6) Conservation Biology; and, (7) Human Macroecology. Each is represented in the following document by its own section. Each section leads off with a summary statement of my research activates in that field, followed by a list of publications, and then by representative examples of published articles.

Section I: Taxonomy, Floristics, and Faunistics

By being independent evolutionary units, species are one of the basic units underlying ecological pattern and process. An accurate understanding of taxonomy and the valid taxa known within a given system is thus a vital foundation for most ecological and biogeographic investigations. For this reason, I maintain an active interest in taxonomy, floristics, and faunistics.

6 of the approximately 75 North American *Vertigo* species

Much of my recent work centers on terrestrial gastropods, where I have named new species, revised taxonomic concepts, and enumerated the taxa and distribution (both geographic and ecological) of both regional and local faunas based on nDNA and mtDNA sequence, shell features, ecological preferences, and biogeography. I have just completed a global phylogenetic analysis of the micro-mollusk genus *Vertigo* based on analysis of nDNA (ITS1 and ITS2), and mtDNA (CytB and 16S) amplicons from 91 putative taxa and 398 individuals. Using a consensus across both sets of DNA sequence, shell features, ecological preferences, and biogeography, six subgenera and 87 species or subspecies are empirically validated. This work demonstrated: (1) a suite of diagnostic shell features usually exists to demarcate each species-level taxon, though these are often not the features historically used; (2) ecological preferences evolve more slowly as compared to shell features; (3) subgeneric transcontinental ranges are ubiquitous; (4) 1/3 of all species possess continental or trans-continental ranges, with very few having range extents <1000 km.; (5) all subgenera and fully 2/3 of the global *Vertigo* taxa reside in North America, more than 2½ times the number found in central and eastern Asia, the second most diverse region. This is similar to several other molluscan groups for which North America serves as the global biodiversity hotspot. Earlier work also documents that diversification in the genus appears synchronous with past episodes of rapid global environment change.

Determination of general trends and potential underlying mechanism requires that these analyses be replicated in other distantly related groups. The Pristilomatidae are an obvious target being not only in a different superfamily but also small (2-8 mm in diameter) and diverse, representing the fifth largest family within the North American fauna (64 recognized species). *Paravitrea* (42 species) is the sixth most speciose genus. Unlike *Vertigo* many Pristilomatidae have very limited ranges (often only a few counties in extent) with 100% of *Pilsbryna* species, 90% of *Paravitrea* species and of 73% *Pristiloma* species being listed as Globally Threatened or higher. Species-level diagnoses have historically relied on the number, shape, and placement of lamellae across shell ontogeny. This is troubling given the significant incidence of ecophenotypic and biogeographic plasticity in these features in other genera. As a result it is unclear how many valid species-level groups actually exist or what their true biodiversity, biogeographic and evolutionary patterns represent.

Representative Publications
[number of citations as of October 27, 2017]

1. Peer-reviewed Books:

Schlicht, D.W., J.C. Downey & **J.C. Nekola**. 2007. *The Butterflies of Iowa*. University of Iowa Press. **[26]**

2. Peer-reviewed Articles:

Nekola, J.C., S. Chiba, B.F. Coles, C.A. Drost, T. vonProschwitz & M. Horsák. *In press.* A phylogenetic overview of the genus *Vertigo* O. F. Müller, 1773 (Gastropoda: Pulmonata: Pupillidae: Vertigininae). *Malacologia.*

Nekola, J.C. & B.F. Coles. 2016. Supraspecific taxonomy in the Vertiginidae (Gastropoda, Stylommatophora). *Journal of Molluscan Studies*. 82:208-212. **[4]**

Nekola, J.C., B.F. Coles & M. Horsák. 2015. Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. *Journal of Molluscan Studies*. 81:196-216. **[12]**

Nekola, J.C. & G. Rosenberg. 2013. *Vertigo marciae* (Gastropoda, Vertiginidae), a new land snail from Jamaica. *The Nautilus*. 127:107-114. **[2]**

Nekola, J.C., A. Jones, G. Martinez, S. Martinez, K. Mondragon, T. Lebeck, J. Slapcinsky & S. Chiba. 2012. *Vertigo shimochii* Kuroda & Amano 1960 synonymized with *Gastrocopta servilis* (Gould, 1843) based on conchological and DNA sequence data. *Zootaxa*. 3161:48-52. **[3]**

Nekola, J.C. & B.F. Coles. 2010. Pupillid land snails of eastern North America. *American Malacological Bulletin*. 28:29-57. **[38]**

Nekola, J.C., B.F. Coles & U. Bergthorsson. 2009. Evolutionary pattern and process in the *Vertigo gouldii* (Mollusca: Pulmonata, Pupillidae) group of minute North American land snails. *Molecular Phylogenetics and Evolution*. 53:1010-1024. **[38]**

Coles, B.F. & **J.C. Nekola**. 2007. *Vertigo malleata*, a new extreme calcifuge land snail from the Atlantic and Gulf coastal plains of the U.S.A. (Gastropoda, Vertiginidae). *The Nautilus*. 121:17-28. **[10]**

Nekola, J.C. & M. Barthel. 2002. Morphometric analysis of the genus *Carychium* in the Great Lakes region of North America. *Journal of Conchology*. 37(5):515-531. **[18]**

Nekola, J.C. & B.F. Coles. 2001. Systematics and ecology of *Gastrocopta (Gastrocopta) rogersensis* (Gastropoda: Pupillidae), a new species from the midwest of the United States of America. *The Nautilus.* 115:105-114. **[16]**

Nekola, J.C. 1998. Butterfly (Lepidoptera: Lycaeniidae, Nymphalidae, and Satyridae) faunas of three peatland habitat types in the Lake Superior drainage basin of Wisconsin. *Great Lakes Entomologist.* 31:27-37. **[10]**

Nekola, J.C. 1994. Environment and vascular flora of northeastern Iowa fen communities. *Rhodora.* 96:121-169. **[23]**

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RESEARCH NOTE

Supraspecific taxonomy in the Vertiginidae (Gastropoda: Stylommatophora)

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The genus *Vertigo* Müller, 1774 consists of *c*. 100 species of terrestrial microsnails *c*. 1.5–3 mm in length with a rounded aperture and 0–6 (sometimes more) apertural lamellae at maturity. As currently defined, the genus is largely Holarctic in distribution with only a few Neotropical species being known (Pilsbry, 1948; Nekola & Rosenberg, 2013).

Consensus does not exist concerning supraspecific taxonomy of the genus. Pilsbry (1919, 1927, 1948) placed *Vertigo*, *Columella* Westerlund, 1878 and *Truncatellina* Lowe, 1852 in the family Pupillidae, subfamily Vertigininae. Based largely on anatomy, he differentiated these from the subfamily Nesopupinae, into which he placed 11 mostly tropical genera: *Bothriopupa* Pilsbry, 1898, *Campolaemus* Pilsbry, 1892, *Costigo* Boettger, 1891, *Cylindrovertilla* Boettger, 1880, *Lyropupa* Pilsbry, 1900, *Nesopupa* Pilsbry, 1900, *Pronesopupa* Iredale, 1913, *Ptychalaea* Boettger, 1889, *Pupisoma* Stoliczka, 1873, *Staurodon* Lowe, 1854 and *Sterkia* Pilsbry, 1898. Bouchet & Rocroi (2005) assigned *Vertigo* to the family Vertiginidae, which in their scheme comprised three subfamilies: Vertigininae, Nesopupinae (both largely as designated by Pilsbry, 1927, but with *Pupisoma* being moved to the Valloniidae) and Gastrocoptinae (including *Gastrocopta* Wollaston, 1878 and 10 related genera). The Gastrocoptinae have subsequently been assigned to the Chondrinidae (Pokryszko *et al*., 2009).

Pilsbry (1919, 1948) recognized four subgenera within *Vertigo*: *Vertigo* s.s. and the monotypic *Angustula* Sterki, 1888, *Vertilla* Moquin-Tandon, 1855 and *Vertillaria* Pilsbry, 1919. He further divided *Vertigo* s.s. into several informal sections and groups. This treatment was followed until Turgeon *et al*. (1998) and Sysoev & Schileyko (2009), respectively, considered the group *Nearctula* Sterki, 1892 and the subgenus *Vertilla* to be of generic rank. Similar intrageneric division has been prominent within *Nesopupa*; e.g. Gittenberger & van Bruggen (2013) recognized nine genera originally proposed as sections by Pilsbry & Cooke (Pilsbry, 1919): *Afripupa*, *Cocopupa*, *Helenopupa*, *Indopupa*, *Infranesopupa*, *Insulipupa*, *Nesodagys*, *Nesopupa* and *Nesopupilla*.

To address these issues empirically, we have assembled and phylogenetically analysed DNA sequence data from the nuclear 28S ribosomal RNA (28S) and mitochondrial 16S ribosomal RNA (16S) genes. The species selected for study included the full conchological, biogeographic and ecological range of *Vertigo*, plus representatives of *Columella*, *Gastrocopta*, *Nearctula* and *Truncatellina*, and a variety of putative nesopupillids and other genera within the Pupillidae (*sensu* Pilsbry, 1927). We also included a representative sampling across the infraorder Orthurethra as designated by Wade, Mordan & Clarke (2001). Among the analysed taxa, the following represent the type species of their respective genera: *Acanthinula aculeata* (Müller, 1774), *Chondrina avenacea* (Bruguière, 1792), *Cochlicopa lubrica* (Müller, 1774), *Columella edentula* (Draparnaud, 1805), *Helix pomatia* Linné, 1758, *Lauria cylindracea* (da Costa, 1778), *Leiostyla anglica* (Wood, 1828), *Nearctula californica* (Rowell, 1862), *Planogyra asteriscus* (Morse, 1857), *Pupilla muscorum* (Linné, 1758) *Pyramidula rupestris* (Draparnaud, 1801), *Solatopupa similis* (Bruguière, 1792), *Sterkia calamitosa* (Pilsbry, 1889), *Strobilops labyrinthica* (Say, 1817), *Vallonia costata* (Müller, 1774), *Vertigo pusilla* (Müller, 1774), *Vertilla angustior* (Jeffreys, 1830) and *Zoogenetes harpa* (Say, 1824). *Carychium tridentatum*, *Helix pomatia* and *Cornu aspersum* were used as comparative outgroups.

Archived GenBank sequences were used for 24 specimens, including data first reported by Armbruster *et al*. (2005) [AY546471], Dinapoli, Zinssmeister & Klussmann-Kolb (2010) [GU331954], Gaitan-Espitia, Nespolo & Opazo (2013) [JQ417194], Ketmaier *et al*. (2010) [|GU046389], Nekola & Rosenberg (2013) [KF214500, KF214496], Nekola *et al*. (2012) [JN941017, JN941032, JN941041, JN941044], Nekola, Coles & Bergthorsson (2009) [GQ921543], Wade, Mordan & Naggs (2006) [AY841284, AY841285, AY841286, AY841333], Wade *et al*. (2001) [AY014019, AY014020, AY014022, AY014023, AY014024, AY014025, AY014027, AY014028, AY014028, AY014030, AY014032, AY014033, AY014040, AY014148] and Weigand *et al*. (2013) [KC206171]. Sequences for the remaining 35 specimens (Table 1) were newly obtained. DNA extraction, purification, PCR amplification and sequencing were performed using previously published methods and primers (see Wade & Mordan, 2000; Nekola & Rosenberg, 2013). The amplified 28S region (Fig. 1) encompasses ITS-2, a region that cannot be aligned because of its intergeneric hypervariability. As a result, all sequence more than 284 bp upstream of the LSU2 primer of Wade & Mordan (2000) was excluded from analysis. The resultant analysed 28S amplicon ranged in length from 809 bp (*Acanthinula aculeta*) to 827 bp (*Columella edentula*). The entire 16S amplicon was used for analysis and ranged in length from 403 bp (*Cornu aspersum*) to 594 bp (*Truncatellina cylindrica*).

Sequences were aligned using ClustalX, with adjustment by eye. Mega v. 5.0 was used to conduct neighbour-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) analyses separately for the 28S and 16S sequences. NJ analysis was based on maximum composite distance including transitions

Table 1. Collection information for specimens analysed in this study.

Taxon	Country	State or equivalent	County or equivalent	Site	Lat./Long.	Collection/ accession no.	16S GenBank acc. no.	28S GenBank acc. no.
Afripupa bisulcata	Ghana			Fetish Grove	5.3356 N, 0.0801 W	deWinter	KT008314	KT008353
Bothriopupa tenuidens	Costa Rica	Puntarenas		Saladera Lodge	8.6988 N, 83.3302 W	Tattersfield		KT008355
Columella edentula	France	Normandy	Calvados	La Valée des Vaux	48.9446 N, 0.4678 W	BC00001	KT008310	KT008360
Leiostyla anglica	UK		Cumbria	Meathop Cliff Seep	54.2066 N, 2.8729 W	JCN	KT008308	KT008363
Nearctula californica	USA	California	Monterey	Moss Landing Beach	36.8095 N, 121.7880 W	JCN13934	KT008315	KT008349
Nearctula rowelli	USA	California	Placer	Auburn	38.9072 N, 121.0520 W	JCN17232	KT008327	KT008347
Nesopupa newcombi	USA	Hawaii	Honolulu	Waianae Forest Reserve	21.5009 N, 158.1680 W	UF469195	KT008307	KT008356
Planogyra asteriscus	USA	Maine	Piscataquis	Atkinson Mills	45.1421 N, 69.0312 W	JCN10494	KT008305	KT008364
Pronesopupa boettgeri	USA	Hawaii	Oahu	Kalihi Valley	21.3585 N, 157.8580 W	Hayes	KT008306	KT008354
Ptychalaea tamagonori	Japan	Tokyo	Ogasawara	Chichijima	27.0948 N, 142.2166 E	Chiba	KT008323	KT008348
Pupilla muscorum	Czech Rep.	Moravia		Brno	49.2509 N, 16.5738 E	Horsak	KT008313	KT008361
Pupisoma dioscoricola	USA	Florida	Alachua	Batram-Carr Woods	29.6436 N, 82.3456 W	Slapcinsky	KT008304	KT008357
Sterkia calamitosa	USA	California	San Diego	Sumner Canyon	32.8734 N, 117.2483 W	JCN18169	KT008324	KT008350
Sterkia clementia	USA	California	San Diego	San Clemente Island	32.9953 N, 118.5516 W	JCN19109	KT008325	KT008351
Sterkia hemphilli	USA	California	San Diego	Border Fields State Park	32.5428 N, 117.1061 W	JCN19780	KT008331	KT008352
Strobilops labyrinthica	USA	Michigan	Mackinac	Brevort Lake	45.9829 N, 84.8618 W	JCN17151	KT008309	KT008362
Truncatellina callicratis	France	Normandy	Calvados	Pont, N. of Falaise	48.9774 N, 0.0902 W	BC00002	KT008302	KT008358
Truncatellina cylindrica	Ukraine	Crimea		Rozovyi	44.6920 N, 34.3190 E	Cameron	KT008303	KT008359
Vallonia costata	USA	New Mexico	Bernalillo	Albuquerque	35.0727 N, 106.6160 W	JCN	KT008312	
Vertigo alabamensis	USA	Florida	Leon	Wolf Trap Bay	30.3680 N, 84.5700 W	JCN12323	KF214500	KT008339
Vertigo antivertigo	UK	Wales	Anglesey	Waun Eraud Fen	53.3008 N, 4.2411 W	JCN	KT008316	KT008338
Vertigo clappi	USA	Tennessee	Carter	Lynn Mountain	36.3545 N, 82.1535 W	UF299578	KT008321	KT008337
Vertigo cristata	USA	Wisconsin	Oneida	Sugar Camp Bog	45.8499 N, 89.2958 W	JCN12213	GQ921543	KT008344
Vertigo gouldii	USA	West Virginia	Lincoln	Big Ugly WMA	38.0859 N, 82.0009 W	Doursen	KT008330	KT008333
Vertigo cf. *okinerabuensis*	Japan	Iwate	Ichinoseki	Sarusawa	38.9869 N, 141.2550 E	Chiba	JN941044	KT008341
Vertigo malleata	USA	North Carolina	Pender	Holly Shelter Game Land	34.5492 N, 77.7817 W	UF449308	KT008318	KT008345
Vertigo meramecensis	USA	Kentucky	Bullitt	Cave Hollow	37.9379 N, 85.6334 W	JCN	KT008329	KT008335
Vertigo milium	USA	Iowa	Buchanan	Rowley North fen	42.3764 N, 91.8507 W	JCN5747	KT008328	KT008346
Vertigo moulinsiana	Netherlands	South Holland	Kaag en Braassem	Woubrugge, Widje Aa	52.1710 N, 4.6119 E	JCN	KT008326	KT008334
Vertigo pseudosubstriata	Russia	Altai Republic		Seminski Pass S	50.9855 N, 85.6817 E	JCN	KT008317	KT008343
Vertigo pusilla	Czech Rep.	Moravia		Podyji National Park	48.8586 N, 15.8960 E	Horsak	KF214496	KT008342
Vertigo pygmaea	Czech Rep.	Moravia		Kotrle Fen	49.3779 N, 18.0236 E	JCN	KT008322	KT008340
Vertigo rugosula	USA	Arkansas	Jefferson	Lock & Dam #5	34.4040 N, 92.1020 W	UF409059	KT008319	KT008332
Vertilla angustior	Czech Rep.	Moravia		Pozdechov Fen	49.2339 N, 17.9864 E	JCN	KT008320	KT008336
Zoogenetes harpa	Canada	Quebec	Manicougan	Pointe-des-Montes	49.3256 N, 67.3700 W	JCN13609	KT008311	

Abbreviations: BC, Coles collection in National Museum of Wales, of which the accession numbers are to be preceded by 'NMW.Z.2015.009'; JCN, Nekola collection in University of New Mexico; UF, material in Florida Museum of Natural History, Gainesville.

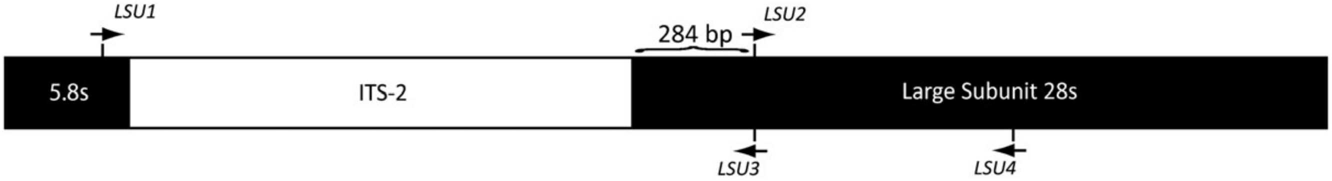

Figure 1. Map of the rRNA gene cluster with primer locations for the analysed segment of 28S in relation to the 5.8S and ITS-2 regions.

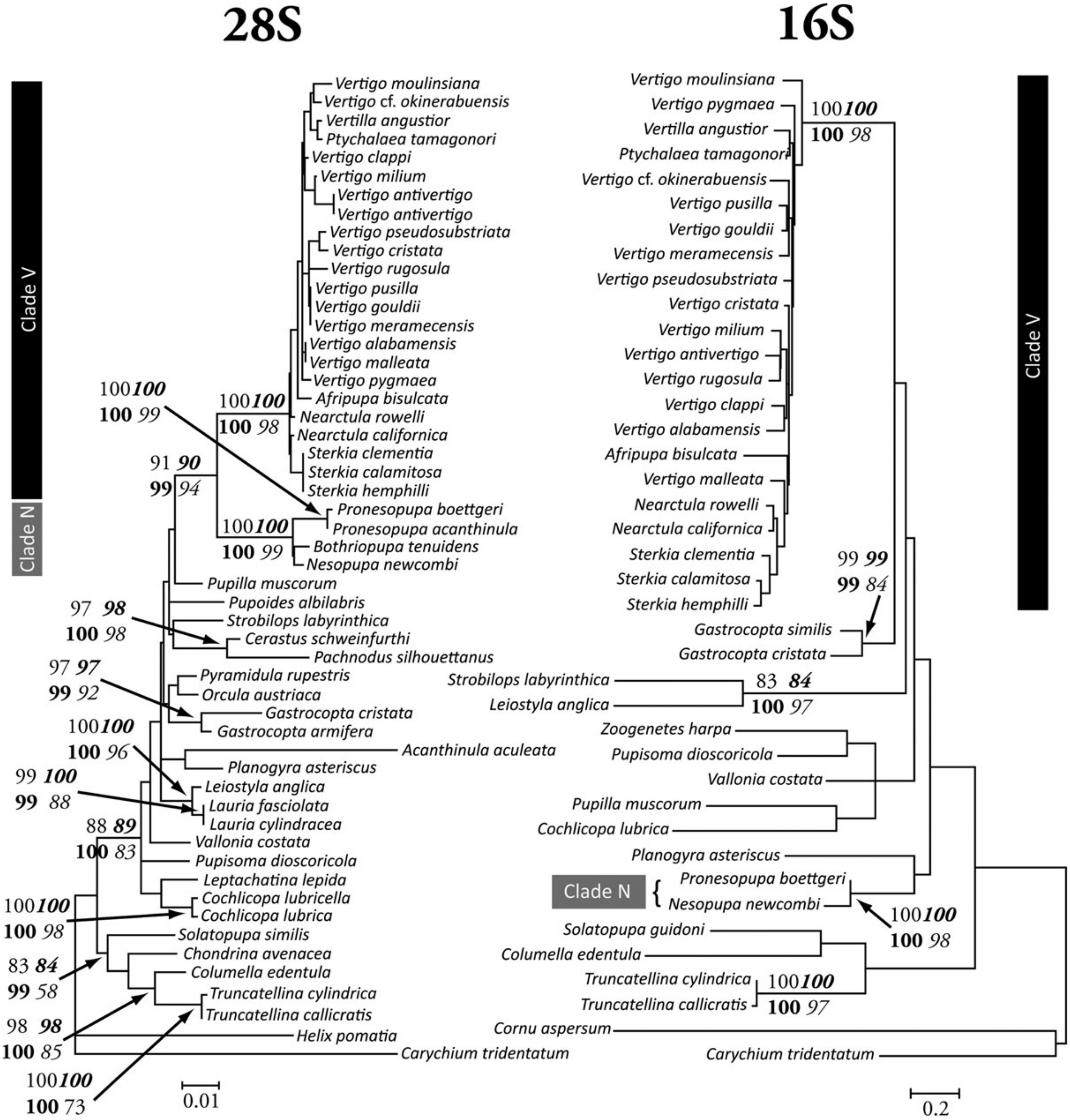

Figure 2. Maximum-likelihood phylogenetic tree reconstruction based on nuclear 28S (left) and mitochondrial 16S (right) data. Nodes with strong to moderate support (≥70) across all four phylogenetic reconstruction methods have been labelled to the left of that node by four support values: upper left (normal font) is for NJ; upper right (***bold italic font***) is for MP; lower left (**bold font**) is for Bayesian; lower right (*italic font*) is for ML.

and transversions with pairwise gap deletion. MP analysis used the close-neighbour interchange search option with the random addition of 10 replicate trees. ML analysis used all sites and was based on the Tamura-Nei substitution model, a five-category gamma distribution for substitution rates and the nearest neighbour interchange ML heuristic method. In all cases support values were estimated from 1,000 bootstrap replicates. Additionally, Bayesian trees were generated using MrBayes v. 3.1 (Huelsenbeck & Ronquist, 2001), with a generalised time reversible substitution model assuming gamma-shaped rate variation over 1,000,000 generations and a sampling frequency of once each 1,000 generations.

Analysis of these data (Fig. 2) demonstrates poorer resolution using the mitochondrial 16S as compared with the nuclear 28S data, presumably due to higher base-pair saturation rates. Therefore, we used the 28S data to deduce phylogenetic relationships and the 16S data for quasi-independent corroboration.

The 28S data show a highly-supported clade composed of two highly-supported sister clades, together including most of the putative Vertigininae (Clade V) and Nesopupinae (Clade N) included in this study. This 'vertiginid' clade in general corresponds with the Vertiginidae as outlined by Bouchet & Rocroi (2005) and Pokryszko *et al*. (2009), with the marked exceptions that: (1) *Gastrocopta* is excluded as it is neither closely related to *Vertigo* nor to the chondrinids, but rather represents a distinct branch within the Orthurethra, and (2) both *Columella* and *Truncatellina* are excluded as both are members of a moderately supported clade that includes *Chondrina*. Wade *et al*. (2001, 2006) have shown that the chondrinids are actually sister to the Orthurethra. The analysis of 16S data in general corroborates these findings, albeit without resolving the sister status of clades V and N.

The 28S and 16S trees both demonstrate that Clade N consists only of tropical species historically assigned to the Nesopupinae. These are known to differ anatomically from the Vertigininae by possessing a penial appendix and a forked retractor muscle (Pilsbry, 1919). Clade V includes not only all analysed *Vertigo*, but also the putative genera *Nearctula* and *Vertilla* and members of some genera historically assigned to the Nesopupinae (*Afripupa*, *Ptychalaea* and *Sterkia*). Pilsbry (1919) lacked anatomical data for any species within these latter three genera and placed them outside of *Vertigo* solely on biogeographical (tropical/subtropical range) and conchological grounds (pustulate shell sculpture, and/or strength and location of angular lamella). Previous analyses have shown that these shell features are not reliable for use in supraspecific taxonomy of pupillids (Coles & Nekola, 2007; Nekola *et al*., 2009; Nekola, Coles & Horsák, 2015).

It should also be noted that for both the 28S and 16S trees, monophyly of *Vertigo* is only preserved when the taxonomic concept of the genus is expanded to include all members of Clade V. Because support levels for this clade are similar to other apparent genus-level clades (including *Cochlicopa*, *Gastrocopta*, *Lauria* and *Truncatellina*), our data suggest that it would be most parsimonious to assign all species within Clade V to the genus *Vertigo*. Our more limited sampling and representation of type species in the narrowly-constrained Nesopupinae (Clade N) makes it impossible for us to say how many generic-level entities might be supported in that group. However it is interesting to note that the genetic divergence between *Bothriopupa* and *Nesopupa* is well within the range found within *Vertigo*. It thus remains an open question how many genera within the Nesopupinae will ultimately be supported by DNA sequence data.

These data do not support subgeneric classification within *Vertigo*, given that no nodes within Clade V possess support values >70 in either 28S or 16S analyses. However, the weakly supported monophyly of *Nearctula*/*Sterkia* suggests that useful subgeneric groupings may in fact exist. Consideration of these issues must await analysis of other amplicons that are more rapidly evolving (therefore with more taxonomically useful sites) than 28S, but more slowly evolving (thus with lower base-pair saturation rates) than 16S.

If retained, the family Vertiginidae represents a highly supported clade possessing only two branches: *Vertigo* on one hand and a subset of nesopupids on the other. But how useful is recognition of so small a family? We agree with Puillandre *et al*. (2015) that such decisions are ultimately matters of taxonomic opinion that cannot be subjected to empirical criteria. In this we freely admit to erring on the side of conservatism, as we do not see the utility of erecting a large number of high-level taxonomic groups that constitute only single branches or simple two-branch entities when a more inclusive division containing more taxa is possible by simply stepping back one level in the tree.

Even though outside our primary focus, these analyses also hint that other traditional supraspecific concepts within the Orthurethra may be in need of revision. In particular, the Valloniidae may be polyphyletic with both *Pupisoma* and *Acanthinula*/*Planogyra* each representing their own unique branches within the Orthurethra. The 16S data also suggest that *Zoogenetes* may be more closely related to *Pupisoma*. Pilsbry (1927: vii) appears to have been prescient when he stated "The division of the Orthurethra into families seems to be largely a matter of expediency." These empirical data validate this statement and strongly suggest that formal reconsideration of supraspecific concepts across the entire infraorder are warranted, based upon DNA sequence data.

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REFERENCES

ARMBRUSTER, G.F.J., BOEHME, M., BERNHARD, D. & SCHLEGEL, M. 2005. The H3/H4 histone gene cluster of land snails (Gastropoda: Stylommatophora): TS/TV ratio, GC3 drive and signals in Stylommatophoran phylogeny. *Journal of Molluscan Studies*, **71**: 339–348.

BOUCHET, P. & ROCROI, J.-P. 2005. Classification and nomenclature of gastropod families. *Malacologia*, **47**: 1–397.

COLES, B.F. & NEKOLA, J.C. 2007. *Vertigo malleata*, a new extreme calcifuge land snail from the Atlantic and Gulf coastal plains of the U.S.A. (Gastropoda, Vertiginidae). *Nautilus*, **121**: 17–28.

DINAPOLI, A., ZINSSMEISTER, C. & KLUSSMANN-KOLB, A. 2010. New insights into the phylogeny of the Pyramidellidae (Mollusca, Gastropoda). *Journal of Molluscan Studies*, **7**: 1–7.

GAITAN-ESPITIA, J.D., NESPOLO, R.F. & OPAZO, J.C. 2013. The complete mitochondrial genome of the land snail *Cornu aspersum* (Helicidae: Mollusca): intra-specific divergence of protein-coding genes and phylogenetic considerations within Euthyneura. *PLoS One*, **8**: E67299.

GITTENBERGER, E. & VAN BRUGGEN, A.C. 2013. Land snails of the islet of Misali, off Pemba Island, Zanzibar, Tanzania. *Zoologische Mededelingen*, **87**: 235–273.

HUELSENBECK, J.P. & RONQUIST, F. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, **17**: 754–755.

KETMAIER, V., MANGANELLI, G., TIEDEMANN, R. & GIUSTI, F. 2010. Prei-Tyrrhenian phylogeography in the land snail *Solatopupa guidoni* (Pulmonata). *Malacologia*, **52**: 81–96.

NEKOLA, J.C., COLES, B.F. & BERGTHORSSON, U. 2009. Evolutionary pattern and process in the *Vertigo gouldii* (Mollusca: Pulmonata, Pupillidae) group of minute North American land snails. *Molecular Phylogenetics and Evolution*, **53**: 1010–1024.

NEKOLA, J.C., COLES, B.F. & HORSÁK, M. 2015. Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. *Journal of Molluscan Studies*, **81**: 196–216.

NEKOLA, J.C., JONES, A., MARTINEZ, G., MARTINEZ, S., MONDRAGON, K., LEBECK, T., SLAPCINSKY, J. & CHIBA, S. 2012. *Vertigo shimochii* Kuroda & Amano 1960 synonymized with *Gastrocopta servilis* (Gould, 1843) based on conchological and DNA sequence data. *Zootaxa*, **3161**: 48–52.

NEKOLA, J.C. & ROSENBERG, G. 2013. *Vertigo marciae* (Gastropoda, Vertiginidae), a new land snail from Jamaica. *Nautilus*, **127**: 107–114.

PILSBRY, H.A. 1919. *Manual of conchology, second series*. Vol. 25: *Pupillidae (Vertigininae, Pupillinae)*. Academy of Natural Sciences, Philadelphia.

PILSBRY, H.A. 1927. *Manual of conchology, second series*. Vol. 28: *Geographic distribution of Pupillidae*. Academy of Natural Sciences, Philadelphia.

PILSBRY, H.A. 1948. *Land Mollusca of North America (north of Mexico)*. Academy of Natural Sciences of Philadelphia Monograph, 3: vol. 2(2).

POKRYSZKO, B.M., AUFFENBERG, K., HLAVÁČ, J. & NAGGS, F. 2009. Pupilloidea of Pakistan (Gastropoda: Pulmonata): Truncatellininae, Vertigininae, Gastrocoptinae, Pupillinae (in part). *Annales Zoologici (Warszawa)*, **59**: 423–458.

PUILLANDRE, N., DUDA, T.F., MEYER, C., OLIVERA, B.M. & BOUCHET, P. 2015. One, four or 100 genera? A new classification of the cone snails. *Journal of Molluscan Studies*, **81**: 1–23.

SYSOEV, A. & SCHILEYKO, A. 2009. *Land snails and slugs of Russia and adjacent Countries*. Pensoft, Sofia.

TURGEON, D.D., QUINN, J.F., Jr., BOGAN, A.E., COAN, E.V., HOCHBERG, F.G., LYONS, W.G., MIKKELSEN, P., NEVES, R.J., ROPER, C.F.E., ROSENBERG, G., ROTH, B., SCHELTEMA, A., THOMPSON, F.G., VECCHIONE, M. & WILLIAMS, J.D. 1998. *Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks*. Edn 2. American Fisheries Society Special Publication 26, Bethesda, MD.

WADE, C.M. & MORDAN, P.B. 2000. Evolution within the gastropod molluscs; using the ribosomal RNA gene-clustre as an indicator of phylogenetic relationships. *Journal of Molluscan Studies*, **66**: 565–570.

WADE, C.M., MORDAN, P.B. & CLARKE, B. 2001. A phylogeny of the land snails (Gastropoda: Pulmonata). *Proceedings of the Royal Society B*, **268**: 413–422.

WADE, C.M., MORDAN, P.B. & NAGGS, F. 2006. Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society*, **87**: 593–610.

WEIGAND, A.M., JOCHUM, A., SLAPNIK, R., SCHNITZLER, J., ZARZA, E. & KLUSSMANN-KOLB, A. 2013. Evolution of microgastropods (Ellobioidea, Carychiidae): integrating taxonomic, phylogenetic and evolutionary hypotheses. *BMC Evolutionary Biology*, **13**: 18.

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Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology

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ABSTRACT

Using the *Pupilla* faunas of Europe, North America, the Altai region of central Asia and eastern Asia, we consider whether the existing taxonomy based primarily on shell apertural characteristics correlates with relationships established on the basis of mitochondrial and nuclear DNA-sequence data. We obtained DNA sequence from nuclear ITS1 and ITS2 and mitochondrial COI and CytB from 80 specimens across 22 putative *Pupilla* taxa. The sequence data were analysed using maximum likelihood, maximum parsimony, Bayesian and neighbour-joining phylogenetic tree reconstruction, as well as base-pair substitution and insertion-deletion analysis. Revised species-level concepts were generated by identifying reciprocally monophyletic clades that exhibited unique conchological features. These analyses document that, although many previously described taxa have biological merit, the highly plastic nature of shell apertural features makes them unreliable indicators of species identity in several independent lineages. However, shell surface sculpture and architecture appear to provide more reliable diagnoses. Because of the traditional reliance of species-level taxonomy in *Pupilla* on plastic apertural features, too many species-level entities have been described in Europe and the Altai. Also, because taxonomically useful shell sculpture features have tended to be ignored, too few species have been described in eastern Asia and North America. As a result, confusion exists about species ranges, ecological tolerances and interpretation of Quaternary fossils within the genus. Based on these analyses three new species are described: *P. alaskensis*, *P. hudsonianum* and *P. hokkaidoensis*.

INTRODUCTION

The use of protein markers and DNA sequence data has shown that conchological traits can be poor indicators of relatedness, for example in eastern North American Polygyridae (Emberton, 1995), Thailand Gastrocoptinae (Tongkerd *et al.*, 2004) and the clausiliid subfamily Alopiinae from Greece (Uit de Weerd *et al.*, 2004). Similarly, our analysis of DNA sequence data in the genus *Vertigo* (Pupilloidea) indicates that while shell features do generally provide accurate assignment of genetically validated species-level entities, they are too labile to resolve evolutionary relatedness (Nekola *et al.*, 2009).

We now extend our molecular studies to include the genus *Pupilla*, a close relative of *Vertigo*. Both genera are in the Orthurethra and have long been considered to be in the same family, the Pupillidae (Pilsbry, 1948; Hubricht, 1985). Like *Vertigo*, *Pupilla* is distributed across the entire Holarctic and members of both genera commonly co-occur within the same sites.

Pupilla species possess a minute shell (<5 mm in height) of conserved cylindrical-ovate form, although shell apertures show considerable variability, ranging from simple to callused and/or lamellate. Consequently, apertural features have been much used as diagnostic species-specific characters (Pilsbry, 1921, 1948). However, preliminary DNA sequence analysis of putative North American *P. muscorum* suggested that this emphasis on shell apertural characters for species assignment was unsatisfactory (Nekola *et al.*, 2009). We have thus undertaken the present study to examine whether the classically used apertural traits used to identify *Pupilla* species are able accurately to assess taxonomy supported by mitochondrial and nuclear DNA sequence data across the Holarctic range of the genus. Because genitalic structure has been found to be of only limited utility in making species-level taxonomic distinctions in this genus (Pokryszko *et al.*, 2009), DNA sequence data offer the only practical non-shell-based method for cross-validation of taxonomic concepts in *Pupilla*.

METHODS

Specimen selection and identification

Specimens used for analysis were primarily obtained from collections made in 2000–2012 (Nekola, 2005; Horsák *et al.*, 2010, 2012; Horsák, Chytrý & Axmanová, 2013; Nekola & Coles, 2010). These include most of the currently recognized *Pupilla* taxa from western and central Europe (east to the Ural Mountains), central Asia (Altai Republic), Japan (Hokkaido) and North America (Canada and the USA including Alaska), as established by original descriptions, authoritative accounts of regional molluscan faunas and monographs (Pilsbry, 1921, 1948; Kerney & Cameron, 1979; Schileyko, 1984; Meng & Hoffman, 2008; Pokryszko *et al.*, 2009; von Proschwitz *et al.*, 2009). We were unable to secure tissue samples from only two species within these target regions: *P. seminskii* Meng & Hoffman, 2009 (Altai Republic) and *P. sterkiana* Pilsbry, 1889 (North America). For each analysed taxon, an attempt was made to select multiple individuals from across their known geographic and ecological range. Six specimens also represent topotype or near-topotype material: AP2 (*P. altaica*), AP13 (*P. alluvionica*), ET7 (*P. muscorum xerobia*), P1 (*P. hebes kaibabensis*), P10 (*P. syngenes*) and P12 (*P. sonorana*). Archival museum material up to 65 years old up to was used to supplement the specimen set for *P. triplicata* (specimens H19-21; Table 1).

Each specimen was taxonomically assigned using currently recognized diagnostic conchological features (Table 2) as reported by Pilsbry (1921, 1948), Kerney & Cameron (1979), Schileyko (1984), Meng & Hoffman (2008), Pokryszko *et al.* (2009) and von Proschwitz *et al.* (2009). In these works, apertural lamellar architecture has been given particular weight, with little variation being reported in their number, shape or placement within a given taxonomic concept. Apertural crest size, callus development and colour are also frequently used as diagnostic features. Shell sculpture, suture depth and shell apex shape have been used less frequently to distinguish some entities.

Based on these diagnoses, shells from all analysed individuals and their respective populations were examined for nine conchological traits (see below).

DNA extraction, PCR amplification and sequence analysis

Live specimens of *Pupilla* were preserved in absolute ethanol, allowed to desiccate at ambient temperature and humidity, or in some cases were used before death. DNA was extracted using the Omega BioTek Mollusk DNA Extraction Kit. Because of the inability of water to displace air within these tightly coiled shells, shell destruction was required to allow access of proteinase to mummified tissue. Thus (with few exceptions) specimens were taken from lots containing multiple examples of each respective taxon, with the actual specimens used for DNA preparation being imaged at 15× magnification prior to shell destruction using methods described by Nekola, Coles & Bergthorsson (2009).

The internal transcribed spacers (plus flanking sequence) of the nuclear ribosomal RNA complex (ITS1 and ITS2), and mitochondrial cytochrome oxidase subunit I (COI) and cytochrome b (CytB) were amplified using published methods with modifications as listed in Table 3. PCR products were sequenced in both forward and reverse directions using Perkin Elmer ABI Big Dye termination and standard protocols. COI and CytB sequences were also obtained from the GenBank database for data analysed by von Proschwitz *et al.* (2009) that could be unambiguously assigned to a single individual (*P. muscorum*, Baden-Würtemberg, Germany; *P. pratensis*, Lagmansro, Östergötland, Sweden; *P. pratensis*, Mecklenburg-Vorpommern, Germany) and for two outgroups (*Vertigo pusilla* and *Gastrocopta cristata*) that were previously analysed by Nekola & Rosenberg (2013).

Phylogenetic analyses

Sequences (excluding primer regions) were aligned using ClustalX with adjustment by eye for ITS1 and ITS2. COI and CytB were concatenated, and ITS1 and ITS2 sequences were analysed as a single construct by omitting 81 invariant base pairs from the intervening 5.8S region. Mega v. 5.0 was used to conduct neighbour-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) analyses separately for the concatenated nuclear and mitochondrial DNA sequences. NJ analysis was based on maximum composite distance including transitions and transversions with pairwise gap deletion. MP analysis used the close-neighbour interchange search option with the random addition of 10 replicate trees. ML analysis used all sites and was based on the Tamura-Nei substitution model, a five-category gamma distribution for substitution rates, and the nearest neighbour interchange ML heuristic method. In all cases support values were estimated from 1000 bootstrap replicates. Additionally, Bayesian trees were generated using MrBayes v. 3.1 (Huelsenbeck & Ronquist, 2001), using a GTR substitution model assuming gamma-shaped rate variation over 1,000,000 generations with a sampling frequency of once each 1000 generations. Because none of these methods makes full informatic use of insertions and deletions, we also constructed a matrix of all variable bases in both the ITS1 and ITS2 regions, including not only base-pair substitutions, but also insertions and deletions.

Post-hoc species delimitation and conchology

Identification of potential species-level (and higher) clades based on DNA sequence data was accomplished by examining the nDNA and mtDNA trees for highly supported, reciprocally-monophyletic clades. This approach was of limited value for the nDNA data, because of low node support due to limited variation of ~90 informative sites across ~1500 bp. To help resolve relationships using these data, we examined the matrix of variable sites by eye for base-pair substitutions, insertions and deletions held in common among groups of sequences. Apparent incongruencies in specimen placement between the nuclear *vs* mitochondrial sequences were identified as potential cases of interspecific mitochondrial introgression or incomplete lineage sorting.

We have not used any of the various methods for species demarcation using single-locus analyses of base-pair variation (e.g. generalized mixed Yule-coalescent functions). Although we have previously used these methods (Nekola *et al.*, 2009), they universally require generation of ultrametric trees, which assume constant evolutionary rates across all clades. As a result, these methods do not function well when base-pair substitution rates are clade-specific. Because assumption of rate homogeneity appeared unjustified within the current *Pupilla* dataset, we have instead opted for reciprocal-monophyly as our decision-rule to identify potential species-level clades based on genetic data.

We then attempted to verify the biological validity of these potential genetically-supported species concepts by reanalysing shell features from the imaged shells as well as additional shells within each analysed population. The range of expressed shell variation within each reciprocally-monophyletic species-level clade was documented for nine conchological traits: height (mm), width (mm), shell form, apex shape, shell sculpture, suture depth, aperture shape, apertural crest and callus strength, and apertural lamellae number and configuration. Potential species-level clades were considered taxonomically validated when some subset of the above shell features was found to be unique to and thus diagnostic of that entity. Based on this revised taxonomy, we then updated biogeographic and ecological information for each species based on our extensive community ecology datasets (e.g. Horsák *et al.*, 2010; Nekola, 2014) in combination with other published accounts.

Table 1. Information for specimens of *Pupilla* used in DNA sequence analysis.

Taxon/location	Latitude/longitude	Specimen code	Collection and lot no.	Name supported by DNA sequence data (when different)	GenBank accession no.			
					CO1	CytB	ITS1	ITS2
Pupilla alluvionica Meng & Hoffman, 2008								
Russia								
Belyashi, Altai	49.2691°N, 87.9838°E	AP13	JN		KM518545	KM518468	KM518390	KM518312
Pupilla alpicola (Charpentier, 1837)								
Russia								
Belyashi, Altai	49.5206°N, 88.0180°E	AP12	JN		KM518546	KM518469	KM518391	KM518313
Slovakia								
Rakša	48.8792°N, 18.8901°E	H6	MH		KM518547	KM518470	KM518392	KM518314
Važec	49.0685°N, 19.9994°E	H11	MH		KM518548	KM518471	KM518393	KM518315
Rakša	48.8792°N, 18.8901°E	H12	MH		KM518549	KM518472	KM518394	KM518316
Liptovská Teplička	48.9632°N, 20.1044°E	H13	MH		KM518550	KM518473	KM518395	KM518317
Pupilla altaica Meng & Hoffman, 2008								
Russia								
Usť-Muny, Altai	51.7297°N, 85.7382°E	AP1	JN	*P. turcmenica*	KM518551	KM518474	KM518396	KM518318
Kurai, Altai	50.3080°N, 87.6485°E	AP2	JN	*P. turcmenica*	KM518552	KM518475	KM518397	KM518319
Kurai, Altai	50.2334°N, 87.7894°E	AP17	MH	*P. turcmenica*	KM518553	KM518476	KM518398	KM518320
Pupilla bigranata (Rossmässler, 1839)								
France								
Pont, Calvados	48.9774°N, 0.0903°W	AP25	BC 2014.013.00081	*P. muscorum*	KM518554	KM518477	KM518399	KM518321
Pupilla blandi Morse, 1865								
Canada								
Irvine, Alberta	49.9595°N, 110.2511°W	AP34	BC 2014.013.00079		KM518555	KM518478	KM518400	KM518322
Moose Jaw, Saskatchewan	50.0434°N, 105.6246°W	AP35	BC 2014.013.00074		KM518556	KM518479	KM518401	KM518323
USA								
Logan Canyon, Utah	41.7426°N, 111.7603°W	P7	JN 18327	*P. hebes*	KM518557	KM518480	KM518402	KM518324
Las Vegas, New Mexico	35.6415°N, 105.1875°W	P15	JN 18417		KM518558		KM518403	KM518325
Ruby Mountains, Nevada	40.7751°N, 115.3364°W	P16	JN 18280	*P. hebes*	KM518559	KM518481	KM518404	KM518326
Wilson Arch, Utah	38.2745°N, 109.3724°W	P18	JN 18237	*P. hebes pithodes*	KM518560	KM518482	KM518405	KM518327
Pupilla blandi charlestonensis Pilsbry, 1948								
USA								
East Tintic Range, Utah	39.9660°N, 112.0484°W	P2	JN 18257	*P. hebes*	KM518561	KM518483	KM518406	KM518328
Bullion Canyon, Utah	38.4171°N, 112.3126°W	AP28	JN 17211	*P. hebes pithodes*	KM518562	KM518484	KM518407	KM518329
Pupilla blandi pithodes Pilsbry & Ferriss, 1917								
USA								
Bullion Canyon, Utah	38.4171°N, 112.3126°W	AP27	JN 17210		KM518563	KM518485	KM518408	KM518330
Tusas Ridge, New Mexico	36.6519°N, 106.0381°W	AP38	JN 13013		KM518564	KM518486	KM518409	KM518331
Bland, New Mexico	35.7504°N, 106.4569°W	P9	JN 14816		KM518565	KM518487	KM518410	KM518332
Pupilla hebes (Ancey, 1881)								
Japan								

Toyokoro, Nakagawa, Hokkaido	42.6050°N, 143.5564°E	VH29	JN	*P.hokkaidoensis*	KM518566	KM518488	KM518411	KM518333
USA								
Knik Island, Anchorage, Alaska	61.5084°N, 149.0343°W	AP29	JN 15390	*P. alaskensis*	KM518567	KM518489	KM518412	KM518334
Ute Creek Canyon, Colorado	38.5848°N, 105.9686°W	AP37	JN 12898	*P. blandi*	KM518568	KM518490	KM518413	KM518335
Happy Valley, Alaska	69.3355°N, 148.7302°W	NS48	JN 15142	*P. alaskensis*	GQ921663	KM518491	KM518414	KM518336
Jarbidge Mountains, Nevada	41.6867°N, 115.5061°W	P5	JN 18292	*P. hebes pithodes*	KM518569	KM518492	KM518415	KM518337
Loope East, California	38.6591°N, 119.7222°W	P14	JN 17254		KM518570	KM518493	KM518416	KM518338
Pupilla hebes kaibabensis Pilsbry & Ferriss, 1911								
U.S.A.								
Kaibab Plateau, Arizona	36.8299°N, 112.2542°W	P1	JN 18400	*P. hebes*	KM518571	KM518494	KM518417	KM518339
Pupilla hebes nefas Pilsbry & Ferriss, 1910								
USA								
Santa Catalina Mts., Arizona	32.4196°N, 110.7311°W	P6	JN 14052	*P. hebes pithodes*	KM518572	KM518495	KM518418	KM518340
Pupilla cf. *khunjerabica* Auffenberg & Pokryszko, 2009								
Russia								
Chagan-Uzun, Altai	50.0869°N, 88.3941°E	AP11	MH		KM518573	KM518496	KM518419	KM518341
Pupilla cf. *limata* Schileyko, 1989								
Russia								
Bestyakh, Yakutia	61.3624°N, 128.8433°E	AP20	MH		KM518574	KM518497	KM518420	KM518342
Kapitonovka, Yakutia	62.3292°N, 129.9282°E	AP39	MH		KM518575	KM518498	KM518421	KM518343
Pupilla loessica Ložek, 1954								
Russia								
Belyashi, Altai	49.4186°N, 87.5928°E	AP5	JN		KM518576	KM518499	KM518422	KM518344
Kosh-Agach, Altai	49.9929°N, 88.5496°E	AP6	JN		KM518577	KM518500	KM518423	KM518345
Belyashi, Altai	49.2804°N, 87.4955°E	AP7	JN		KM518578	KM518501	KM518424	KM518346
Kosh-Agach, Altai	49.6609°N, 88.2278°E	AP8	JN		KM518579	KM518502	KM518425	KM518347
Belyashi, Altai	49.2691°N, 87.9838°E	AP9	JN		KM518580	KM518503	KM518426	KM518348
Belyashi, Altai	49.5206°N, 88.0180°E	AP10	JN		KM518581	KM518504	KM518427	KM518349
Ulagan, Altai	50.4767°N, 87.6301°E	AP19	MH		KM518582	KM518505	KM518428	KM518350
Pupilla muscorum (Linnaeus, 1758)								
Europe								
Czech Republic								
Brno, Moravia	49.2509°N, 16.5738°E	mtG-Pup	MH		KM518583	KM518506	KM518429	KM518351
USA (naturalized)								
Cedar Rapids, Iowa	41.9866°N, 91.7400°W	22	JN 14592		GQ921664			
Syracuse, New York	43.0074°N, 76.1105°W	AP26	JN 13955		KM518584	KM518507	KM518430	KM518352
Canada								
Cochrane, Alberta	51.2642°N, 114.7326°W	AP36	BC 2014.013.00058	*P. hudsonianum*	KM518585	KM518508	KM518431	KM518353
Churchill, Manitoba	58.7086°N, 94.1230°W	P8	JN 11098	*P. hudsonianum*	KM518586	KM518509	KM518432	KM518354
La Grande Pointe, Quebec	50.2059°N, 63.3968°W	P13	BC 2014.013.00001	*P. hudsonianum*	KM518587	KM518510	KM518433	KM518355
USA								
Bullion Canyon, Utah	38.4171°N, 112.3303°W	P17	JN 17219	*P. hebes*	KM518588	KM518511	KM518434	KM518356

Continued

Table 1. *Continued*

Taxon/location	Latitude/longitude	Specimen code	Collection and lot no.	Name supported by DNA sequence data (when different)	GenBank accession no.			
					CO1	CytB	ITS1	ITS2
Lake Bemidji, Minnesota	47.5328°N, 94.8247°W	23	JN 9054	*P. hudsonianum*	GQ921662			KM518357
Lake Bemidji, Minnesota	47.5328°N, 94.8247°W	AP33	JN 9054	*P. hudsonianum*	KM518589	KM518512	KM518435	KM518358
Pupilla muscorum xerobia Pilsbry, 1914								
USA								
Bannon Ranch, New Mexico	36.9166°N, 103.7800°W	ET7	JN 16491	*P. blandi*	KM518590	KM518513	KM518436	KM518359
Lake Bemidji, Minnesota	47.5328°N, 94.8247°W	P4	JN 9054	*P. blandi*	KM518591	KM518514	KM518437	KM518360
Pupilla pratensis (Clessin, 1871)								
Russia								
Aktash, Altai	50.4472°N, 87.6078°E	H3	MH	*P. alpicola*	KM518592	KM518515	KM518438	KM518361
Ulagan, Atlai	50.4767°N, 87.6218°E	H4	MH	*P. alpicola*	KM518593	KM518516	KM518439	KM518362
Europe								
Czech Republic								
Pozděchov, Moravia	49.2339°N, 17.9864°E	H1	MH	*P. alpicola*	KM518594	KM518517	KM518440	KM518363
Vysoké Mýto, Bohemia	49.9611°N, 16.1892°E	H7	MH	*P. alpicola*		KM518518	KM518441	KM518364
Slovakia								
Závod	48.5331°N, 16.9963°E	H5	MH	*P. alpicola*	KM518595	KM518519	KM518442	KM518365
Pupilla sonorana (Sterki, 1899)								
USA								
Sacramento Mountains, New Mexico	32.7141°N, 105.7541°W	P12	BC 2005.011.03117		KM518596	KM518520	KM518443	KM518366
Pupilla sterrii (Forster, 1840)								
Albania								
Periferi Dibre	41.8172°N, 20.5003°E	AP16	MH		KM518597	KM518521	KM518444	KM518367
Czech Republic								
Pavlov, Moravia	48.8773°N, 16.6635°E	H8	MH		KM518598	KM518522	KM518445	KM518368
Praha-Hlubočepy, Bohemia	50.0419°N, 14.3761°E	H14	MH		KM518599	KM518523	KM518446	KM518369
Klentnice, Moravia	48.8467°N, 16.6405°E	AP22	MH		KM518600	KM518524	KM518447	KM518370
Russia								
Verkhne Bikberda, Bashkortostan	52.3207°N, 56.8032°E	AP15	MH		KM518601	KM518525	KM518448	KM518371
Slovakia								
Valaská Dubová	49.1511°N, 19.6441°E	AP21	MH		KM518602	KM518526	KM518449	KM518372
Pupilla syngenes (Pilsbry, 1890)								
USA								
Mogollon, New Mexico	33.3944°N, 108.8056°W	AP30	BC 2005.011.02961		KM518603	KM518527	KM518450	KM518373
Kaibab Plateau, Arizona	36.6918°N, 112.2989°W	P10	BC		KM518604	KM518528	KM518451	KM518374
Pupilla syngenes dextroversa Pilsbry & Vanatta, 1900								
USA								
Kaibab Plateau, Arizona	36.6918°N, 112.2989°W	P11	BC	*P. syngenes*	KM518605	KM518529	KM518452	KM518375
Pupilla triplicata (Studer, 1820)								
Russia								

Ozero Kureevo, Altai	52.4811°N, 85.7605°E	AP32	MH	KM518606	KM518530	KM518453	KM518376
Czech Republic							
Točník, Bohemia	49.8905°N, 13.8866°E	H2	MH	KM518607	KM518531	KM518454	KM518377
Pavlov, Moravia	48.8773°N, 16.6635°E	H9	MH	KM518608	KM518532	KM518455	KM518378
Milešov, Bohemia	50.5344°N, 14.9437°E	H10	MH	KM518609	KM518533	KM518456	KM518379
Kamýk, Bohemia	50.5643°N, 14.0887°E	H15	MH	KM518610	KM518534	KM518457	KM518380
Chroustov, Moravia	49.1718°N, 16.0502°E	H16	MH	KM518611	KM518535	KM518458	KM518381
Hracholusky, Bohemia	49.9974°N, 13.7904°E	H17	MH	KM518612	KM518536	KM518459	KM518382
Louny, Bohemia (1948)		H19	VL	KM518613	KM518537	KM518460	KM518383
Kamýk, Bohemia (1970)		H20	VL	KM518614	KM518538	KM518461	KM518384
Pupilla triplicata (Studer, 1820)							
Czech Republic							
Srdov, Bohemia (1950)		H21	VL	KM518615	KM518539	KM518462	
France							
Cahors, Dordogne	44.4772°N, 1.4303°E	AP31	BC 2014.013.00082	KM518616	KM518540	KM518463	KM518385
Russia							
Nugush, Bashkortostan	53.0066°N, 56.5356°E	AP23	MH	KM518617	KM518541	KM518464	KM518386
Pupilla turcmenica (O. Boettger, 1889)							
Russia							
Kosh-Agach, Altai	50.0729°N, 88.7201°E	AP3	MH	KM518618	KM518542	KM518465	KM518387
Belyashi, Altai	49.2955°N, 87.7344°E	AP4	MH	KM518619	KM518543	KM518466	KM518388
Kurai, Atlai	50.2334°N, 87.7894°E	AP18	MH	KM518620	KM518544	KM518467	KM518389

All specimens from the Nekola collection (JN) are currently maintained at the University of New Mexico before ultimate deposition at the Academy of Natural Sciences at Drexel University (ANSP). All specimens from the Coles collection (BC) are housed at the National Museum of Wales; all accession numbers for this material are preceded by ‘NMW.Z’. All specimens from the Horsák collection (MH) are housed at the Department of Botany and Zoology at Masaryk University, Brno. Material from the Vojen Ložek collection (VL) is housed at Charles University, Prague.

Table 2. Historical taxonomic and traditional conchological concepts for analysed *Pupilla*.

Taxon	Height (mm)	Width (mm)	Shell form	Apex shape	Shell sculpture	Suture depth	Apertural crest	Apertural callus	Apertural lamellae
alluvionica	3.3–4.3	2.2–2.4	Wide cylindrical	Tapered/domed	Smooth/weak striae		Clearly evident	Hardly thickened, clearly white	0–1 (rare weak parietal)
alpicola	2.8–3.3	1.8–1.9	Wide cylindrical	Domed	Obvious	Deep	Weak - absent		0–1 (rare weak parietal)
altaica	2.5–3.2	1.6–1.8	Cylindrical ovoid	Domed	Fine ribs with dermal edges		Pronounced	Thick, white	2–3 (angular pad; palatal rare)
bigranata	3.0–3.6	1.6	Cylindrical ovoid	Tapered	Almost smooth; fine lines only	Shallow	Present	Thick, white	2–3 (rare columellar)
blandi	2.5–3.3	1.5–1.6	Cylindrical	Domed	Delicate striations	Deep	Present	Yellow/tan	3
blandi charlestonensis	3.0	1.4	Cylindrical	Domed	Slightly striate	Deep	Well developed	Brown	3 (palatal, parietal strong, long)
blandi pithodes	3.1–3.7	1.7–1.8	Wide cylindrical	Domed	Delicate striae	Deep	Low - strong	Weak; brown	3
hebes	3.1–4.0	1.6–1.9	Subcylindric	Domed	Minute striae	Deep	None - weak	None	0–1 (rare parietal)
hebes kaibabensis	2.7–2.8	1.5	Subcylindric	Domed	Minute striae	Deep	None - weak	None	0–1 (rare parietal)
hebes nefas	3.2–4.2	1.7–1.9	Subcylindric, sinistral	Domed	Minute striae	Deep	None - weak	None	1 (parietal)
cf. *khunjerabica*	3.2–4.0	1.7–1.9	Cylindrical ovoid	Tapered/domed	Almost smooth, striae faint, irregular	Moderately deep	Weak	Thin - lacking	0
cf. *limata*	2.8–3.1	1.6–1.7	Cylindrical ovoid	Tapered/domed	Delicate striae	Moderately deep	Absent - weak	None	0
loessica	3.0–3.4	1.7–1.75	Cylindrical ovoid	Tapered/domed	Finely, irregularly ribbed	Deep	Absent - weak	None	0
muscorum	3.2–4.0	1.7	Cylindrical ovoid	Tapered	Almost smooth; fine lines only	Shallow	Strong	Thick, white	0–2
muscorum xerobia	2.3–2.8	1.4–1.5	Cylindrical ovoid	Domed	Almost smooth; fine lines only	Shallow	Strong	Thick, white	1 (parietal)
pratensis	3.5–4.5	1.9–2.1	Cylindrical ovoid	Domed	Fine striation	Deep	Weak	Weak, white	0–2 (weak if present); no depression over palatal
sonorana	2.5–3.3	1.3–1.4	Cylindrical	Domed	Fine striae	Deep	Strong	Thick, white	3 (all long)
sterrii	2.8–3.5	1.6	Cylindrical	Tapered/domed	Coarse striae	Very deep	Weak - moderate	Moderately thick, white	2 (both peg-shaped)
syngenes	3.0–4.2	1.7–1.8	Biconic, widest at *c.* 4th whorl; 8 narrow whorls; sinistral	Tapered/domed	Delicate striae	Shallow	Strong		3
syngenes dextroversa	3.0–4.5	1.6–1.8	Biconic, widest at *c.* 4th whorl; 8 narrow whorls; dextral	Tapered/domed	Delicate striae	Shallow	Strong		3
triplicata	2.2–2.8 (4)	1.4	Cylindrical	Domed	Fine, close striation	Deep	Moderate	Distinct, white	3 (blade shaped)
turcmenica	3.0–3.2	1.1–1.4	Cylindrical; shell thinner	Tapered/domed	Coarse striae	Very deep	Weak	Weak, white	0–2 (weak parietal and/or palatal)

Table 3. Primers used for genetic analysis.

Region	Direction	Anneal	Sequence	Source
COI	f	45°C	5′-ATTCAACGAATCATAAAGATATTGG-3′	Author Design
	r		5′-TATACTTCAGGATGACCAAAAAACCA-3′	Author Design
CytB	f	47°C	5′-TGAGGTGCAACAGTNATTAC-3′	Author Design
	r		5′-GCAAATAAAAAGTATCACTCTGG-3′	Author Design
ITS1	f	52°C	5′-TAACAAGGTTTCCGTATGTGAA-3′	Armbruster & Bernhard (2000)
	r		5′-TCACATTAATTCTCGCAGCTAG-3′	Author Design
ITS2	f	52°C	5′-CTAGCTGCGAGAATTAATGTGA-3′	Wade & Mordan (2000)
	r		5′-GGTTTCACGTACTCTTGAAC-3′	Author Design

RESULTS

DNA sequence data

A total of 80 specimens from 22 putative *Pupilla* taxa underwent DNA extraction (1–12 individuals/taxon, see Table 1). DNA sequences were obtained for 79 specimens for COI, 77 specimens for CytB and 77 specimens for ITS1 and ITS2. All COI and CytB amplicons consisted of 655 and 377 bp, respectively, and could be unambiguously aligned. The COI amplicon contained 240 and CytB 137 variable sites. The ITS1 amplicon length was 615–635 bp and the ITS2 amplicon length was 868–874 bp. All *Pupilla* ITS sequences could be unambiguously aligned, but those of the outgroup (*Vertigo pusilla* and *Gastrocopta cristata*) could not. The 5.8S region between the ITS amplicons (based on 23 *Pupilla* specimens for which it was determined) consisted of 81 invariant bases so that the entire contiguous sequence between the 5′-end of the ITS1 amplicon and the 3′-end of the ITS2 amplicon is 1569–1593 bp. The total informative sites in ITS consisted of 56 bp substitutions and 36 bp comprising 12 insertions/deletions.

Phylogenetic reconstructions and supported taxonomic entities

Phylogenetic tree reconstruction and base-pair variation maps based on concatenated COI + CytB mtDNA and ITS1 + ITS2 nDNA sequences support the presence of 17 putative reciprocally-monophyletic species or subspecies-level taxa (Figs 1 and 2, Table 4): *P. alluvionica, P. alpicola, P. blandi, P.* cf. *khunjerabica, P.* cf. *limata, P. hebes, P. hebes pithodes, P. loessica, P. muscorum, Pupilla* n. sp. (Alaska), *Pupilla* n. sp. (Hokkaido), *Pupilla* n. sp. (Hudsonian), *P. sonorana, P. sterrii, P. syngenes, P. triplicata* and *P. turcmenica*. The three new species identified by these analyses are formally described below and will be referred to hereafter as *P. alaskensis, P. hokkaidoensis* and *P. hudsonianum*, respectively.

Pupilla alluvionica is a xeric rock outcrop and steppe species that differs from all other analysed *Pupilla* by possessing adult shells >2.1 mm in diameter with a smooth or very weakly striate shell, a crest and a white callus. The single individual analysed for DNA sequence possessed an ITS1 + ITS2 sequence with four bases different from all other *Pupilla* (111C and 577A in ITS1; 333G and 490C in ITS2). However, its COI + CytB sequence was part of the same highly supported clade defining *P. turcmenica*, which consistently co-occurs with *P. alluvionica* in the Altai.

Pupilla alpicola is a wetland species whose shells are up to 2.1 mm wide with a shallow suture and a body whorl often slightly narrower than the penultimate whorl. This species is defined by 92C and usually 340C in ITS2. Two subpopulations are noted, one with AC at 171–172 in ITS1 and the other maintaining the consensus GT at these positions. While the former subpopulation is more prevalent in Europe and the latter in central Asia, individuals characteristic of either occur throughout its known range. *Pupilla pratensis* has been traditionally differentiated from *P. alpicola* by lacking a depression or flattening on the palatal wall of the aperture and having a rather pronounced shell apex (von Poschwitz *et al.*, 2009). However, *P. pratensis* shares the same unique ITS2 bases as *P. alpicola,* with individuals referable to *P. pratensis* occurring in both of the unique ITS1 subpopulations. Additionally, *P. pratensis* mtDNA occurs throughout the same highly supported clade that contains all analysed *P. alpicola*. If *P. pratensis* is considered a shell form of *P. alpicola*, then *P. alpicola* is monophyletic for both nDNA and mtDNA.

According to Pilsbry (1948), *P. blandi* is characterized by a cylindrical shell with a prominent crest, a yellow to tan callus and three apertural lamellae. Using these criteria, individuals conchologically assignable to *P. blandi* demonstrate polyphyly both in ITS1 + ITS2 and COI + CytB, occurring within three well-supported species-level clades. However, if these traditional conchological characteristics are abandoned in favour of surface sculpture, with *P. blandi* being differentiated by its irregular, very weak striae, shiny shell surface and shallow suture, this species becomes a strongly supported monophyletic entity for COI + CytB that uniquely possesses a GAC insertion at 181–183 in ITS2. Because this entity varies in apertural lamella number from 0 to 3, and has a crest and callus ranging from weak to strong, it includes a number of shell forms that were previously assigned to other taxa including *P. hebes* and *P. muscorum xerobia*.

Pilsbry (1948) characterized *P. hebes* as possessing a minutely striate, subcylindric shell with no apertural callus, an absent to rarely weak apertural crest and absent to rarely weak parietal lamella. Shells displaying these traits demonstrate polyphyly among three different species-level clades. However, as with *P. blandi*, monophyletic grouping is apparent when a different suite of shell features is used to diagnose *P. hebes*, including a cylindrical-ovoid shell tapered for the upper 1/3-1/4 of the shell height, a normal to deep suture and possession of numerous sharp thread-like striae. Shells possessing these features all uniquely possess 508T in ITS1, while sharing 495A in ITS1 with *P. blandi* and *P. hebes pithodes*. Using the shell characters of Pilsbry (1948) for identification causes some individuals within this group to be incorrectly assigned to *P. blandi*, *P. blandi charlestonensis* and *P. muscorum*. It should be noted that COI + CytB suggests that *P. hebes* exists as two discrete subpopulations, one ranging throughout the Great Basin from California to north-central Utah (samples P5, P7, P14 and P16) and the other being restricted to the canyonlands region of the Colorado Plateau (samples P1, P2 and P17). This latter subpopulation would equate to *P. hebes kaibabensis* of Pilsbry (1948). However, as the shells of this clade completely overlap with typical material as well as possessing identical ITS1 + ITS2 sequence, it seemed best not to formally recognize this subpopulation at this time.

Pilsbry (1948) characterized *P. blandi pithodes* as being wider than *P. blandi*, with a weak to absent crest and callus. He hypothesized that it was intermediate between *P. blandi* and *P. hebes*. ITS1 + ITS2 indicate that in fact this entity is more

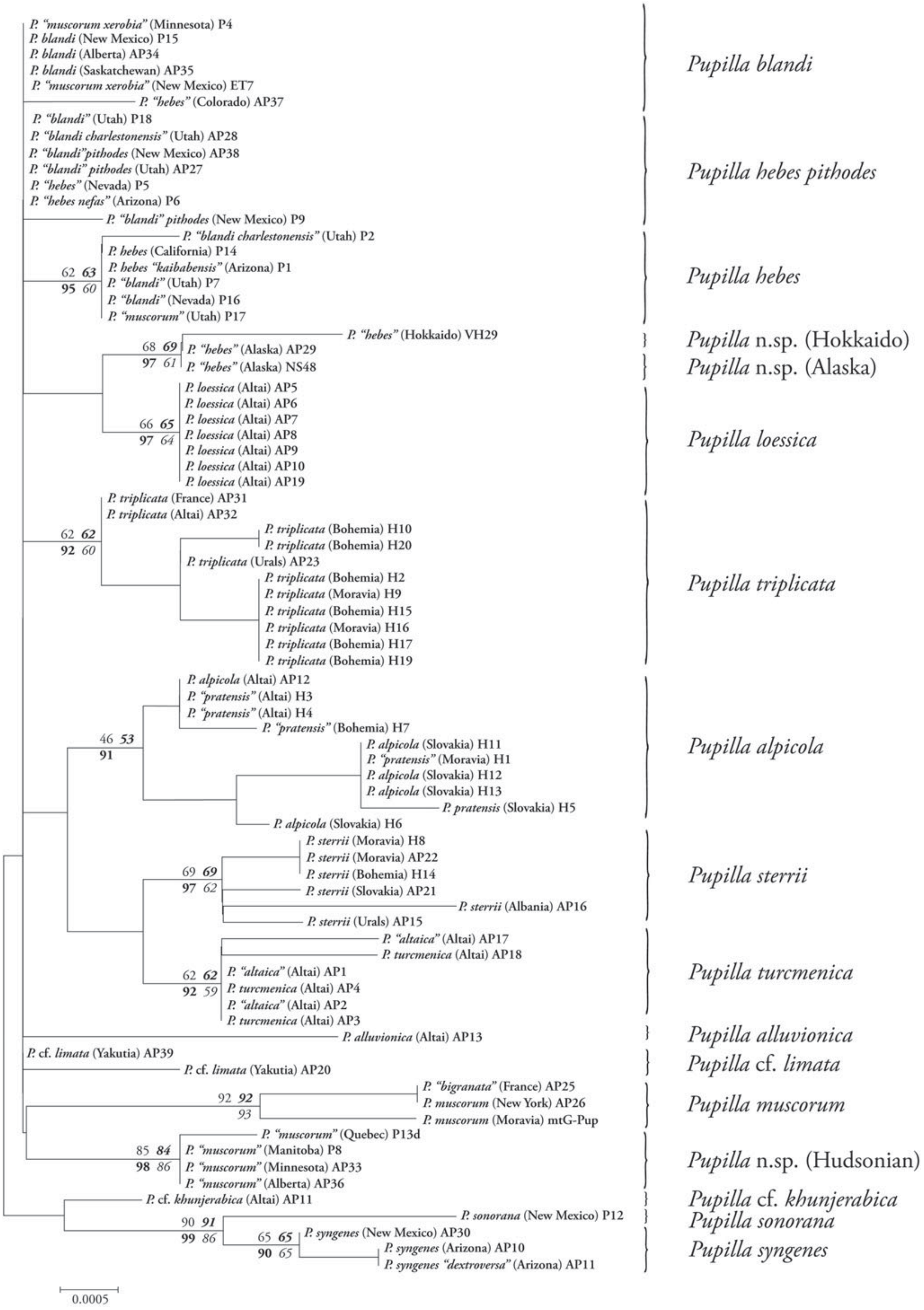

Figure 1. Maximum-likelihood phylogenetic tree reconstruction for *Pupilla* based on concatenated ITS1 + ITS2 data. Nodes with strong to moderate support across all four phylogenetic reconstruction methods have been labelled to the left of that node by four support values: upper left (normal font) is for NJ; upper right (bold italic font) is for MP; lower left (bold font) is for Bayesian; lower right (italic font) is for ML. Branch tip labels represent initial identifications based on traditional conchological features, whereas labels to the right of brackets represent valid names supported by both nDNA and mtDNA sequence analysis.

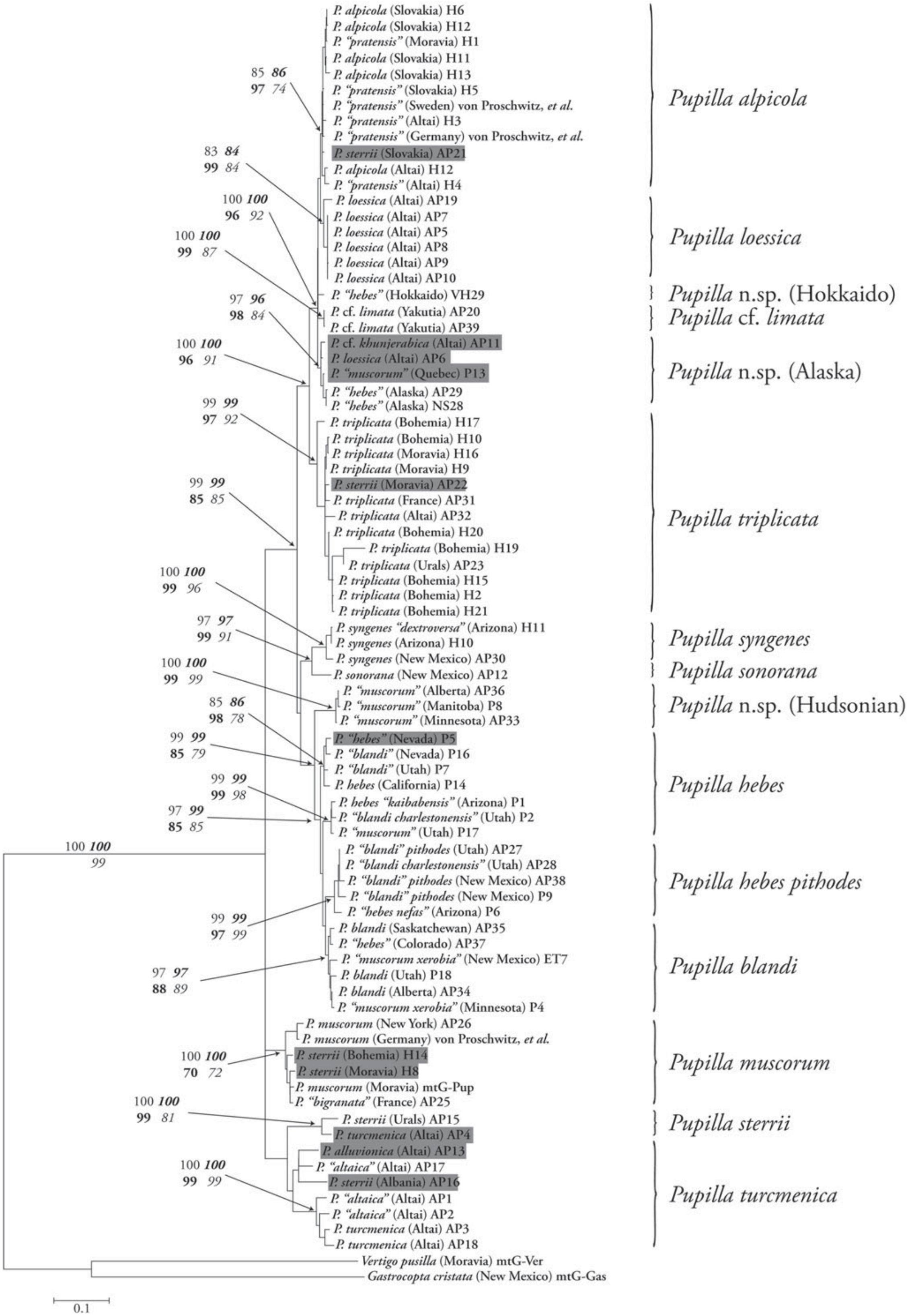

Figure 2. Maximum-likelihood phylogenetic tree reconstruction for *Pupilla* based on concatenated COI + CytB. Labelling conventions as in Figure 1. Specimens that have a significantly different topological location as compared with the nDNA tree are highlighted in gray.

Table 4. Matrix of variable bases in ITS1 and ITS2.

Species / Sample information	ITS1	ITS2	SG
	11122222333333444445555556666	1111111222222333333344445555555677	
	3344444444466777777917700166113557345890035670122	577893457888000379133455111990002458814	
	8901234567889012345511227867129585743858989179759	669327367123017385436068456014569113870	
Pupilla blandi			
P. blandi (New Mexico); P15	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATATGAC--TGATGCTTC----TA---AATTACA	1
P. blandi (Alberta); AP34	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATATGAC--TGATGCTTC----TA---AATTACA	1
P. blandi (Saskatchewan); AP35	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATATGAC--TGATGCTTC----TA---AATTACA	1
P. m. xerobia (New Mexico); ET7	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATATGAC--TGATGCTTC----TA---AATTACA	1
P. m. xerobia (Minnesota); P4	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATATGAC--TGATGCTTC-GCCTA---AATTACA	1
P. hebes (Colorado); AP37b	GCGGCCCAGGC--------TTGATATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATATGAC--TGATGCTTC----TA---AATTACA	1
Pupilla hebes			
P. h. kaibabensis (Arizona); P1	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-ATAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. blandi (Utah); P7	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-ATAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. hebes (California); P14	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-ATAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. blandi (Nevada); P16	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-ATAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. muscorum (Utah); P17	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-ATAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. b. charlestonensis (Utah); P2	GCGGCCCAGGC--------TTGTTATGTGTAC-TGTC-ATAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
Pupilla hebes pithodes			
P. b. pithodes (New Mexico); AP38	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. b. pithodes (Utah); AP27	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. b. charlestonensis (Utah);AP28	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. h. nefas (Arizona); P6	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. blandi (Utah); P18	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. b. pithodes (New Mexico); P9	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AACTACA	1
Pupilla* cf. *limata			
P. cf. *limata* (Yakutia); AP39	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC-AGAT-TGGTAT	-GTGTATAT-----TGATGCTTC----TA---AATTACA	1
P. cf. *limata* (Yakutia); AP20	GCGGCCCAGGC--------TTGTTATGTGTAC-TTCC-AGAT-TGGTAT	-GTGTATAT-----TGGTGCTTC----TA---AATTACA	1
Pupilla hudsonianum			
P. muscorum (Minnesota); AP33	NCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT	AGTGTATAT-----TGATGCTTC----TA---AGTCACA	2
P. muscorum (Alberta); AP36	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT	AGTGTATAT-----TGATGCTTC----TA---AGTCACA	2
P. muscorum (Manitoba); P8	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT	AGTGTATAT-----TGATGCTTC----TA---AGTCACA	2
P. muscorum (Quebec); P13	GCGGCCCAGGCGGCA----TTGTTATGTGTAC-TTTC--GAT-TGGTAT	AGTGTATAT-----TGATGCTTC----TA---TGTCACA	2
Pupilla syngenes			
P. syngenes (Arizona); P10	GCGGCCCAGGC--------CTGTTATGTGTAC-TTTT--GAT-TGGTAT	-GTATATGT-----TAATGCTTC----TA---AATTACA	3
P. s. dextroversa (Arizona); P11	GCGGCCCAGGC--------CTGTTATGTGTAC-TTTT--GAT-TGGTAT	-GTATATGT-----TAATGCTTC----TA---AATTACA	3
P. syngenes (New Mexico); AP30	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTT--GAT-TGGTAT	-GTATATGT-----TAATGCTTC----TA---AATTACA	3
Pupilla sonorana			
P. sonorana (New Mexico); P12	GCGGCCCAGGCGGCA----TTGTTAAGTGTAC-TTTT--GAC-TGGTAT	-GTGTATGT-----TAATGCTTA----TA---AATTACA	3
Pupilla* cf. *khunjerabica			
P. cf. *khunjerabica* (Altai);AP11	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT	-GTGTCTGT-----TGATGCTTC----TA---AATTACA	3
Pupilla loessica			
P. loessica (Altai); AP5	GCGGCCCAGGC--------TTGTTATCTGTAC-TTTC--GAT-TGGTAT	-GTGTATAT-----AGATGCTTC----TA---AATTACA	4
P. loessica (Altai); AP6	GCGGCCCAGGC--------TTGTTATCTGTAC-TTTC--GAT-TGGTAT	-GTGTATAT-----AGATGCTTC----TA---AATTACA	4
P. loessica (Altai); AP7	GCGGCCCAGGC--------TTGTTATCTGTAC-TTTC--GAT-TGGTAT	-GTGTATAT-----AGATGCTTC----TA---AATTACA	4
P. loessica (Altai); AP8	GCGGCCCAGGC--------TTGTTATCTGTAC-TTTC--GAT-TGGTAT	-GTGTATAT-----AGATGCTTC----TA---AATTACA	4
P. loessica (Altai); AP9	GCGGCCCAGGC--------TTGTTATCTGTAC-TTTC--GAT-TGGTAT	-GTGTATAT-----AGATGCTTC----TA---AATTACA	4
P. loessica (Altai); AP10	GCGGCCCAGGC--------TTGTTATCTGTAC-TTTC--GAT-TGGTAT	-GTGTATAT-----AGATGCTTC----TA---AATTACA	4
P. loessica (Altai); AP19	GCGGCCCAGGC--------TTGTTATCTGTAC-TTTC--GAT-TGGTAT	-GTGTATAT-----AGATGCTTC----TA---AATTACA	4
Pupilla alaskensis			
P. hebes (Alaska); NS48	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT	-GTGTATAG-----AGATGCTTC----TA---AATTACA	4
P. hebes (Alaska); AP29	GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT	-GTGTATAG-----AGATGCTTC----TA---AATTACA	4
Pupilla hokkaidoensis			
P. hebes (Hokkaido); VH29	-------------------TTGTTATGAGTAC-TTTC--GAT-TGGTAT	-GCGTATAG-----AGATGCTTC----TA---AATTACA	4
Pupilla alluvionica			
P. alluvionica (Altai); AP13	GCGGCCCAGGC--------TCGTTATGTGTAC-TTTC--GAT-TAGTAT	-GTGTATAT-----TGATGGTTC----CA---AATTACA	5

```
Species / Sample information
                                    ITS1                                              ITS2                                    SG
                                                        11122222333333444445555556666      1111111222222333333344445555555677
                                    3344444444466777777917700166113557345890035670122 577893457888000379133455111990002458814
                                    8901234567889012345511227867129585743858989179759 669327367123017385436068456014569113870
Pupilla alpicola
 P. alpicola (Slovakia); H6         GCGGCCCAGGC--------TTACTATGTGTAC-TTTC--GAT-TGGTAT -GTGYATAT-----TGATGCTTC----TA---AATTATA 6
 P. alpicola (Slovakia); H11        GCGGCCCAGGC--------TTACTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATGCTCC----TA---AATTACA 6
 P. alpicola (Slovakia); H12        GCGGCCCAGGC--------TTACTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATGCTCC----TA---AATTACA 6
 P. alpicola (Slovakia); H13        GCGGCCCAGGC--------TTACTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATGCTCC----TA---AATTACA 6
 P. pratensis (Moravia); H1         GCGGCCCAGGC--------TTACTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATGCTCC----TA---AATTACA 6
 P. pratensis (Slovakia); H5        GCGGCCCAGGC--------TTACTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATTCTCC----TA---AATTACA 6
 P. pratensis (Bohemia); H7         GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATTCTCC----TA---AATTACA 6
 P. alpicola (Altai); AP12          GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATGCTCC----TA---AATTACA 6
 P. pratensis (Altai); H3           GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATGCTCC----TA---AATTACA 6
 P. pratensis (Altai); H4           GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT -GTGCATAT-----TGATGCTCC----TA---AATTACA 6
Pupilla muscorum
 P. bigranata (France); AP25        GCGGCCCAGGC--------TTGTTATGTGTAC-CTTC--GAT-TGATAC -GTGTAGAT-----TGATGCCTC----TA---AATTACA 7
 P. muscorum (New York); AP26       GCGGCCCAGGC--------TTGTTATGTGTAC-CTTC--GAT-TGATAC -GTGTAGAT-----TGATGCCTC----TA---AATTACA 7
 P. muscorum (Moravia); mtG-Pup     GCGGCCCAGGC--------TTGTCATGTGTAC-CTTC--GAT-TGATAT -GTGTATAT-----TGATGCCTC----TA---GATTACA 7
Pupilla triplicata
 P. triplicata (France); AP31       GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGTAT -GTGTATAT-----TGAAGCTTC----TA---AATTACA 8
 P. triplicata (Altai); AP32        GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GATATGGTAT -GTGTATAT-----TGAAGCTTC----TA---AATTACA 8
 P. triplicata (Urals); AP23        GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACA 8
 P. triplicata (Bohemia); H10       GCGGCCCAGGC--------TTGTTATGTTTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACA 8
 P. triplicata (Bohemia); H20       GCGGCCCAGGC--------TTGTTATGTTTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACA 8
 P. triplicata (Bohemia); H2        GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACG 8
 P. triplicata (Moravia); H9        GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACG 8
 P. triplicata (Bohemia); H15       GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACG 8
 P. triplicata (Bohemia); H16       GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACG 8
 P. triplicata (Bohemia); H17       GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACG 8
 P. triplicata (Bohemia); H19       GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GAT-TGGCAT -GTGTATAT-----TGAAGCTTC----TA---AATTACG 8
Pupilla sterrii
 P. sterrii (Moravia); H8           GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GTT-TGGTGT -GTGTATAT-----TGATGCTTC----TA---AATTATA 9
 P. sterrii (Moravia); AP22         GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GTT-TGGTGT -GTGTATAT-----TGATGCTTC----TA---AATTATA 9
 P. sterrii (Bohemia); H14          GCGGCCCAGGC--------TTGTTATGTGTAC-TTTC--GTT-TGGTGT -GTGTATAT-----TGATGCTTC----TA---AATTATA 9
 P. sterrii (Slovakia); AP21        GCGGCCCAGGCGGCAGGCATTGTTATGTGTAC-TTTC--GTT-TGGTAT -GTGTATAT-----TGATGCTTC----TAGGTAATTATA 9
 P. sterrii (Albania); AP16         GCGGCCCAGGC--------TTGTTATGTGTTTGTTTC--GTT-TGGTAT -GTGTATAT-----TGATGCTTC----TA---AATTGTA 9
 P. sterrii (Urals); AP15           GCGGCCCAGGC--------TTGTTATGTGTAC-TTTCT-GTT-TGGTAT -ATGTATAT-----TGATGCTTC----TA---AATTATA 9
Pupilla turcmenica
 P. altaica (Altai); AP1            GCGGCCCAGGC--------TTGTTGTGTGTAC-TTTC--GAT-TGGTAT -GTGTATAT-----TGATGCTTC----TA---AATTATA 9
 P. altaica (Altai); AP2            GCGGCCCAGGC--------TTGTTGTGTGTAC-TTTC--GAT-TGGTAT -GTGTATAT-----TGATGCTTC----TA---AATTATA 9
 P. turcmenica (Altai); AP3         GCGGCCCAGGC--------TTGTTGTGTGTAC-TTTC--GAT-TGGTAT -GTGTATAT-----TGATGCTTC----TA---AATTATA 9
 P. turcmenica (Altai); AP4         GCGGCCCAGGC--------TTGTTGTGTGTAC-TTTC-AGAT-TGGTAT -GTGTATAT-----TGATGCTTCT---TA---AATTATA 9
 P. turcmenica (Altai); AP18        GCGGCCCAGGC--------TTGTTGTGTGCAC-TTTC--GAT-AGGTAT -GTGTATAT-----TGATGCTTC----TA---AATTATA 9
 P. altaica (Altai); AP17           GCGACCCAGGC--------TTGTTGTGTGTAC-TTTC--GAT-TGGTAT -GTGTATAT---CTTGATGCTTC----TG---AATTATA 9
```

For both amplicons, numbers refer to the base pairs downstream of the termination of the forward primer. Base pairs invariant across all samples are omitted, while base pairs that diverge from the genus consensus are highlighted. Dash indicates base-pair deletion. Samples are sorted by post-hoc supported species names (in bold italic), while initial names used prior to DNA analysis, and based on traditional conchological features, are listed in the Sample information. Potential groupings of related species are noted in the farthest-right column, labelled SG. Note that the insertions: ITS1 68–71 and 72–75; and ITS2 181–183 and 504–506, are microsatellite repeats.

closely related to *P. hebes*, lacking the GAC insertion at 181–183 in ITS2. However, it is distinguished from this species by possessing 508G in ITS1. The COI + CytB of *P. hebes pithodes* exists as a highly supported clade. Because we observed a gradation from barrel-shaped *P. pithodes* to more cylindrical *P. hebes* shells, we have chosen to consider *P. pithodes* as a subpopulation that occurs to the east of the main range of *P. hebes*, ranging from eastern Arizona and central Utah into Colorado, New Mexico and Texas. Use of traditional shell characteristics (Pilsbry, 1948) results in some *P. hebes pithodes* being incorrectly assigned to *P. blandi charlestonensis*. ITS1 + ITS1 and COI + CytB both indicate that the sinistral *P. hebes nefas* of southeastern Arizona should be regarded as a shell form of *P. hebes pithodes*.

DNA analysis also demonstrates that *P. alaskensis* and *P. hokkaidoensis*, which have previously been confused with *P. hebes*, actually represent undescribed species related to the central Asian *P. loessica*, as all share 207A in ITS2. Both of these new species uniquely share 177G in ITS2, with *P. hokkaidoensis* differing from *P. alaskensis* based on an 11-bp deletion at 38–48 in ITS1, 111C in ITS1 and 79C in ITS2. *Pupilla alaskensis* shells differ from *P. hebes* in their widely spaced, coarse, somewhat anastomosing striae. *Pupilla hokkaidoensis* shells differ from *P. hebes* in their rotund cylindrical shape with shallow suture and anastomosing coarse striae (see taxonomic descriptions below).

Pupilla cf. *khunjerabica* is represented in the sample by a single population from a riparian forest corridor in the Altai. This specimen possesses a cylindrical-ovoid shell tapered for the upper half of the shell height, very weak irregular thread-like striae, a moderately deep suture, a weak to absent callus or crest, and no apertural lamellae. Although its COI + CytB sequence fell within the highly supported clade defining *P. alaskensis*, it uniquely possessed 137C in ITS2, and was the only taxon outside the southwestern North America *P. syngenes/sonorana* group to possess 156G in ITS2.

Pupilla cf. *limata* was sampled from riparian forest in the Yakutia region of eastern Siberia and is characterized by a cylindrical-ovoid shell with numerous, sharp, somewhat anastomosing striae, a weak crest and no callus or apertural lamellae. While this taxon is highly supported as a monophyletic entity in COI + CytB, one of the two analysed individuals possessed ITS1 + ITS2 identical with *P. hebes pithodes* from western North America. The other individual uniquely possessed 444C in ITS1.

Pupilla loessica is a steppe-tundra species that in modern times is restricted to central Asia, although Pleistocene fossils extend west into central Europe (e.g. Horsák *et al*., 2010). It is distinguished by its numerous strong rounded anastomosing striae and lack of callus and apertural lamellae. It uniquely possessed 266C in ITS1 and shares 207A in ITS2 with *P. alaskensis* and *P. hokkaidoensis*. *Pupilla loessica* exists as a strongly supported clade in COI + CytB. While one individual (AP6) possessed COI + CytB characteristic of *P. alaskensis*, this individual had ITS1 + ITS2 characteristic of *P. loessica*.

Pupilla muscorum has traditionally been characterized by its cylindrical shell with smooth sculpture, shallow suture, strong crest, thick white callus and from zero to two parietal lamellae (Pilsbry, 1948; von Proschwitz *et al*., 2009). This species exists as a well defined clade in ITS1 + ITS2 by uniquely possessing 375C and 609A in ITS1 and 336C in ITS2. It also exists as a strongly supported clade in COI + CytB. *Pupilla bigranata*, which is distinguished from *P. muscorum* by its three strong apertural lamellae, was found to have COI + CytB sequence identical with Moravian *P. muscorum* and ITS1 + ITS2 sequence identical with New York *P. muscorum*. Individuals from the High Plains and Rocky Mountains of the western USA, which have been previously identified as *P. muscorum* using the above conchological characteristics, were shown by DNA sequence analysis actually to represent *P. blandi* or *P. hebes*.

In North America *P. muscorum* was thought to exist in two disjunct populations, one ranging from the northeastern Atlantic seaboard west through the Great Lakes to Iowa, and the other ranging across the northern taiga (Oughton, 1948; Hubricht, 1985). This latter entity (*P. hudsonianum*) exists as a well defined monophyletic group uniquely possessing 56A, 541G and 583C in ITS2. It also exists as a strongly supported clade in COI + CytB, although one individual (P13) possessed sequence characteristic of *P. alaskensis*. It is easily differentiated from *P. muscorum* by the strong taper over the top half of its shell height and its sculpture of dense thread-like striae (see taxonomic description below).

Pupilla syngenes possesses a distinctive shell that is widest in the top half and has three apertural lamellae including a long, curved blade-like parietal lamella. This species of wooded, xeric rock outcrops in the southwestern USA uniquely possessed 83A in ITS2 and also exists as a strongly supported clade in COI + CytB. The dextral individual of this typically sinistral species, termed *P. syngenes dextroversa*, had ITS1 + ITS2 and COI + CytB sequences identical to a typical individual within the same population.

Pupilla sonorana was compared by Pilsbry (1948) with *P. triplicata* and distinguished by its small size, columnar shell, strong crest and three apertural lamellae including a curved blade-like parietal lamella. It appears closely related to *P. syngenes* by sharing 453T in ITS1 and 156G and 233A in ITS2. However, it differed from that species in possessing 218A and 538C and a GGCA insertion from 68 to 71 in ITS1 and 83G and 356A in ITS2. As only one individual was analysed, no species-level clade can be assigned in COI + CytB. However, it differed from *P. syngenes* by 54 bp at these loci.

Pupilla triplicata of rock outcrops from western Europe to central Asia has shells that differ from *P. sonorana* only by their weak, rounded (rather than sharp) striae. This species uniquely possesses 295A in ITS2. Most individuals also exhibit 617C in ITS1. COI + CytB of this species form a highly supported clade. While two distinct subpopulations are suggested by 740A *vs* 740G in ITS2, there is no correspondence in COI + CytB or in any noted conchological features. As such, this grouping appears to have no taxonomic merit.

Pupilla sterrii of dry calcareous grasslands from central Europe to the Urals is characterized by its very deep suture and sharp, coarse, anastomosing striae. It is defined by uniquely possessing 509T in ITS1. The mtDNA of this species is highly variable, with individuals variously possessing COI + CytB characteristic of *P. alpicola*, *P. muscorum*, *P. triplicata* or *P. turcmenica*. No analysed individual from Europe was found to possess mtDNA sequence with the expected topological position as sister to *P. turcmenica*. However the Urals specimen did and it may represent the only individual with both nDNA and mtDNA characteristic of *P. sterrii*.

Pupilla turcmenica is a species of xeric calcareous grasslands that ranges across Asia Minor and central Asia. It is conchologically distinguished from the similar *P. sterrii* by its less deep sinus and more widely spaced striae. It uniquely displays 207G in ITS1, with its COI + CytB forming a highly supported clade. *Pupilla altaica* has been recently differentiated from this species by its larger crest, more massive white callus and the presence of an angular pad on the parietal wall of the aperture (Meng & Hoffman, 2008). However, this entity did not possess any unique ITS1 + ITS2 distinctions from *P. turcmenica*, being distributed throughout the same highly supported COI + CytB clade encompassing that species. As such it appears to simply represent the high-calcificiation endpoint within the normal conchological range of *P. turcmenica*.

These supported entities could be further associated into nine groups using ITS1 + ITS2 data (used to order Table 4). Group

1 consists of *P. blandi*, *P. hebes*, *P. hebes pithodes* and *P.* cf. *limata* and is characterized by insertion 495A in ITS1. Group 2 is represented only by *P. hudsonianum* and is characterized by the 56A insertion, 541G and 583C in ITS2. Group 3 consists of *P. syngenes*, *P. sonorana* and *P.* cf. *khunjerabica* and is characterized by 156G in ITS2. Group 4 consists *of P. loessica*, *P. alaskensis* and *P. hokkaidoenis* and is characterized by 207A in ITS2. Group 5 includes only *P. alluvionica* and is characterized by 111C and 577A in *ITS1* and 333G and 490C in ITS2. Group 6 includes only *P. alpicola* and is characterized by 92C and typically 340C in *ITS2*. Group 7 consists only of *P. muscorum* and is characterized by 375C and 609A in ITS1 and 336C in ITS2. Group 8 is represented only by *P. triplicata* and is characterized by 295A in ITS2. Group 9 consists of *P. sterrii* and *P. turcmenica* and is characterized by 717T in ITS2. Because no variable bases are shared between groups, however, possible relationships between them cannot be inferred.

The greater amount of variation within COI + CytB allows resolution of deeper relationships. The nine interspecific groups suggested by ITS1 + ITS2 are generally validated with high support by the mtDNA tree topology. The major exception is Group 1, whose members are spread across two major mtDNA clades: *P. blandi*, *P. hebes hebes* and *P. hebes pithodes* belong to one strongly supported clade, while *P.* cf. *limata* appears more related to *P. loessica* and *P. alpicola* in the mtDNA tree.

Topological incongruence between mitochondrial and nuclear DNA phylogenies

Comparison of the mtDNA tree with nDNA tree and base-pair variation matrix reveals topological incongruence in eleven specimens, or almost 15% of the total. These are largely limited to two groups: *P. alaskensis* and the *P. sterrii/turcmenica* clade. The highly supported mtDNA species-level clade containing both *P. alaskensis* specimens also harbours individuals with nDNA characteristic of *P. loessica*, *P.* cf. *khunjerabica* or *P. hudsonianum*. Individuals harbouring mtDNA characteristic of *P. turcmenica* may possess nDNA characteristic of either *P. alluvionica* or *P. sterrii*. In *P. sterrii*, specimens possessing nDNA characteristic of that species may harbour mtDNA characteristic of *P. alpicola*, *P. triplicata*, *P. muscorum* or *P. turcmenica*. While the current analysis is not capable of resolving the cause of these incongruencies, it does seem likely that mitochondrial introgression is responsible in the case of *P. sterrii* as European individuals variously possess mtDNA from all other known European species.

Conchological variation: traditional vs *other traits*

Comparison of conchological features among genetically-identified individuals demonstrates that the size of the apertural crest, degree of callus deposition, callus colour and number, shape and placement of apertural lamellae are of little taxonomic value (Table 5). For instance, in Europe *P. alpicola*, *P. muscorum* and *P. triplicata* all show variation ranging from zero to multiple apertural lamellae, and from absent/weak to strong crest and callus (Fig. 3). This same pattern is repeated in central Asia with *P. turcmenica* (Fig. 4) and in North America with *P. blandi* and *P. hebes* (Fig. 5). The reliance of traditional taxonomy on these traits is thus responsible for oversplitting in some regions (e.g. *P. bigranata* and *P. pratensis* in Europe and *P. altaica* in central Asia; Figs 3, 4) and for the abysmal initial sorting of western North American material (Fig. 5).

However, other conchological traits do accurately reflect genetic relationships and are capable of accurately sorting individuals into species-level groups (Table 5; Figs 3–5). The most important of these are shell sculpture, including not only shape, strength, density and complexity of shell striae, but also the lustre of the underlying shell surface. Suture depth and apex architecture were also found to be valuable for species identification, as was shell width, which appeared to be relatively independent of shell height.

SYSTEMATIC DESCRIPTIONS

Pupillidae
Pupilla Leach, in Fleming, 1828

Pupilla alaskensis Nekola & Coles, n. sp.

(Fig. 6A–H, K)

Types: Holotype (Fig. 6A–D, K): ANSP 458632, Happy Valley, North Slope Borough, Alaska, USA (69°20′7″N, 148°43′48″W). Paratypes: 10 shells, ANSP 458633, collected with holotype; ~100 shells, NMW.Z.2014.013.00013, collected with holotype; 5 shells ANSP 458634, Sukakpak Mountain, Yukon-Koyukuk Census Area, Alaska, USA (67°35′55″N, 149°47′4″W); ~60 shells NMW.Z.2014.013.00011, same loc. as preceding; 5 shells ANSP 458635, Livengood East, Yukon-Koyukuk Census Area, Alaska, USA (65°27′55″N, 148°20′40″W); 3 shells ANSP 458636, Knik I., Matanuska-Susitna Borough, Alaska, USA (61°30′30″N, 149°2′3″W).

Zoobank registration: urn:lsid:zoobank.org:act:D98DD52C-BFAE-4752-A9D4-18F116CE8957

Other material examined: NMW.Z.2005.011.01468, NMW.Z.2014.013.00002 – 00023 *c.* 1000 shells from Alaska, USA; 30 lots (3739 individuals) from Alaska, USA in Nekola collection.

Etymology: Specific name *alaskensis* refers to region in which species is known to occur.

Diagnosis: Shell small, cylindrical-ovoid, similar to *P. hebes* but differing by its deeper suture and shell sculpture of widely-spaced, anastomosing radial striae.

GenBank: GQ921663, KM518334, KM518336, KM518412, KM518414, KM518489, KM518491, KM518567.

Description: Shell 2.6–3.3 mm tall × 1.6–1.8 mm wide, opaque to translucent, yellowish-brown to cinnamon-brown; ~6–6.5 whorls; apical whorls rounded-conical, remainder ovate-cylindrical to cylindrical; suture typically deep though sometimes of only normal depth with whorls consequently appearing swollen; shell surface silky in general appearance, the post-neanic whorls bearing sharp, irregular, often widely spaced, anastomosing radial striae occasionally developed into fine lamellae superimposed on a minutely and irregularly papillate surface (Fig. 6K); aperture ~1/4 of shell height, ranging from slightly wider than tall (Fig. 6A, E, G) through circular (Fig. 6F) to slightly taller than wide (Fig. 6H), in profile ascending onto body whorl (Fig. 6B); umbilicus closed by preceding whorls (Fig. 6C); peristome interrupted by body whorl, apertural lip flared (Fig. 6B, D), shell slightly contracted behind (Fig. 6D); crest absent or weakly developed but not thickened or callused (Fig. 6A–H); apertural lamellae generally absent, though a vestigial, plate-shaped columellar is occasionally present (Fig. 6E, G).

Geographical distribution: Currently known from just south of Arctic Ocean coastal plain in far northern Alaska to Pacific Coast near Anchorage, Alaska. It seems likely that this species will be found in adjacent areas of the Yukon and northwestern British Columbia, Canada. The published records for *P. hebes*

Table 5. *Pupilla* shell features for those taxonomic units validated by DNA sequence data.

Taxon	Height (mm)	Width (mm)	Shell form	Apex shape	Shell sculpture	Suture depth	Aperture shape	Apertural crest and callus	Apertural lamellae
alaskensis	2.6–3.3	1.6–1.8	Cylindrical ovoid to cylindrical	Tapered	Widely spaced, sharp, somewhat anastomosing coarse striae; dull shell	Normal to deep	Slightly wider than tall to slightly taller than wide	Absent to weak crest; no callus	0–1 (vestigal, plate-like columellar only)
alluvionica	3.3–4.3	2.0–2.4	Cylindrical ovoid	Tapered/domed	Low, rounded, irregular, wide spaced striae; shell shiny	Shallow/ normal	Taller than wide	Weak to very strong crest and white callus	0–1 (occasional weak parietal)
alpicola	2.8–4.2	1.6–2.1	Cylindrical ovoid; body whorl often narrower than penultimate	Tapered	Fine, rounded, close, irregular striae; shell shiny/ satiny	Shallow	Round to slightly wider than tall; small in proportion to shell size	Weak to strong crest; absent to moderate white callus	0–2 (occasional weak parietal and palatal) mostly palatal depression
blandi	2.3–3.2	1.2–1.6	Cylindrical	Domed	Irregular, very weak striae; shell shiny	Shallow	Round to slightly wider than tall	Weak to strong crest, absent to strong, brown to white callus	0–3
hebes	2.6–3.5	1.4–1.7	Cylindrical ovoid	Tapered for upper ⅓–¼ of shell height	Sharp, numerous thread striae; shell silky	Normal/deep	Round to taller than wide	Weak to strong crest; absent to strong, brown to white callus	0–3
hebes pithodes	2.9–3.3	1.6–1.8	Cylindrical ovoid; body whorl often narrower than penultimate	Tapered for upper ⅓–¼ of shell height	Sharp, numerous thread striae; shell silky	Normal/deep	Round to wider than tall	Weak to very strong crest; absent to strong brown to white callus	1–3
hokkaidoensis	3.0–3.1	1.7–1.8	Ovoid cylindrical	Tapered	Anastomosing coarse striae; shell silky to dull	Shallow	Round to wider than tall	Weak absent crest; no callus	0
hudsonianum	3.3–3.6	1.7–1.8	Cylindrical ovoid	Strongly tapered for upper ½	Dense thread striae; shell silky to dull	Normal to deep	Taller than wide (rarely) to wider than tall	Weak to strong; white callus	0–2 (weak parietal and vestigal columellar occasionally present)
cf. *khunjerabica*	2.9–3.5	1.7–1.8	Cylindrical ovoid	Tapered for upper ½ of shell height	Very weak, irregular thread striae; dull shell	Moderately deep	Taller than wide	Thin - lacking	0
cf. *limata*	2.7–3.1	1.6–1.7	Cylindrical ovoid	Tapered	Sharp, numerous, somewhat anastamosing striae; dull shell	Shallow	Taller than wide	Weak crest; no callus	0
loessica	2.6–3.6	1.6–2.0	Cylindrical ovoid	Tapered	Strong but rounded numerous, anastamosing striae; dull shell	Normal	Round	Weak to moderate crest; no callus	0
muscorum	2.7–4.0	1.6–1.8	Cylindrical ovoid	Tapered	Low, rounded, somewhat irregular striae; shell shiny to silky	Shallow	Round	Strong to very strong crest and white callus	1–2 (columellar absent)
sonorana	2.5–3.3	1.3–1.4	Ovoid cylindrical, widest in upper ½	Domed	Weak, irregular sharp thread striae; shell silky	Normal	Round	Strong crest; strong to very strong white callus	3 (palatal ranging from peg to long blade)

sterrii	2.6–3.5	1.5–1.8	Cylindrical ovoid	Tapered/domed	Sharp, anastomosing coarse striae; shell silky to dull	Very deep	Round	Weak to strong crest; absent to strong white callus	1–2 (peg shaped palatal)
syngenes	3.0–4.5	1.6–1.8	Biconic, widest in upper ⅓ of shell; 8 + whorls	Tapered/domed	Weak thread striae; shell dull	Shallow	Taller than wide	Very strong crest; weak to moderate brown callus	3
triplicata	2.2–3.1 (rarely to 4)	1.3–1.6	Cylindrical to cylindrical ovoid	Tapered	Low, rounded, irregular striae; shell shiny to silky	Normal to deep	Round	Moderate to strong crest; absent to strong white callus	0–3 (columellar often absent or weak)
turcmenica	2.7–3.2	1.5–1.6	Cylindrical ovoid	Tapered/domed	Regular remote, somewhat anastomising coarse striae; shell dull	Deep	Round	Weak to strong crest; absent to very strong white callus	0–3 (columellar absent; angular pad sometimes present)

from Anchorage, Alaska in Forsyth (2004) refer to material of the present authors and represent *P. alaskensis*.

Habitat: This species has been found in upland and lowland tundra, taiga, fens, herb-rich meadows, coastal grasslands and riparian forest.

Remarks: Shell reminiscent of *P. loessica*, but differs from that species by its widely-spaced, sharp and only slightly anastomosing striae, deeper suture and weaker (or absent) crest. It differs from *P. hokkaidoensis* in its deep suture, darker shell colour and more regular striae (Table 5).

Pupilla hudsonianum **Nekola & Coles, n. sp.**

(Fig. 7A–H, K)

Types: holotype (Fig. 7A–D, K): ANSP 458637, Lake Bemidji State Park, Beltrami County, Minnesota, USA (47°31′58″N, 94°49′28″W). Paratypes: 10 shells, ANSP 458638, collected with holotype; ∼50 shells, NMW.Z.2005.011.00835, collected with holotype; 2 shells, ANSP 458639, highway 40 at Rabbit Hill Road, east of Benchlands (Calgary), Bighorn #8 Municipal District, Alberta, Canada (51°15′51″N, 114°43′57″W); ∼100 shells, NMW.Z.2014.013.00058, same loc. as preceding; 5 shells, ANSP 458640, Goose Creek Road, Churchill, Manitoba, Canada (58°42′30″N, 94°7′22″W); 1 shell, ANSP 458641, La Grande Pointe, Duplessis District, Quebec, Canada (50°12′21″N, 63°23′48″W); ∼30 shells, NMW.Z.2014.013.00001, same loc. as preceding.

Zoobank registration: urn:lsid:zoobank.org:act:B9E21337-42C7-4BFD-87B9-EFE157D2A5A2.

Other material examined: NMW.Z.2014.01300054-00060, 00066-00071, 00080; *c.* 500 shells. Ten lots from Nekola collection (including one of Pleistocene fossil material; 651 individuals).

Etymology: The specific name *hudsonianum* refers to Hudson Bay and to the Hudsonian life zone, which has been used to refer to the North American taiga, and which defines much of this species' range.

Diagnosis: Shell ovoid-cylindrical, similar to *P. hebes*, but differentiated by its more ovate shell shape with a surface sculpture consisting of densely packed radial thread-like striae, giving shell a silky lustre.

GenBank: GQ921662, KM518353, KM518354, KM518355, KM518357, KM518358, KM518431, KM518432, KM518433, KM518435, KM518508, KM518509, KM518510, KM518512, KM518585, KM518586, KM518587, KM518589.

Description: shell 3.3–3.6 mm tall × 1.7–1.8 mm wide; opaque to translucent yellowish-brown; *c.* 6.5–7 whorls; apical whorls rounded-conical in outline, remainder cylindrical; suture moderately deep; shell surface silky in general appearance, postneanic whorls bearing irregular, dense, closely-spaced, weakly anastomosing radial thread-like striae superimposed on a minutely scaly surface, with minute papillae present between the scales (Fig. 7K); aperture *c.* $\frac{1}{4}$ of shell height, approximately circular (Fig. 7F) to wider than tall (Fig. 7A, E, G), rarely taller than wide (Fig. 7H), in profile ascending onto body whorl (Fig. 7B); umbilicus closed by preceding whorls (Fig. 7C); peristome interrupted by body whorl; apertural lip expanded, shell slightly contracted behind; lip thickened by a weakly to strongly developed pale callus of shallow depth corresponding to a weakly to strongly developed crest (Fig. 7A, B, D, E); apertural

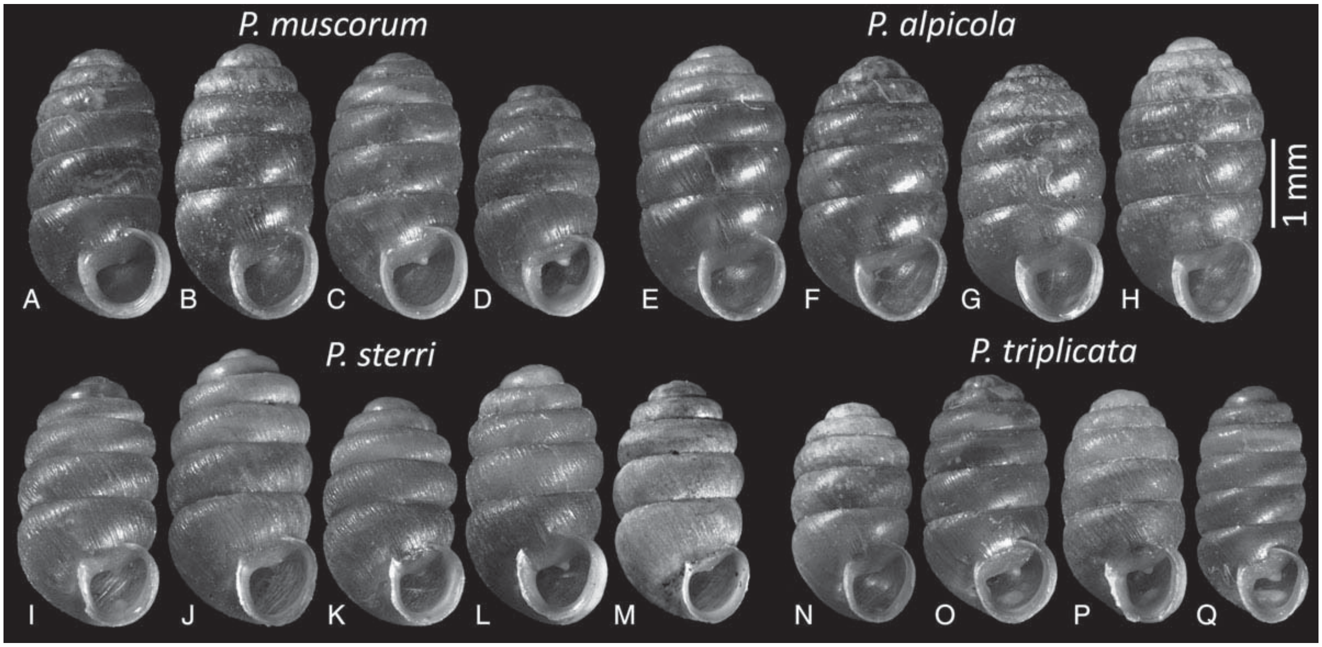

Figure 3. *Pupilla* species of primarily European distribution. Names are those supported by DNA sequence analysis. **A–D.** *P. muscorum*. **A.** Cedar Rapids, Iowa, USA (22). **B.** Brno, Moravia, Czech Republic (mtG-Pup) **C.** Syracuse, New York, USA (AP26). **D.** Pont, Calvados, France (AP25). **E–H.** *P. alpicola*. **E.** Rakša, Slovakia (H6). **F.** Belyashi, Altai, Russia (AP12). **G.** Závod, Slovakia (H5). **H.** Pozděchov, Moravia, Czech Republic (H1). **I–M.** *P. sterrii*. **I.** Verkhne Bikberda, Bashkortostan, Russia (AP15). **J.** Periferi Dibre, Albania (AP16). **K.** Klentnice, Moravia, Czech Republic (AP22). **L.** Pavlov, Moravia, Czech Republic (H8). **M.** Valaská Dubová, Slovakia (AP21). **N–Q.** *P. triplicata*. **N.** Hracholusky, Bohemia, Czech Republic (H17). **O.** Ozero Kureevo, Altai, Russia (AP32). **P.** Pavlov, Moravia, Czech Republic (H9). **Q.** Cahors, Dordogne, France (AP31).

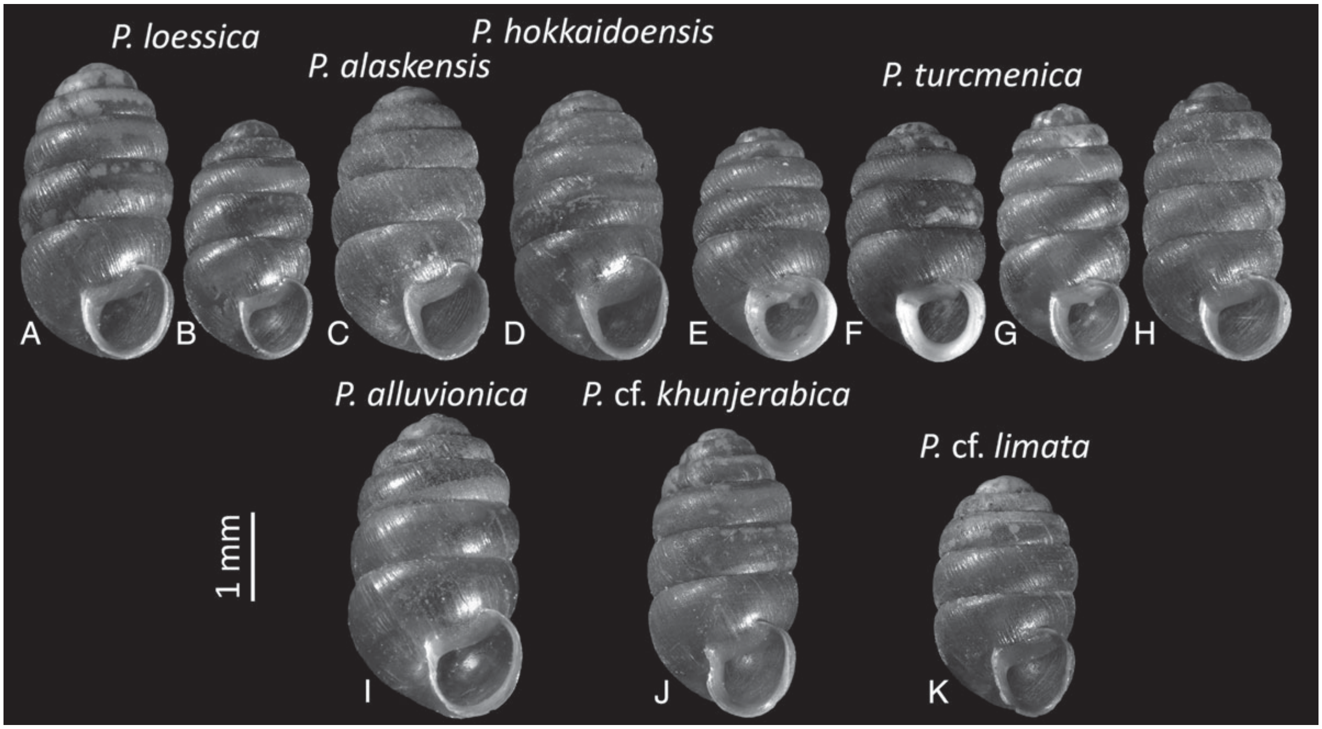

Figure 4. *Pupilla* species primarily of Asian/Beringian distribution. Names are those supported by DNA sequence analysis. **A, B.** *P. loessica*. **A.** Belyashi, Altai, Russia (AP7). **B.** Belyashi, Altai, Russia (AP9). **C.** *P. alaskensis*, Knik Island, Anchorage, Alaska, USA (AP29). **D.** *P. hokkaidoensis*, Toyokoro, Nakagawa, Hokkaido, Japan (VH29). **E–H.** *P. turcmenica*. **E.** Ust'-Muny, Altai, Russia (AP1). **F.** Kurai, Altai, Russia (AP17). **G.** Kurai, Altai, Russia (AP18). **H.** Kosh-Agach, Altai, Russia (AP3). **I.** *P. alluvionica*, Belyashi, Altai, Russia (AP13). **J.** *P.* cf. *khunjerabica*, Chagan-Uzun, Altai, Russia (AP11). **K.** *P.* cf. *limata*, Kapitonovka, Yakutia, Russia (AP39).

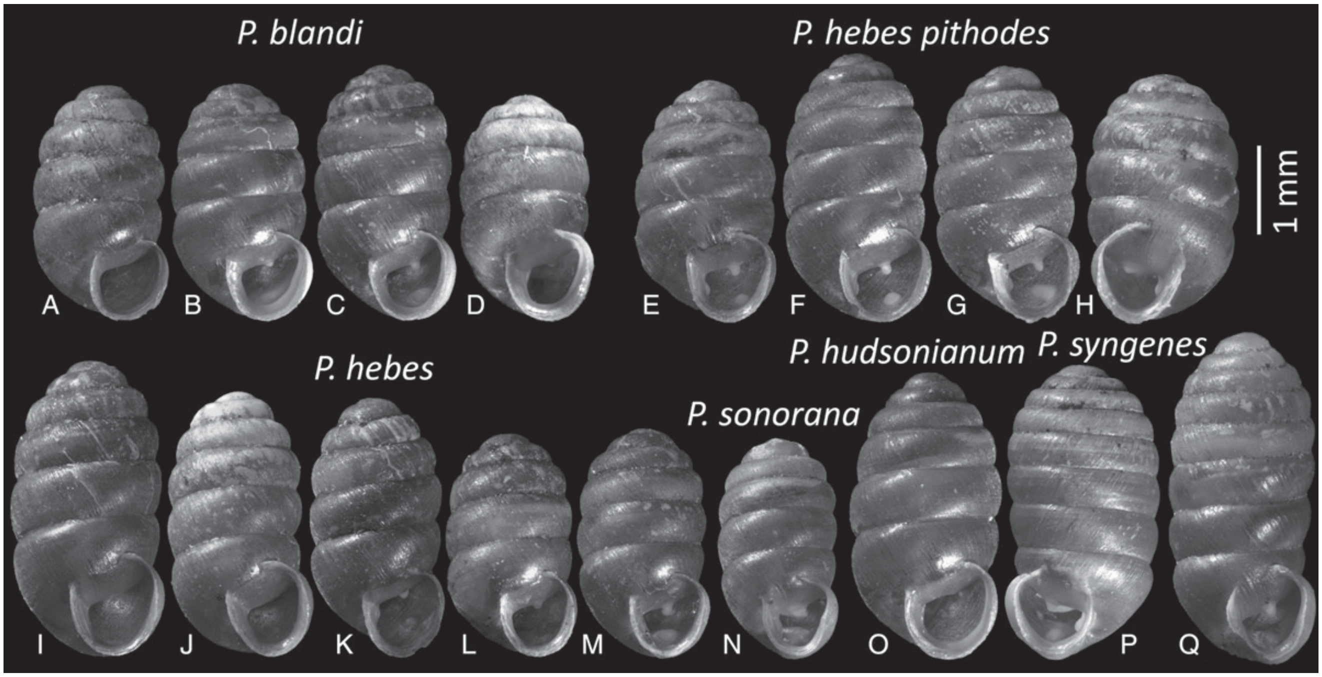

Figure 5. *Pupilla* species of North American distribution. Names are those supported by DNA sequence analysis. **A–D.** *P. blandi*. **A.** Ute Creek Canyon, Colorado, USA (AP37). **B.** Irvine, Alberta, Canada (AP34). **C.** Moose Jaw, Saskatchewan, Canada (AP35). **D.** Bannon Ranch, New Mexico, USA (image for ET7 was lost, so a similar shell from same population is figured). **E–H.** *P. hebes pithodes*. **E.** Tusas Ridge, New Mexico, USA (AP38). **F.** Bullion Canyon, Utah, USA (AP27). **G.** Bullion Canyon, Utah, USA (AP28). **H.** Bear Wallow, Arizona, USA (P6). **I–M.** *P. hebes hebes*. **I.** Loope East, California, USA (P14). **J.** Bullion Canyon, Utah, USA (P17). **K.** Ruby Mountains, Nevada, USA (P16). **L.** Kaibab Plateau, Arizona, USA (P1). **M.** East Tintic Range, Utah, USA (P2). **N.** *P. sonorana*, Sacramento Mountains, New Mexico, USA (P12). **O.** *P. hudsonianum*, Lake Bemidji, Minnesota, USA (AP33). **P, Q.** *P. syngenes*. P. Mogollon, New Mexico, USA (AP30). **Q.** Kaibab Plateau, Arizona, USA (P11).

lamellae generally absent (Fig. 7G, H), but a weak parietal (Fig. 7E) and vestigial plate-like columellar lamella (Fig. 7A, F) occasionally present.

Geographical distribution: Currently documented from DNA sequence data from the foothills of the Rockies in western Alberta, Canada east through the northern (Churchill, Manitoba, Canada) and southern (Lake Bemidji, Minnesota, USA) taiga limits in central North America to the north shore of the Gulf of St Lawrence in Quebec. Shell lots at the Academy of Natural Sciences at Drexel University (ANSP 106909, 141759, 141770, 141776, 141783, 150006, 150026), Carnegie Museum (CM 86989, 87010, 62.20823), Museum of Comparative Zoology (MCZ 048304, 201542), National Museum of Canada (NMC 2892, 69132), Royal Ontario Museum (ROM 21464) and University of Michigan Museum of Zoology (UMMZ 55951, 109819, 109829, 168485, 180110, 180112) indicate that *P. hudsonianum* occurs across the southern shore of Hudson Bay in Ontario and along the Gulf of St Lawrence shore from the Gaspé and Anticosti Island in Quebec to the west shore of Newfoundland All reports of *P.* '*muscorum*' from Pleistocene sediments in central North America (Hubricht, 1985) represent *P. hudsonianum* (Fig. 6J).

Habitat: This species occurs has been found in mesic taiga, calcareous fens, dry sandy lakeshores and tundra-like turfs on shoreline limestone pavements.

Remarks: *Pupilla hudsonianum* is most readily distinguished from *P. muscorum*, with which it has been previously confused, by its deeper suture, less massive and more yellow apertural callus, and sharp, fine striae which give the shell a matte luster (Table 5).

Pupilla hokkaidoensis Nekola, Coles & S. Chiba, n. sp.

(Fig. 8A–K)

Types: holotype (Fig. 8A–D, K): ANSP 458642, Toyokoro, Nakagawa District, Hokkaido Prefecture, Japan (42°36′18″N, 143°33′23″E). Paratypes: 10 shells, ANSP 458643, collected with holotype; 11 shells, NMW.Z.2014.013.00061, collected with holotype; 5 shells, ANSP 458644, Kushiro Marsh, Kushiro District, Hokkaido Prefecture, Japan (43°2′2″N, 144°23′24″E); 12 shells, NMW.Z.2014.013.00062, same loc. as preceding; 5 shells, ANSP 458645, Betsukai, Notsuke District, Hokkaido Prefecture, Japan (43°20′50″N, 145°19′6″E); 5 shells, ANSP 458646, Hama-koshimizu, Shari District, Hokkaido Prefecture, Japan (43°56′1″N, 144°26′38″E); ~25 shells, NMW.Z.2014.013.00064, same loc. as preceding.

Zoobank registration: urn: lsid:zoobank.org:act:891CB0E8-E4AA-43BB-9BDB-8F579461E48A.

Other material examined: 6 shells NMW.Z.2005.011.03876, 03878; 4 lots from Nekola collection (176 individuals).

Etymology: The specific name *hokkaidoensis* refers to the island of Hokkaido, where all known populations reside.

Diagnosis: Shell small, ovoid-cylindrical, similar to *P. hebes* but differentiated by a more ovate shell with shallower sutures and shell surface sculpture of coarse, anastomosing, radial striae.

GenBank: KM518566, KM518488, KM518411, KM518333.

Description: Shell 3.0–3.1 mm tall × 1.7–1.8 mm wide; opaque to translucent, yellow-brown; *c.* 6 whorls; apical whorls conical

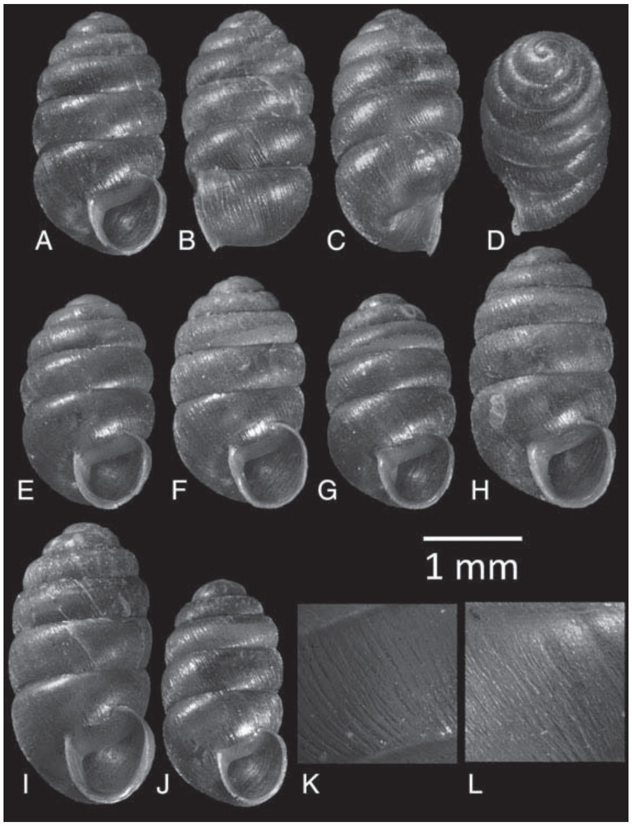

Figure 6. A–H. *Pupilla alaskensis*, n. sp. **A–D, K.** Holotype, ANSP 458632; Happy Valley, North Slope Borough, Alaska, USA. **E.** Paratype, ANSP 458633; Happy Valley, North Slope Borough, Alaska, USA. **F.** Paratype, ANSP 458635; Livengood East, Yukon-Koyukuk Census Area, Alaska, USA. **G.** Paratype, ANSP 458634; Sukakpak Mountain, Yukon-Koyukuk Census Area, Alaska, USA. **H.** Paratype, ANSP 458636; Knik I., Matanuska-Susitna Borough, Alaska, USA. **I, L.** *P. hebes*, JCN 17254; Loope East, Alpine Co., California, USA. **J.** *P. loessica*, Belyashi, Altai Republic, Russia; 49°16′8″N, 87°59′2″E.

in outline, remainder ovoid-cylindrical giving shell slight barrel shape; suture shallow; shell surface silky in general appearance, post-neanic whorls bearing irregular, anastomosing radial striae most strongly developed on mid whorls, superimposed on a minutely and irregularly papillate surface (Fig. 8K); aperture *c.* $\frac{1}{4}$ of shell height, ranging in shape from approximately circular (Fig. 8A, E, H) to taller than wide (Fig. 8F, G), in profile ascending onto body whorl (Fig. 8B); umbilicus closed by preceding whorls (Fig. 8C); peristome interrupted by body whorl; apertural lip flared (Fig. 8B–D), shell slightly contracted behind; crest absent or weakly developed (Fig. 8D), callus absent; apertural lamellae absent.

Geographical distribution: Currently known only from the eastern coast of Hokkaido, Japan.

Habitat: This species was found in beach grasslands, wetland margins and old fields.

Remarks: *Pupilla hokkaidoensis* differs from *P. loessica* in its more ovate shell, more yellow shell colour, shallower suture and coarser, more widely spaced and irregular striae. It differs from *P. alaskensis* in its more yellow shell colour, shallower suture and more irregular striae. It differs from *P.* cf. *limata* from Yakutia, Siberia, in its larger size, lighter shell colour and presence of anastomosting striae.

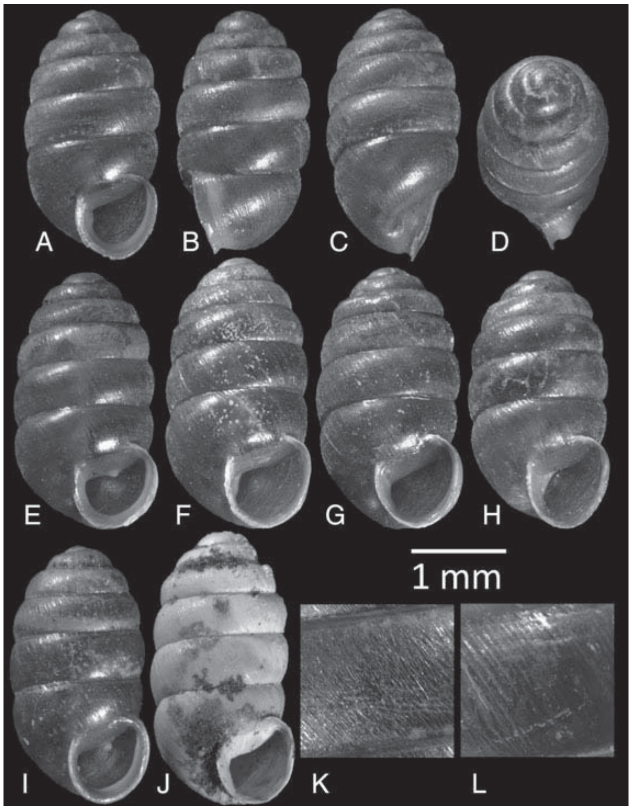

Figure 7. A–H, J, K. *Pupilla hudsonianum*. **A–D, K.** Holotype, ANSP 458637; Lake Bemidji State Park, Beltrami County, Minnesota, USA. **E.** Paratype, ANSP 458638; Lake Bemidji State Park, Beltrami County, Minnesota, USA. **F.** Paratype, ANSP 458641; La Grande Pointe, Duplessis District, Quebec, Canada. **G.** Paratype, ANSP 458639; East of Benchlands, Bighorn #8 Municipal District, Alberta, Canada. **H.** Paratype, ANSP 458640; Goose Creek Road, Churchill, Manitoba, Canada. **J.** Pleistocene loess fossil, Wenig Road, Cedar Rapids, Linn Co., Iowa, USA; 42°0′8″N, 91°40′40″ W; JCN 3650. **I, L.** *P. muscorum*; Syracuse University South Campus, Syracuse, Onondaga Co., New York, USA; 43°0′27″N, 76°6′38″W; JCN 13955.

DISCUSSION

These analyses show that in three widely separated geographic regions the understanding of species-level taxonomy within the genus *Pupilla* has been hampered by the traditional reliance on a suite of highly plastic shell apertural features that are of little taxonomic value. As a result, too many species have been described in Europe and central Asia, and too few species in North America and eastern Asia, with confusion existing about actual species ranges and ecological tolerances. However, DNA sequence analysis also confirms that most previously described taxa have biological merit, with alternative conchological traits such as shell sculpture and architecture being able accurately to distinguish these entities.

Because traditional taxonomic concepts within *Pupilla* have been based on unstable shell features, larger patterns regarding biodiversity, biogeography and ecology must also be reconsidered. While we cannot deal here with these issues for the entire genus, the current analysis does allow for reconsideration within each of our three study regions.

Reassessment of Pupilla *biodiversity*

In Europe oversplitting has been predominant, with both *P. bigranata* and *P. pratensis* having been differentiated from *P.*

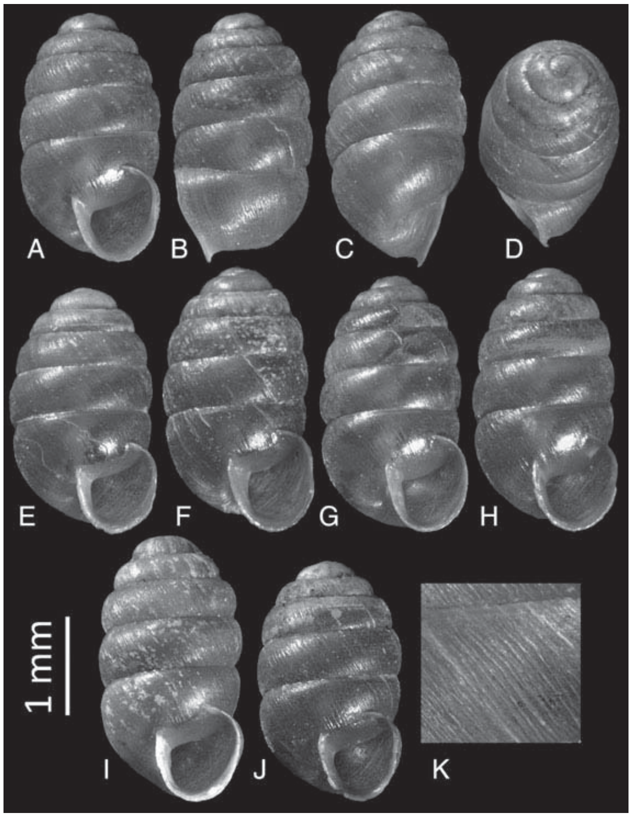

Figure 8. A–H. *Pupilla hokkaidoensis*. **A–D, K.** Holotype, ANSP 458642; Toyokoro, Nakagawa District, Hokkaido Prefecture, Japan. **E.** Paratype, ANSP 458643; Toyokoro, Nakagawa District, Hokkaido Prefecture, Japan. **F.** Paratype, ANSP 458644; Kushiro Marsh, Kushiro District, Hokkaido Prefecture, Japan. **G.** Paratype, ANSP 458646; Hama-koshimizu, Shari District, Hokkaido Prefecture, Japan. **H.** Paratype, ANSP 458645; Betsukai, Notsuke District, Hokkaido Prefecture, Japan. **I.** *P. hebes*, Charleston, Elko Co., Nevada, USA; 41°41′12″N, 115°30′22″W; JCN 18292. **J.** *P.* cf. *limata*, Kapitonovka, Yakutia Republic, Russia; 62°19′45″N, 129°55′42″E.

muscorum and *P. alpicola*, respectively, based upon unstable shell apertural characters. It is fortunate that degree of apertural calcification has never been used to split *P. triplicata*, as its development of lamellae can range from three very strong (French Pyrenees) to absent (basalt talus in northern Bohemia).

In central Asia, oversplitting has also been an issue. While some recently described taxa are strongly demarcated (e.g. *P. alluvionica* and *P.* cf. *khujerabica*), others (*P. altaica* and *P. pratensis*) appear to represent high-calcification endpoints in apertural development within previously described species (*P. turcmenica* and *P. alpicola*, respectively). Perhaps it is not surprising that such high-calcification shell forms tend to originate from drier, lower elevation sites, which would have higher calcium availability due to lower leaching and higher potential evapotranspiration rates (Lapenis *et al.*, 2008).

In North America, overlumping and ignorance of taxonomically valid shell traits has led to considerable confusion. First, *P. muscorum* is not a native North American species, with all examined putative native populations representing either *P. hebes* (southwestern USA) or *P. hudsonianum* (central/eastern taiga and tundra) and with *P. muscorum xerobia* being a junior synonym of *P. blandi*. *Pupilla blandi* should be distinguished from other North American species not by apertural features, but rather by its weak to obsolete striation and shining shell lustre. *Pupilla hebes* should be distinguished by its strong thread-like striae and narrow, columnar shell. *Pupilla hebes pithodes* is most closely related to *P. hebes*, but differs in its wider and more barrel-shaped shell. Additionally, *P. alaskensis* has been variously regarded as *P. muscorum* or *P. hebes* in spite of its coarser striation, ovate shell shape and deeper suture than either of these species.

Reassessment of Pupilla *biogeography*

In Europe, *P. alpicola* cannot be considered a central European endemic with a disjunct set of populations in the Altai (Horsák *et al.*, 2010). Rather, it extends continuously northwest into southern Scandinavia and Ireland (as the former *P. pratensis*) and east into central Asia. Although demarcation between the central Asian and European populations is evident in nDNA, the central Asian subpopulation extends at least as far west as Bohemia. The amount of mixing of these two populations during full glacial stages is thus unclear. *Pupilla triplicata* occurs as far east as the Altai in central Asia. *Pupilla sterrii* is the western sibling of *P. turcmenica*, with populations extending from central Europe east to the Urals. *Pupilla muscorum* is not a Holarctic species, but is a European endemic with confirmed Pleistocene fossil occurrences in loess deposits of central Europe.

In the Altai, species status for two putative central Asian endemics (*P. alluvionica* and *P.* cf. *khunjerabica*) was established. However, another (*P. altaica*) was found to be simply a shell form within *P. turcmenica*, which ranges from western China and Tibet to the Iran–Turkmenistan border (Pilsbry, 1921). *Pupilla loessica* was shown to be a member of a Beringian group that also includes *P. hokkaidoensis* and *P. alaskensis*.

In North America, the lack of true *P. muscorum* as a Pleistocene fossil suggests that it is an exotic species ranging from the western Great Lakes east to Virginia and north into the Canadian maritime provinces. The identical COI haplotype of the Brno and Cedar Rapids *P. muscorum* specimens suggest that both populations were sourced from the same pool. This is not surprising given that extensive immigration from the Czech Republic to eastern Iowa happened during the mid-1800s. *Pupilla hudsonianum*, which has been previously regarded as *P. muscorum*, extends west from the north shore of the St Lawrence River in Quebec to the southern border of Hudson Bay, northwestern Minnesota and the foothills of the Rockies in Alberta. It also represents the putative Pleistocene fossil '*P. muscorum*' reported by Hubricht (1985) across the central Midwestern USA and Plains. *Pupilla blandi* is limited to the Plains (NE New Mexico to NW Minnesota to southern Saskatchewan and Alberta) and rarely penetrates west into the Rockies as far as the continental divide. *Pupilla hebes* is characteristic of the Great Basin from Arizona and California to Utah and Idaho, with a well-demarcated subpopulation from the Colorado Plateau being demonstrated by mtDNA. While this subpopulation would equate to *P. hebes kaibabensis*, its shells and nDNA do not differ in any meaningful way from typical *P. hebes*, and we have not chosen to recognize it here. *Pupilla hebes pithodes* is found to the south and east of typical *P. hebes*, ranging from eastern Arizona and SE Utah to the eastern foothills of the Rockies in Colorado and New Mexico. *Pupilla alaskensis*, formerly confused with *P. hebes*, is actually a sibling of the western Beringian *P. loessica*.

Reassessment of Pupilla *ecology*

The existence of so much apertural variation within species across *Pupilla* begs for an explanation. In particular, how much of these differences are due to genetic variation and how much to ecophenotypic response? Little empirical data exist to address this question. However, we typically noted limited variation in apertural features within populations. Populations expressing a poorly developed apertural callus and lamellae tended to be found in sites with low calcium availability, such as *P. blandi*

(AP37) on acid metamorphic rock in the Colorado Rockies, and *P. triplicata* on basalt talus slopes in Bohemia (e.g. H10). In contrast, the most heavily calcified *P. turcmenica* in the Altai tend to be restricted to xeric, low-elevation steppe, often on calcium-rich metamorphic rock or limestone. Individual age and the season when maturity is reached may also play important factors. While these observations suggest that ecophenotypic or developmental response is responsible for much of the observed variation, different shell forms have nevertheless been observed in co-occurring individuals that share identical mtDNA and nDNA haplotypes (e.g. AP27, AP28), suggesting that multiple factors may be operating.

ACKNOWLEDGEMENTS

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We initially embarked on this project to discern whether *P. triplicata* with vestigal or absent lamellae from the basalt screes of northern Bohemia warranted erection as a new species. Had our initial hypothesis been validated, we intended to name this taxon after Dr Ložek. While this work ultimately documented an entirely different story, we would still like to thank Dr Ložek for his lifetime of work on Eurasian land snails, including the initial description of *P. loessica*.

REFERENCES

ARMBRUSTER, G.F.J. & BERNHARD, D. 2000. Taxonomic significance of ribosomal ITS-1 sequence markers in self-fertilizing land snails of *Cochlicopa* (Stylommatophora, Cochlicopidae). *Zoosystematics & Evolution*, **76**: 11–18.

EMBERTON, K.C. 1995. When shells do not tell—145-million years of evolution in North American polygyrid land snails, with a revision and conservation priorities. *Malacologia*, **37**: 69–109.

FORSYTH, R.G. 2004. *Land snails of British Columbia*. Royal BC Museum, Victoria, Canada.

HORSÁK, M., CHYTRÝ, M. & AXMANOVÁ, I. 2013. Exceptionally poor land snail fauna of central Yakutia (NE Russia): climatic and habitat determinants of species richness. *Polar Biology*, **36**: 185–191.

HORSÁK, M., CHYTRÝ, M., POKRYSZKO, B.M., DANIHELKA, J., ERMAKOV, N., HÁJEK, M., HÁJKOVÁ, P., KINTROVA, K., KOČÍ, M., KUBEŠOVÁ, S., LUSTYK, P., OTÝPKOVÁ, Z., PELÁNKOVÁ, B. & VALACHOVIČ, M. 2010. Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. *Journal of Biogeography*, **37**: 1450–1462.

HORSÁK, M., HÁJEK, M., SPITALE, D., HÁJKOVÁ, P., DÍTĚ, D. & NEKOLA, J. 2012. The age of island-like habitats impacts habitat specialist species richness. *Ecology*, **93**: 1106–1114.

HUBRICHT, L. 1985. The distributions of the native land mollusks of the eastern United States. *Fieldiana, New Series*, **24**: 1–191.

HUELSENBECK, J.P. & RONQUIST, F. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, **17**: 754–755.

KERNEY, M.P. & CAMERON, R.A.D. 1979. *Field guide to the land snails of the British Isles and northwestern Europe*. Collins, London.

LAPENIS, A.G., LAWRENCE, G.B., BAILEY, S.W., APARIN, B.F. & SHIKLOMANOV, A.I. 2008. Climatically driven loss of calcium in steppe soil as a sink for atmospheric carbon. *Global Biogeochemical Cycles*, **22**: GB2010, doi:10.1029/2007GB003077.

MENG, S. & HOFFMAN, M.H. 2008. *Pupilla altaica* n. sp. and *Pupilla alluvionica* n. sp., two new species of the Pupillidae (Gastropoda: Pulmonata: Pupilloidea) from the Russian Altay. *Mollusca*, **26**: 229–234.

MENG, S. & HOFFMAN, M.H. 2009. *Pupilla seminskii* n. sp. (Gastropoda: Pulmonata: Pupilloidea) from the Russian Altay. *Mollusca*, **27**: 83–86.

NEKOLA, J.C. 2005. Latitudinal richness, evenness, and shell size gradients in eastern North American land snail communities. Records of the Western Australian Museum, Supplement, **68**: 39–51.

NEKOLA, J.C. 2014. North American terrestrial gastropods through either end of a spyglass. *Journal of Molluscan Studies*, **80**: 238–248.

NEKOLA, J.C. & COLES, B.F. 2010. Pupillid land snails of eastern North America. *American Malacological Bulletin*, **28**: 29–57.

NEKOLA, J.C., COLES, B.F. & BERGTHORSSON, U. 2009. Evolutionary pattern and process in the *Vertigo gouldii* (Mollusca: Pulmonata, Pupillidae) group of minute North American land snails. *Molecular Phylogenetics and Evolution*, **53**: 1010–1024.

NEKOLA, J.C. & ROSENBERG, G. 2013. *Vertigo marciae* (Gastropoda, Vertiginidae), a new land snail from Jamaica. *Nautilus*, **127**: 107–114.

OUGHTON, J. 1948. A zoogeographical study of the land snails of Ontario. *University of Toronto Studies. Biological Series*, **57**: 1–126.

PILSBRY, H.A. 1921. *Manual of conchology, second series. Vol. 26: Pupillidae (Vertigininae, Pupillinae)*. Academy of Natural Sciences, Philadelphia.

PILSBRY, H.A. 1948. *Land Mollusca of North America (north of Mexico)*. Academy of Natural Sciences of Philadelphia Monograph 3, vol. 2.

POKRYSZKO, B.M., AUFFENBERG, K., HLAVÁČ, J.Č. & NAGGS, F. 2009. Pupilloidea of Pakistan (Gastropoda: Pulmonata): Truncatellininae, Vertigininae, Gastrocoptinae, Pupillinae (in part). *Annales Zoologici (Warszawa)*, **59**: 423–458.

SCHILEYKO, A.A. 1984. Nazemnye molljuski podotryda Pupillina fauny SSSR (Gastropoda, Pulmonata, Geophila). *Fauna SSSR, Molljuski*, **3**: 1–399 (In Russian).

TONGKERD, P., LEE, T., PANHA, S., BURCH, J.B. & Ó FOIGHIL, D. 2004. Molecular phylogeny of certain Thai Gastrocoptinae micro land snails (Stylommatophora: Pupillidae) inferred from mitochondrial and nuclear ribosomal DNA sequences. *Journal of Molluscan Studies*, **70**: 139–147.

UIT DE WEERD, D.R., PIEL, W.H. & GITTENBERGER, E. 2004. Widespread polyphyly among Alopiinae snail genera: when phylogeny mirrors biogeography more closely than morphology. *Mollecular Phylogenetics and Evolution*, **33**: 533–548.

VON PROSCHWITZ, T., SCHANDER, C., JUEG, U. & THORKILDSEN, S. 2009. Morphology, ecology, and DNA-barcoding distinguish *Pupilla pratensis* (Clessen, 1871) from *Pupilla muscorum* (Linnaeus, 1758) (Pulmonata: Pupillidae). *Journal of Molluscan Studies*, **75**: 315–322.

WADE, C.M. & MORDAN, P.B. 2000. Evolution within the gastropod molluscs; using the ribosomal RNA gene-clustre as an indicator of phylogenetic relationships. *Journal of Molluscan Studies*, **66**: 565–570.

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Vertigo marciae (Gastropoda: Vertiginidae), a new land snail from Jamaica

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ABSTRACT

Vertigo marciae, a new species of gastropod mollusk (Pupilloidea: Vertiginidae), is described from Jamaica. This species is known in the Recent fauna only from John Crow Peak in the Blue Mountains, but also occurs as a Pleistocene fossil at Red Hills Road Cave. *Vertigo marciae* has been confused with *Vertigo gouldii*, but differs by its smaller shell size, lack of distinct shell striation, lack of an angular lamella, and presence of a flared aperture base. DNA sequence analyses document that *V. marciae* possesses unique mtDNA and nDNA sequences and is most closely allied with *Vertigo alabamensis*, *Vertigo hebardi*, and *Vertigo oscariana*. This group of species comprises a highly supported clade whose members are limited either to the Caribbean or the southeastern USA.

Additional Keywords: Vertigo, biogeography, southeastern USA, Caribbean, DNA sequence analysis

INTRODUCTION

In their synopsis of the Jamaican land snail fauna, Rosenberg and Muratov (2006) reported three species from the genus *Vertigo*, all of which possess ranges extending into the eastern half of North America (Nekola and Coles, 2010): *V. gouldii*, *V. milium*, and *V. ovata*. However, images of putative Jamaican '*V. gouldii*' on the Discover Life website (http://pick4.pick.uga.edu/mp/20q?search=Vertigo+gouldii&guide=1) illustrate a shell quite unlike *V. gouldii* from eastern North America (Nekola and Coles, 2010) in its light-yellow shell color, lack of sharp shell striation, and absence of a basal lamella. Observation of the three known Jamaican lots for this entity in the Academy of Natural Sciences of Philadelphia (ANSP) collections confirmed these differences. Although they looked most like *V. hebardi* Vanatta, 1912 of the Florida Keys, these lots clearly differed from that species by their taller shell, reduced striation, and absence of an angular lamella. Thus, rather than representing a population of *V. gouldii* isolated by 2000 km from its nearest neighbors (Nekola and Coles, 2010), these specimens appear to represent an undescribed new species. Based on shell descriptions, reports of *Vertigo gouldii* from the Pleistocene Red Hills Road Cave deposits of Jamaica (Paul and Donovan, 2005) also appeared to represent this new species. This conclusion was subsequently confirmed via observation of digital images.

We therefore investigated this putative new species via analyses of both shell morphology and DNA sequence data, and are now in the unusual situation of describing and reporting a new species simultaneously from both living and fossil material, while also being able to report on its phylogenetic relationships.

MATERIALS AND METHODS

Field Collection: The three known Recent lots of the putative new Jamaican species (ANSP 402244, 403039, and 403040) were collected on John Crow Peak in the Blue Mountains of eastern Jamaica on May 22, 1999, during the Jamaican Biotic Survey. Collecting methods were detailed in Rosenberg and Muratov (2006), and included drying of soil litter samples over a Berlese Funnel. This encouraged snails to enter aestivation, allowing them to mummify upon death. For this reason, it was possible to successfully extract, amplify, and sequence selected amplicons from both their mitochondrial and nuclear genomes (Nekola et al., 2009).

Shell Measurements: Measurements were determined in 0.1 mm increments for adult shells with aperture facing up, using a dissecting microscope with a calibrated ocular micrometer. Height and width were measured as the dimensions of a bounding box with long axis parallel to the shell axis and sides tangent to the tip of the protoconch, the base of the lip, the right-most margin of the aperture and the left-most margin of the body whorl.

Imaging: Shells were imaged at 20× magnification using a digital camera attached to a stereomicroscope.

Approximately 14 separate 1388×1040 pixel images were made of each specimen with the image focal lengths positioned at 75 µm increments from the front to back of the shell. CombineZ5 freeware (http://www.hadleyweb.pwp.blueyonder.co.uk/CZ5/combinez5.htm) was used to assemble a final image from the focused parts of each separate image. Assembled images were imported into Adobe Photoshop, where brightness and contrast were optimized and the background made uniformly black. These images were then compiled into a single plate.

DNA Sequence Analysis: Mitochondrial cytochrome b (*CytB*), 16S ribosomal RNA (*16S*) and the internal transcribed spacers 1 (*ITS–1*) and 2 (*ITS-2*) of the nuclear ribosomal RNA gene were investigated to test the distinctiveness of the putative new Jamacian species and to resolve its nearest evolutionary neighbors. The mitochondrial cytochrome oxidase subunit 1 (*CO1*) was not analyzed as we were unable to amplify this gene in the Jamaican species.

Sixteen specimens were chosen for analysis (Table 1). This set includes not only two specimens of the Jamaican species but also *Vertigo alabamensis, V. gouldii, V. hebardi,* and *V. oscariana*. We attempted to maximally spread these individuals across the known geographic range of each species (see Nekola and Coles, 2010). Because *V. conecuhensis* is likely a simple shell form of *V. alabamensis* (Nekola and Coles, 2010), only a single individual of this taxon was included. Topotype or near-topotype material was selected for *V. conecuhensis* (Pond Creek, Covington Co., Alabama, about 50 km from the type locality in Evergreen, Alabama) and *V. hebardi* (Long Key, Florida which is the type locality). Previously analyzed *16S* sequence data from three *Vertigo gouldii* specimens analyzed by Nekola et al. (2009) were retrieved from GeneBank (Table 1). *Vertigo pusilla*, the type species of the genus, was also included, as were *Gastrocopta cristata* and *Pupilla muscorum* for outgroup comparisons.

Genomic DNA was extracted from live, ethanol-preserved, or mummified material using the OmegaBioTek Mollusk DNA Extraction Kit. Because shell destruction was required, all shells were imaged prior to extraction using the methods detailed above. PCR amplification and sequencing of *CytB, 16S, ITS-1,* and *ITS-2* were accomplished using standard methods (Nekola et al., 2009). Resultant traces were examined, primer ends removed, and aligned by eye. Because of their lower evolutionary rates, the nDNA *ITS-1* and *ITS-2* regions were concatenated to provide a roughly similar number of nucleotide differences to either of the mtDNA amplicons. Mega 5.0 (Tamura et al., 2011) was used to calculate the average number of nucleotide differences in the *CytB*, *16S*, and concatenated *ITS-1* + *ITS-2* regions between all putative species-level taxa. Substitutions included both transitions and transversions with pairwise gap deletion.

Table 1. Specimen information for material used in DNA sequence analysis.

Taxon		GENBANK Accession number			
Location	Latitude/Longitude	*CytB*	*16S*	*ITS-1*	*ITS-2*
Vertigo marciae new species					
John Crow Peak, St. Andrew Parish, Jamaica	18.1132 N., 76.6685 W.	KF214513	KF214503		
John Crow Peak, St. Andrew Parish, Jamaica	18.1132 N., 76.6685 W.	KF214514	KF214502	KF214489	KF214477
Vertigo alabamensis Clapp, 1915					
Johnson Mill Bay, Bladen Co., North Carolina, USA	34.7125 N., 78.5261 W.	KF214515	KF214501	KF214490	KF214478
Wolf Trap Bay, Leon Co., Florida, USA	30.3680 N., 84.5700 W.	KF214516	KF214500	KF214491	KF214479
Vertigo conecuhensis Clapp, 1915					
Pond Creek, Covington Co., Alabama	31.1036 N., 86.5343 W.	KF214517	KF214499	KF214492	KF214480
Vertigo gouldii (A. Binney, 1843)					
Brush Creek Canyon, Fayette Co., Iowa, USA	42.7796 N., 91.6890 W.	KF214508	GQ921506	KF214484	KF214472
Panther Creek, Searcy Co., Arkansas, USA	36.0858 N., 92.5649 W.	KF214509	GQ921507	KF214485	KF214473
11-Point River, Oregon Co., Missouri, USA	36.7931 N., 91.3334 W.	KF214510	KF214506	KF214486	KF214474
Vertigo hebardi Vanatta, 1912					
Long Key, Monroe County, Florida, USA	24.8146 N., 80.8211 W.	KF214511	KF214505	KF214487	KF214475
Elliott Key, Miami-Dade County, Florida, USA	25.4553 N., 80.1925 W.	KF214512	KF214504	KF214488	KF214476
Vertigo oscariana (Sterki, 1890)					
Blanchard Springs, Stone Co., Arkansas, USA	35.9582 N., 92.1778 W.	KF214518	KF214498	KF214493	KF214481
Wadboo Creek, Berkeley Co., South Carolina, USA	33.1971 N., 79.9461 W.	KF214519	KF214497	KF214494	KF214482
Vertigo pusilla Müller, 1774					
Podyji National Park, Moravia, Czech Republic	48.8586 N., 15.8960 E.	KF214520	KF214496	KF214495	KF214483
Gastrocopta cristata (Pilsbry and Vanatta, 1900)					
Albuquerque, Bernalillo Co., New Mexico, USA	35.0727 N., 106.6160 W.	KF214522	JN941032		
Pupilla muscorum (Linnaeus, 1758)					
Masaryk University, Brno, Moravia, Czech Republic	49.2509 N., 16.5738 E.	KF214521	KF214507		

Mega 5.0 was used to conduct nearest–neighbor joining (NNJ), maximum parsimony (MP), and maximum likelihood (ML) trees for the three focal regions. NNJ was based on Maximum Composite Distance including transitions and transversions with pairwise gap deletion. MP used the close neighbor interchange search option with the random addition of 10 replicate trees. ML used all sites and was based on the Tamura–Nei substitution model, a five–category Gamma Distribution for substitution rates, and the Nearest Neighbor Interchange ML heuristic method. In all cases support values were estimated from 1000 bootstrap replicates. Additionally, Bayesian trees were generated using MrBayes 3.1 (Huelsenbeck and Ronquist, 2001) using a GTR substitution model assuming gamma-shaped rate variation over 1,000,000 generations with a sampling frequency of once each 1000 generations.

Nomenclature: Taxonomic names and concepts follow Nekola and Coles (2010). Apertural lamellae and fold nomenclature follows that of Pilsbry (1948: 869, fig. 469), i.e., parietal “teeth” are referred to as “folds” and all other “teeth” are termed “lamellae”, whatever their form. Also, we follow Pilsbry (1948) by referring to the raised riblets on the surface of *Vertigo* shells as “striae.”

SYSTEMATICS

Class Gastropoda
Subclass Pulmonata
Order Stylommatophora
Family Vertiginidae

Genus *Vertigo* Müller, 1773

Vertigo marciae new species

(Figures 1–6; Tables 1, 2)

GenBank Accessions KF214477, KF214489, KF214502, KF214503, KF214513, KF214514

Diagnosis: Minute shell reminiscent of *Vertigo hebardi* but taller, less striate, and lacking angular lamella; shell surface smooth and glossy with indistinct wrinkles; aperture flared toward bottom; four lamellae/folds present, including parietal, columellar, and two palatals.

Description: Shell 1.4–1.6 mm tall × 0.8–1.0 mm wide (holotype 1.5 × 0.8 mm), columnar-ovoid to ovoid, approximately 4–4.5 whorls, with moderately shallow suture and domed apex. Translucent, pale yellow-brown color. Body whorl approximately 60% of total height (Figures 1–3, 5, 6). Protoconch and neanic whorls smooth (Figure 4), with subsequent whorls having irregular, infrequent, and weak wrinkles. Immediately behind aperture sculpture takes the form of irregular low striae (Figure 2). Aperture flared on bottom, making it taller than wide and approximately 1/3 of shell height. Lip unthickened and slightly reflexed, sinulus moderate-weak, sometimes expressed as simple flattening of palatal wall. Basally aperture abruptly inflates to form rounded swelling but not crest (Figure 4). Umbilicus closed (Figure 3). Aperture with four lamellae/folds: parietal lamella strong, slightly sinuous (Figures 1, 2, 5, 6); columellar lamella downward-sloping, peg-shaped; two palatal folds with lower being approximately twice as long as upper and extending approximately 0.2 whorls into body whorl, lower slightly more immersed than upper, both highest at mid length (Figures 1, 2, 5, 6). Apertural end of lower palatal fold coincides with abrupt inflation of basal aperture. Externally shell only slightly impressed over palatal folds (Figure 4).

Type Material: Holotype (Figures 1–4), ANSP 450580, from type locality, May 22, 1999; paratypes (Figures 5–6), ANSP 402244, 8 shells and Institute of Jamaica, 2 shells, from type locality; ANSP 403039, Jamaica, St. Andrew Parish, John Crow Peak, Blue Mountains, elfin forest with bamboo near summit, 18°05′45″ N, 76°40′08.4″ W, altitude 1755 m, May 22, 1999; sta. JBS4a, 16 shells; ANSP 403040, Jamaica, St. Andrew Parish, Vinegar Hill Trail near head of Clyde River, 18°05′ N, 76°39′18″ W, altitude 1520 m, May 22, 1999, sta. JBS 5, 3 shells.

Type Locality: Jamaica, St. Andrew Parish, John Crow Peak, Blue Mountains; litter sample collected at base of limestone cap, 18°5′50″ N, 76°40′5″ W, altitude 1550 m, May 22, 1999, sta. JBS4c.

Other Material Examined: Digital images of two specimens from Red Hills Road Cave, Jamaica (Paul and Donovan, 2005), Paul collection.

Etymology: The specific name *marciae* refers to Dr. Marcia Mundle, then of the Jamaica Conservation and Development Trust. Dr. Mundle arranged for the vehicle used and park ranger guide that accompanied the expedition to the type location, and was present when the species was first collected.

RESULTS AND DISCUSSION

Variation: *Vertigo marciae* is rather constant in general appearance in terms of its shape, color, sculpture, and development of the apertural lamellae. While some variation in size (especially height) was noted, this was minor—only 16% difference between the largest and smallest shells was observed.

Comparison with Other *Vertigo* Species: *Vertigo marciae* differs from all other *Vertigo* species by its small (<1.7 mm in height) yellow shell with indistinct striae/wrinkles, flared aperture base, and lack of angular and basal lamellae. It is closest in appearance to *V. hebardi* of the Florida Keys (Figure 7), with which it shares a small yellow shell, the lack of a basal lamella, and preference for accumulations of tropical forest leaf litter. However, it differs from this species in its taller shell with less distinct striae and absence of an angular lamella. It is also reminiscent of *Vertigo marki* Gulick,

Figures 1–12. Stereomicroscope images of *Vertigo marciae* and related taxa. **1–4.** *Vertigo marciae,* holotype, Jamaica, St. Andrew Parish, John Crow Peak, Blue Mountains, 18°5′45″ N, 76°40′8″ W to 18°5′50″ N, 76°40′5″ W, ANSP 450580. **1.** Apertural view. **2.** Profile. **3.** Umbilical view showing parietal and upper palatal lamellae. **4.** Apical view showing protochonch and the basal apertural dilation. **5.** *Vertigo marciae*, ANSP 402244, Paratype, second specimen from the type locality, exhibiting a shorter shell. **6.** *Vertigo marciae,* ANSP 402244, Paratype, third specimen from the type locality, exhibiting a slightly more worn shell. **7.** *Vertigo hebardi*, Long Key, Monroe County, Florida, 24°48′52″ N, 80°49′14″ W, JCN 17479. **8.** *Vertigo gouldii* (small southern form), Tellico Gorge, Monroe Co., Tennessee, 35°19′49″ N, 84°10′59″ W, BFC 1332. **9.** *Vertigo alabamensis*, Lanier Quarry, Pender Co., North Carolina, 34°37′49″ N, 77°40′27″ W, JCN 10781. **10.** *Vertigo "conecuhensis*," Pond Creek seep, Covington Co., Alabama, 31°6′12″ N, 86°32′3″ W, JCN 12364. **11.** *Vertigo oscariana*, Wadboo Creek, Berkeley Co., South Carolina, 33°11′50″ N, 79°56′46″ W, JCN 10908. **12.** *Vertigo gouldii* (normal form), Deer Creek, Fillmore Co., Minnesota, 43°43′56″ N, 92°20′39″ W, JCN 14646.

1904 from Bermuda, with which it shares a smooth, yellowish shell that lack both basal and angular lamellae (Pilsbry, 1919). However, *V. marciae* differs from this species by its smaller shell height and lack of a callus on the palatal wall of the aperture. *Vertigo oscariana* from the southeastern USA (Figure 11) also has a small, smooth yellow shell without a basal lamella, but this species also lacks an upper palatal fold, has a callus on the outer apertural margin, and a shell that is widest in the middle, tapering both to base and apex. *Vertigo alabamensis* of the southeastern North American coastal plain (Figures 9, 10) also has a yellowish shell lacking striae, but this species is larger (generally >=1.8 mm tall), possessing both angular and basal lamellae, a strong crest on the apertural margin, and a strong sinulus on the palatal wall of the aperture.

Rosenberg and Muratov (2006) identified *Vertigo marciae* as *Vertigo gouldii* (Figures 8, 12) because of its general shell shape and placement of the parietal lamella and palatal folds, and also because *V. gouldii* was reported from Jamaica by Pilsbry and Cooke (1919: 99). However, *V. gouldii* has a larger shell of brown color, has a duller shell luster from the presence of abundant strong but irregular striae, and always possesses a basal lamella. Specimens documenting the Pilsbry and Cooke record have not been traced, and are apparently based on personal communication between Victor Sterki and Pilsbry. Bequaert and Miller (1973: 95) rejected Antillean records of *V. gouldii*.

While *Vertigo milium*—which also occurs in Jamacian tropical forest leaf litter—possesses a shell <1.7 mm tall; this species is easily distinguished from *V. marciae* in its dark red-brown color, presence of both angular and basal lamellae, and its long, curved lower palatal fold which deeply enters the shell.

Geographic Distribution and Ecology: *Vertigo marciae* is currently known in the Recent fauna only from the crest of John Crow Peak and its immediate vicinity in the Blue Mountains of eastern Jamaica at elevations of 1520–1755 m. John Crow Peak is capped by an isolated limestone outlier known to have distinctive plant communities, including endemic species (Grossman et al., 1993). (Note that John Crow Peak is not the same location as the John Crow Mountains, the easternmost range of Jamaica.) *Vertigo marciae* is found mainly on or adjacent to limestone boulders and outcrops in tropical as well as scrub forest with bamboo, but has also been found at one site (JBS 5) that lacks exposed limestone.

As a Pleistocene fossil, it is known only from Red Hills Road Cave, which is about 21 km west of Rosenberg and Muratov's sites on John Crow Peak and 1000 m lower in elevation (520 m, Paul and Donovan, 2005). *Vertigo marciae* joins the two *Radiodiscus* species and the *Punctum* reported by Paul and Donovan (2005) on the basis of personal communication from Rosenberg as species known in Jamaica only from John Crow Peak and from the Red Hills Road Cave. Paul and Donovan interpreted the faunal changes from the Red Hills Road Cave fauna to the recent fauna around the cave as suggesting drying of the climate since the Pleistocene. As *Vertigo marciae* was found nowhere else in Jamaica among the hundreds of sites sampled by Rosenberg and Muratov, its current occurrence might represent a relict distribution.

Although it must currently be considered a Jamaican endemic, the general lack of local endemism in the genus *Vertigo* (Nekola, 2009) suggests the possibility that it may occur elsewhere in the adjacent Caribbean, especially on carbonate substrates in mid- to high-elevation montane forest.

Table 2. Average number of base-pair differences between all pairwise combinations of *Vertigo marciae* and related species.

A. *CytB* amplicon (355 base pairs)

V. oscariana	53.1			
V. alabamensis	65.6	54.3		
V. hebardi	62.3	52.0	8.3	
V. marciae	63.8	46.5	38.7	36.0
	V. gouldii	*V. oscariana*	*V. alabamensis*	*V. hebardi*

B. *16S* amplicon (443–447 base pairs)

V. oscariana	40.9			
V. alabamensis	37.3	44.5		
V. hebardi	35.8	44.5	4.0	
V. marciae	42.5	42.0	18.0	18.0
	V. gouldii	*V. oscariana*	*V. alabamensis*	*V. hebardi*

C. Concatenated *ITS-1* and *ITS-2* amplicons (1274–1284 base pairs)

V. oscariana	34.8			
V. alabamensis	32.3	20.5		
V. hebardi	34.3	22.5	5.0	
V. marciae	37.3	23.5	9.0	12.0
	V. gouldii	*V. oscariana*	*V. alabamensis*	*V. hebardi*

Genetic Distinctness and Phylogenetic Relationships: DNA sequence analysis clearly demonstrates that *V. marciae* is distinct at the species level. It possesses an average of 36 and 39 base pair differences with *V. hebardi* and *V. alabamensis*, respectively, in the 355 bp *CytB* amplicon (Table 2). This equates to a 10–11% variation across the entire amplicon. In addition, it possessed an average of 46.5 base pair differences in *CytB* (13%) with *V. oscariana* and 63.8 differences (18%) with *V. gouldii*. In the more slowly evolving 443 to 447 bp *16S* region *V. marciae* differed by 18 bases (4.0%) from *V. hebardi* and *V. alabamensis*, 42 bases (9.4%) from *V. oscariana*, and 42.5 bases (9.6%) from *V. gouldii*. In the concatenated 1274–1284 bp *ITS-1* + *ITS-2* nDNA amplicon, *V. marciae* possessed an average of 9 base-pair (0.7%) differences with *V. alabamensis*, 12 (0.9%) with *V. hebardi*, 23.5 (1.8%) with *V. oscariana*, and 37.3 (2.9%) with *V. gouldii*. These levels of difference were considerably larger than those exhibited between the conchologically distinct *V. alabamensis* and *V. hebardi* (Figures 7, 9, 10), which amounted to an average difference of 8.3 bases (2.3%) in *CytB*, 4.0 (0.9%) in *16S*, and 5.0 (0.4%) in concatenated *ITS-1* and *ITS-2*.

The topologies across phylogenetic reconstructions were largely compatible, with the same highly supported nodes being identified in all cases (Figures 13–15). These demonstrate that *V. marciae* is clearly a member of the genus *Vertigo*, being within the same highly supported clade in *CytB* and *16S* that includes *V. pusilla*, the type species of the genus. While it was not possible to root the concatenated *ITS-1* + *ITS-2* tree because of profound differences with both *Gastrocopta cristata* and *Pupilla muscorum* sequences, *V. marciae* was easily aligned with all *Vertigo* sequences.

The phylogenetic reconstructions also demonstrate that *V. marciae* is a member of a highly supported clade that includes both *V. alabamensis* and *V. hebardi*. The existence of a single ancestor to all of these species implies long distance dispersal from the southeastern United States to Jamaica, perhaps with migrating birds as a vector. This is not an unreasonable scenario, given that much longer feats of long distance dispersal via migrating birds have been documented in the eastern Atlantic (Gittenberger et al., 2006).

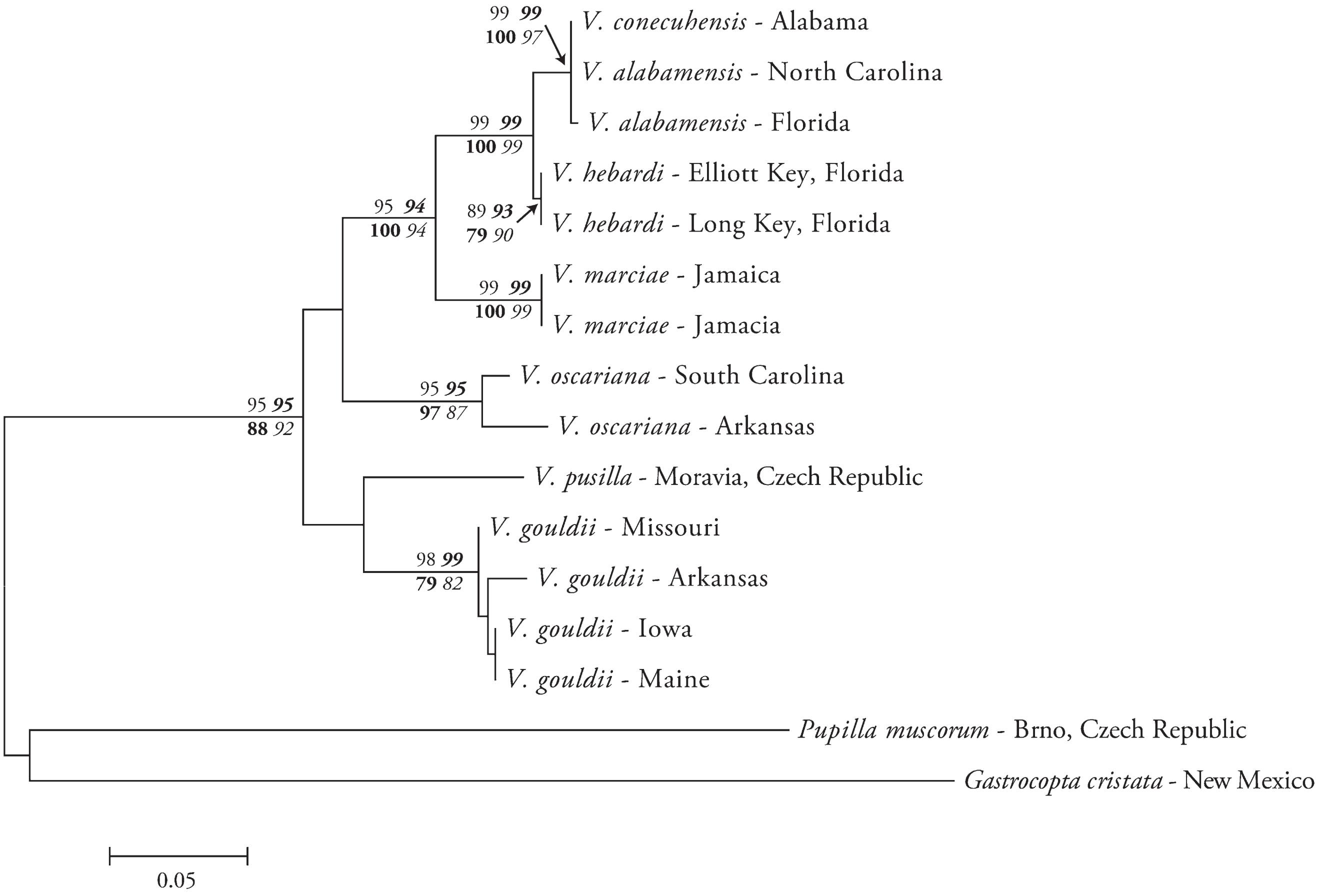

Figure 13. The phylogenetic relationships of *Vertigo marciae* as reconstructed by maximum-likelihood analysis from the *CytB* amplicon. Nodes with strong to moderate support across all four phylogenetic reconstruction methods have been labeled to the left of that node by four support values: The upper left (normal font) is for nearest neighbor joining. The upper right (***bold italic font***) is for maximum parsimony. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for maximum likelihood.

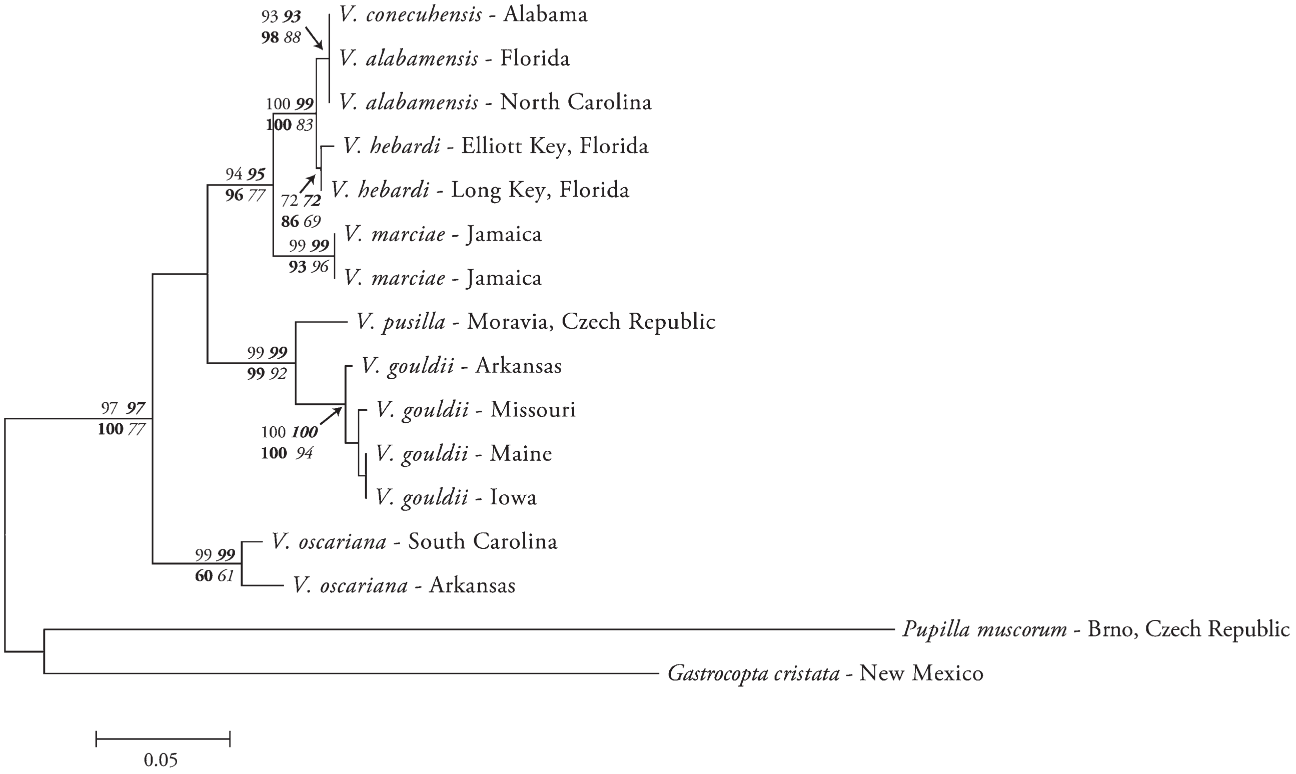

Figure 14. The phylogenetic relationships of *Vertigo marciae* as reconstructed by maximum-likelihood analysis from the *16S* amplicon. Nodes with strong to moderate support across all four phylogenetic reconstruction methods have been labeled to the left of that node by four support values: The upper left (normal font) is for nearest neighbor joining. The upper right (***bold italic font***) is for maximum parsimony. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for maximum likelihood.

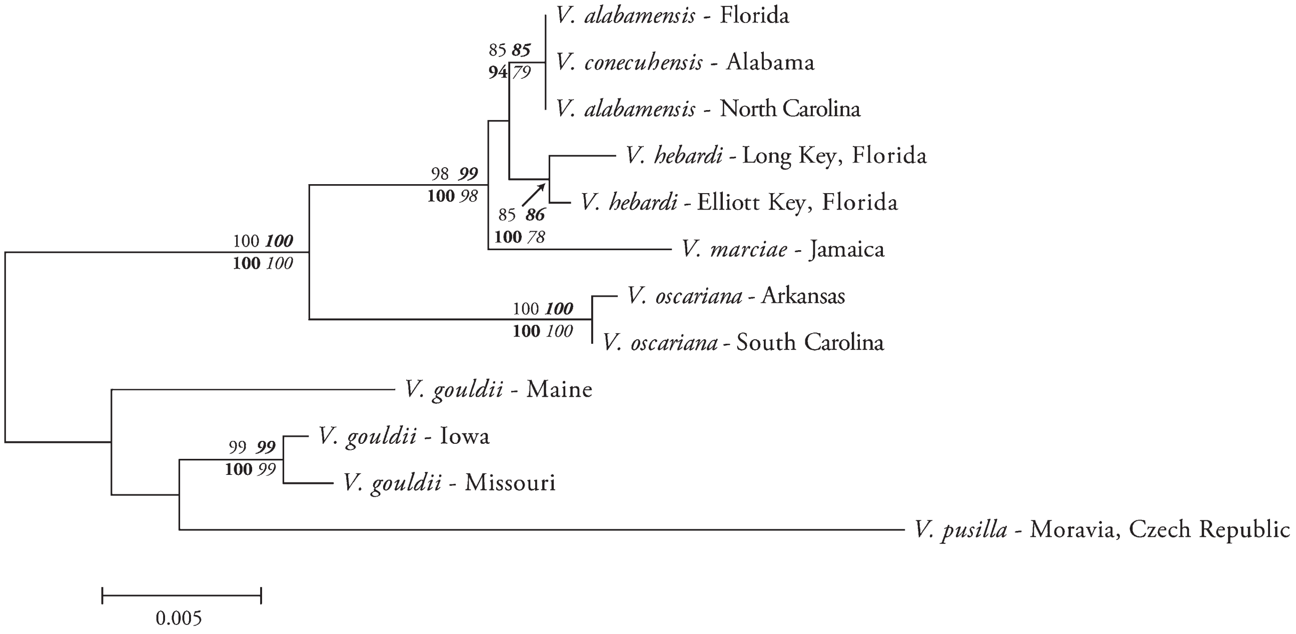

Figure 15. The phylogenetic relationships of *Vertigo marciae* as reconstructed by maximum-likelihood analysis from the concatenation of the ITS-1 and ITS-2 amplicons. Nodes with strong to moderate support across all four phylogenetic reconstruction methods have been labeled to the left of that node by four support values: The upper left (normal font) is for nearest neighbor joining. The upper right (***bold italic font***) is for maximum parsimony. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for maximum likelihood.

While resolution of deeper nodes within the genus *Vertigo* was not possible in the *CytB* and *16S* mtDNA amplicons (Figures 13, 14), presumably due to base-pair saturation, the concatenated *ITS-1*+ *ITS-2* data (Figure 15) demonstrated a very highly supported node connecting the *V. marciae* / *V. hebardi* / *V. alabamensis* clade to *V. oscariana*. This radiation includes some of the most distinct members of the genus (Pilsbry, 1948). Additional field work across the Caribbean—especially in Cuba, Hispaniola, Puerto Rico, and Bermuda—will be required to determine the actual number of species contained within this group.

ACKNOWLEDGMENTS

John Slapcinsky of the Florida Museum of Natural History provided ethanol-preserved tissue samples of *Vertigo hebardi*, while Michal Horsak of Masaryk University in Brno, the Czech Republic, provided live samples for *Vertigo pusilla* and *Pupilla muscorum*. *CytB* and *16S* sequences for *V. pusilla*, *P. muscorum*, and *Gastrocopta cristata* were retrieved from full mitochondrial genomic sequences provided by Jason Marquardt and Ulfar Bergthorsson of the University of New Mexico. Christopher Paul, University of Bristol, provided digital images of the Red Hills Road Cave fossils. Field work which established the persistence of *Vertigo hebardi* in the Florida Keys was supported by The Bailey-Matthews Shell Museum through an R.T. Abbott Visiting Curatorship to JCN. Additional funding for PCR and sequencing analysis was provided by Michal Horsak. The field work which resulted in the Recent samples of the new species being collected was supported by NSF Grant DEB-9870233 to Gary Rosenberg.

LITERATURE CITED

Bequaert, J.C. and W.B. Miller. 1973. The Mollusks of the Arid Southwest. University of Arizona, Tucson, xvi+271 pp.

Gittenberger, E., D.S.J. Groenenberg, B. Kokshoorn and R.C. Preece. 2006. Molecular trails from hitch-hiking snails. Nature 439: 409.

Grossman, D.H., S. Iremonger, and D.M. Muchoney. 1993. Jamaica: map of natural communities and modified vegetation types. Jamaica: a rapid ecological assessment. Phase 1: An island-wide characterization of mapping of natural communities and modified vegetation types. The Nature Conservancy, Washington, D.C., USA.

Huelsenbeck, J.P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17: 754–755.

Nekola, J.C. and B.F. Coles. 2010. Pupillid land snails of eastern North America. American Malacological Bulletin 28: 29–57.

Nekola, J.C. 2009. Big ranges from small packages: North American vertiginids more widespread than thought. The Tentacle 17: 26–27.

Nekola, J.C., B.F. Coles, and U. Bergthorsson. 2009. Evolutionary pattern and process in the *Vertigo gouldii* (Mollusca: Pulmonata, Pupillidae) group of minute North American land snails. Molecular Phylogenetics and Evolution 53: 1010–1024.

Paul, C.R.C. and S.K. Donovan. 2005. Quaternary and Recent land snails (Mollusca: Gastropoda) from Red Hills Road Cave, Jamaica Bulletin of the Mizunami Fossil Museum 32: 109–144.

Pilsbry, H.A. 1919. American Species of *Vertigo*. Manual of Conchology. Second Series (Pulmonata) 25: 74–150, pls. 6–13.

Pilsbry, H.A. 1948. Land Mollusca of North America (North of Mexico). Academy of Natural Sciences of Philadelphia Monographs 3, vol. 2(2): i–xlvii, 521–1113.

Rosenberg, G. and I.V. Muratov. 2006. Status report on the terrestrial mollusca of Jamaica. Proceedings of the Academy of Natural Sciences of Philadelphia 155: 117–161.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28: 2731–2739.

BUTTERFLY (LEPIDOPTERA: LYCAENIDAE, NYMPHALIDAE, AND SATYRIDAE) FAUNAS OF THREE PEATLAND HABITAT TYPES IN THE LAKE SUPERIOR DRAINAGE BASIN OF WISCONSIN

Jeffrey C. Nekola[1]

ABSTRACT

The butterflies which complete their entire life cycle within peatland habitats were documented in the Lake Superior drainage basin of northwestern Wisconsin. Seventy peatlands were inventoried over the course of the 1996 growing season, and were classified as either muskeg, kettlehole, or coastal sites. Muskeg peatlands were of similar elevation to the surrounding uplands, possessed drier and more nutrient-poor substrates, and were typically larger than other peatland types. Kettlehole peatlands were wetter and had floating *Sphagnum* mats which fringed lake margins or were in depressions much lower than the surrounding uplands. Coastal peatlands were located in estuaries along the Lake Superior coast, and possessed relatively eutrophic, wet soils. Muskeg sites harbored the most diverse total fauna, and possessed the highest average number of taxa per site. A highly significant correlation between habitat size and butterfly richness was observed in both muskeg and kettlehole peatlands. The muskeg fauna included five taxa not found in other peatland habitats. These species have arctic-boreal affinities and reach their southern range limit in eastern North America on these sites.

Even though peatlands are moderately frequent and widely distributed across northern Wisconsin, relatively few systematic studies of their biodiversity has been conducted. Curtis (1959) described only a single peatland community type (open bog) in northern Wisconsin, and characterized its vegetation based upon only 17 stands. Contemporary ecological investigations of Wisconsin peatlands have been largely limited to fens in the southeastern counties (e.g., Reed 1985, Carpenter 1990). The first intensive butterfly surveys of northern Wisconsin peatlands (e.g., Ebner 1970, Masters 1971a, 1971b, 1972, Ferge & Kuehn 1976) uncovered a group of boreal and/or arctic taxa (*Clossiana eunomia dawsonii* (Barnes & McDunnough), 1916; *Clossiana freija* (Thunberg), 1791; *Clossiana frigga saga (*Staudinger), 1816; *Erebia discoidalis* (Kirby), 1837; *Oeneis jutta* (Hübner), 1805) which reach the southern limit of their eastern North American range on these sites. However, these studies did not systematically inventory all peatland sites within a region, or compare faunas of different types of peatlands.

Recent ecological analyses of peatlands in northern Minnesota (Glaser 1987) and Michigan (Crum 1992) have documented a great diversity of peat-

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lands, ranging from highly minerotrophic fens to ombotrophic bogs. Based on these investigations it appears that any monolithic view of northern Wisconsin peatlands is an oversimplification. Unpublished plant community, water, and soil chemistry data (Eric Epstein and James Meeker, pers. comm.) suggest that three broad classes of peatland habitats can be recognized in northern Wisconsin. Muskeg sites are dominated by an open Black Spruce (*Picea mariana* (Mill.) BSP.)—*Carex oligosperma* Michx.—*Eriophorum spissum* Fern.—*Sphagnum* savanna, are relatively dry (except in the proximity to moats or bog lakes) and are oligotrophic. These sites usually have an elevation similar to their surrounding uplands. Kettlehole peatlands are much wetter and commonly contain floating *Sphagnum*—Leatherleaf (*Chamaedaphne calyculata* (L.) Moench.) mats. These sites range from very oligotrophic to eutrophic, depending upon the nature of infiltrating groundwater, and typically fringe lakes or occur in depressions much lower than their surrounding uplands. Coastal wetlands, located in estuaries along the Lake Superior Coast, are wet and relatively eutrophic sites dominated by Tamarack (*Larix laricina* (DuRoi) K.Koch) and *Carex lasiocarpa* Ehrh. Acid *Sphagnum*-dominated microhabitats are limited to small islands or ridges typically situated near upland margins.

In conjunction with a Wisconsin Department of Natural Resources (WDNR) investigation of Lake Superior coastal wetlands, butterfly faunas were documented in all accessible peatlands within the Lake Superior drainage basin in Ashland, Bayfield, Douglas, and Iron counties of northwestern Wisconsin. From these data it was possible to assess the faunistic similarities and species diversity patterns between peatland sites, as well as the adult behavior and microsite preferences of individual peatland-obligate species.

METHODS

Site selection. Identification of all high-quality peatlands within or adjacent to the Lake Superior drainage basin was accomplished by a fly-over of the study area on May 20, 1996 in a small aircraft. Approximately 5½ hours of flight time were required to survey the entire region at an altitude of 5000-6000 feet in north-south transects running approximately 6 miles apart. Potential survey sites were marked on USGS topographic quads. Other high-quality sites were identified through review of the Biological Conservation Database (BCD) of the WDNR Bureau of Endangered Resources (WBER). A few additional sites were also recommended by Eric Epstein and others in the staff of the WBER. Through this process a total of 70 sites were selected for inventory: 37 were muskegs, 23 were kettleholes, and 10 were coastal sites. While an attempt was made to inventory all high-quality peatlands within the region, some (like the Kakagon Sloughs) were not surveyed due to difficulty in political and/or physical access.

Sampling. The location in longitude-latitude of each surveyed site was determined through digitization of USGS 7.5 minute topographic quads. The centroid, area and perimeter of each was calculated using the Atlas Draw software package.

Sites were surveyed at approximately 1–2 week intervals throughout the 1996 growing season for a total of 4–6 visits. Visits were made at more frequent intervals early in the season when a number of closely spaced emergences occur. Later in the season when emergences were more temporally separated and when individual populations were in flight for longer periods of time, intervals increased to three weeks. Each visit lasted for 15–90 minutes, depending upon site size. During this time a list was made of all encountered butterfly and skipper taxa. Observations were also made of the spatial location of individuals within sites, their preferred areas of occurrence, nectar sources, and oviposition locations. Voucher specimens for most peatland-limited taxa were made from each site. These specimens are housed at the University of Wisconsin—Green Bay.

Cumulative species lists for all taxa which live out their entire life-cycle within peatland habitats (*Clossiana eunomia dawsonii*; *Clossiana freija*; *Clossiana frigga saga*; *Clossiana titania* (Esper), 1793; *Coenonympha inornata* Edwards, 1861; *Erebia discoidalis, Incisalia augustinus* (Kirby), 1837; *Lycaena dorcas* Kirby, 1837; *Lycaena epixanthe* (Boisduval & LaConte), 1833; *Oeneis jutta*) were generated. No obligate peatland taxa from the families Hesperiidae, Papilionidae, or Pieridae were observed. Throughout this report, nomenclature of Opler and Krizek (1984) has been used for butterflies, and Fernald (1950) for vascular plants.

Site-specific species lists were augmented with any additional reports or collections from the Milwaukee Public Museum or the WBER BCD of species which were not observed during this work, but have been previously documented. Only 5 such occurrences were added to the entire data set. By comparison, 155 individual occurrences of peatland-obligate populations were noted through field sampling.

Data analysis. The frequency of peatland butterfly taxa within each peatland group was measured by counting the total number of occurrences of each species across all examples of each habitat type. Significant differences between these frequencies were tested using Log-likelihood Ratio contingency table analysis (Zar 1984). Pearson's chi-square statistic was not used due to the high number of taxa absent from kettlehole and coastal peatland habitats.

Differences between the average size and richness of the three peatland types were analyzed using ANOVA. For richness, this analysis was also conducted on the subset of sites falling within the range of overlap in habitat size for the three peatland types (2.68–34.31 ha).

The relationship between species richness vs. natural log of habitat size for each of the habitats was analyzed using linear regression. Natural-log transformed habitat size was used as the independent variable in these models as it provided a better fit for the assumptions of linear regression than the untransformed data. The testing of differences between the best-fit slopes and intercepts for those habitats demonstrating a significant species-area relationship were determined by analyzing the significance of a binary variable (representing habitat type) which was added into the models (following methods outlined in Kleinbaum et al. 1988).

RESULTS

Size and distribution of peatland sites. A strong statistical difference (p=0.007; r^2=0.136) was observed in mean size of the three peatland types (Table 1). Average muskeg size was 300% greater than average coastal peatland size, which was 50% greater than average kettlehole peatland size.

Muskegs were found to be limited to the general vicinity of the divide basin (Figure 1). While occurring in all four counties, none were located in the pitted outwash plain extending from eastern Douglas to eastern Bayfield County. Kettlehole peatlands occurred in all four counties, but were most frequently encountered in the pitted outwash plain extending from Brule in Douglas County to Lake Owen in central Bayfield County. Coastal peatland sites were essentially limited to the Bayfield Peninsula, although three sites

Table 1. ANOVA of peatland size (in hectares) vs. peatland type.

Peatland Type	Min	Max	Mean	Standard Deviation
Muskeg	1.59	288.1	37.41	50.22
Kettlehole	0.49	67.24	6.98	14.36
Coastal	2.68	34.31	11.55	9.79

Summary of ANOVA analysis: r^2=.136; p=0.007

were also encountered on Madeline Island. A number of additional coastal peatland sites occur in the Apostle Islands (Judziewicz and Koch 1993) and the Kakagon Slough, but were not sampled due to logistical and time constraints.

Butterfly faunas of peatland habitats. A total of ten peatland-obligate butterfly taxa were from muskeg sites (Table 2). The most frequent of these were *Incisalia augustinus* (recorded from 81% of surveyed sites), *Clossiana eunomia dawsonii* (43%), *Oeneis jutta* (41%), *Lycaena dorcas* (35%), and *Clossiana freija* (32%). Five peatland-obligate taxa were located from kettlehole sites. The most frequent of these were *Clossiana eunomia dawsonii* (recorded from 58% of surveyed sites), *Incisalia augustinus* (33%), and

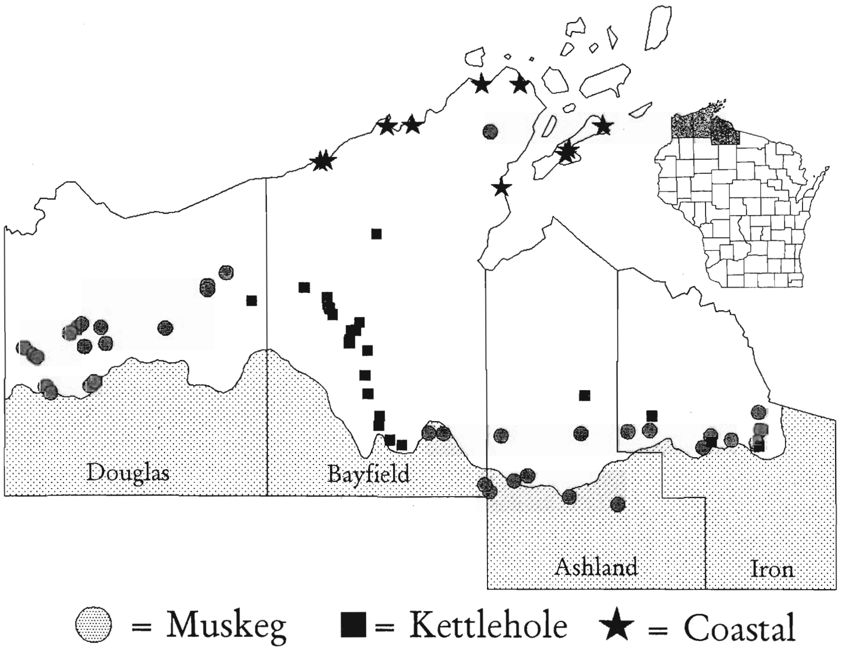

Figure 1. Location of the Lake Superior drainage basin in northwestern Wisconsin and of surveyed peatland sites.

Table 2. Absolute and relative occurrence frequency of peatland-obligate butterfly taxa among the three peatland types

	Peatland Type					
	Muskeg		Kettlehole		Coastal	
Taxon	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.
Incisalia augustinus	30	81%	8	35%	1	10%
Clossiana eunomia dawsonii	16	43%	14	61%	4	40%
Oeneis jutta	15	41%	3	13%	0	
Lycaena dorcas	13	35%	0		0	
Clossiana freija	12	32%	0		0	
Lycaena epixanthe	7	19%	7	30%	9	90%
Clossiana titania	6	16%	0		0	
Coenonympha inornata	4	11%	1	4%	4	40%
Clossiana frigga saga	2	5%	0		0	
Erebia discoidalis	2	5%	0		0	
Total Sites Sampled	37		23		10	

Log-liklihood Ratio test statistic: 66.68
Degrees of freedom: 18
p: <0.00001

Table 3. ANOVA of peatland-obligate butterfly richness per site as a function of peatland type.

Peatland Type	All sites			Sites within range of habitat size overlap		
	n	Mean	Std. Dev.	n	Mean	Std. Dev.
Muskeg	37	3.00	2.07	22	2.46	1.68
Kettlehole	23	1.38	1.14	9	2.33	1.23
Coastal	10	2.00	1.16	10	2.00	1.16

Summary of ANOVA analysis for: All sites—$r^2 = .168$; $p = 0.002$
Sites within overlap range—$r^2 = .017$; $p = 0.725$

Lycaena epixanthe (29%). Four peatland-obligate taxa were located from coastal peatland sites. The most frequent of these were *Lycaena epixanthe* (recorded from 90% of surveyed sites), *Clossiana eunomia dawsonii* (40%), and *Coenonympha inornata* (40%). These differences in species frequency between peatland types proved to be highly statistically significant ($p<.00001$)

Species diversity patterns . Significant differences ($p<0.002$; $r^2=0.168$) were observed in mean site richness of peatland-obligate species across the three peatland types (Table 3), with muskegs typically being the richest (3 taxa/site), followed by coastal (2 taxa/site), and kettlehole (1.38 taxa/site) sites. A strong relationship was also found between log-transformed habitat size and species richness in all but coastal peatland habitats (Figure 2; Table 4). Natural-log transformed habitat area was found to explain 41%, 52%, and 14% of the observed variation in peatland-restricted species richness of muskeg, kettlehole, and coastal peatland habitats, respectively.

When the ANOVA of richness by peatland type was recalculated using only those sites within the range of overlap in habitat size between all three

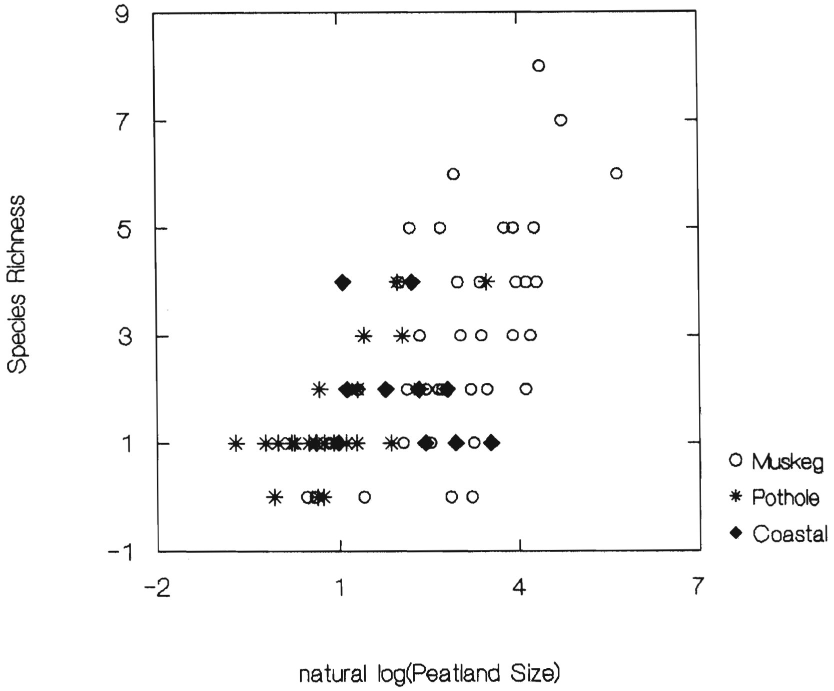

Figure 2. Relationship between richness of peatland taxa and natural-log transformed site area for all three peatland types.

habitats, no significant differences (p=0.725) were noted between groups. Comparison of the species-area relationships for muskeg and kettlehole peatlands (Table 4) also demonstrated no significant differences between their best-fit intercepts (p=0.179) and slopes (p=0.460).

Table 4. Summary statistics for obligate-peatland butterfly species richness vs. peatland area for the three peatland types. The independent variable in this analysis is the natural-log transformed habitat size of each peatland site in hectares.

	Muskeg	Kettlehole	Coastal
Intercept	–0.385	0.628	3.037
Intercept Std. Error	0.737	0.236	0.996
Intercept p	0.605	0.015	0.016
Slope	1.123	0.854	–0.488
Slope Std. Error	0.228	0.178	0.437
Slope p	0.000	0.000	0.297
r^2	0.409	0.521	0.135

p-value for difference in intercept between muskeg and kettlehole sites: 0.179
p-value for difference in slope between muskeg and kettlehole sites: 0.460

Peatland taxa distribution, ecology and behavior

LYCAENIDAE

Incisalia augustinus Westwood

This is the most frequent peatland-obligate butterfly in northwestern Wisconsin, being observed at 6 Ashland, 7 Bayfield, 17 Douglas, and 9 Iron county stations. While occurring in all peatland types, populations were most frequently encountered in muskegs, and almost completely avoided coastal sites. Individuals were often found roosting and nectaring on Heaths, particularly Leatherleaf.

Lycaena dorcas Kirby

This taxon was limited to 6 Ashland, 1 Bayfield, 3 Douglas, and 3 Iron County muskeg sites. No more than 5 individuals were noted at any site. Most adults were observed in relatively dry, open site centers. No oviposition or nectaring was observed. Shrubby Cinquefoil (*Potentilla fruticosa* L.), the host plant typically listed for this species (e.g., Newcomb 1910, Opler and Malikul 1992), does not occur on any of the observed stations, and is not known to occur within 150 km of the study region. While Laplante (1985) also lists Marsh Cinquefoil (*Potentilla palustris* (L.) Scop.) as a host for eastern Canadian populations, only once during field work were individuals observed flying in its vicinity. Strangely, no populations were found from coastal peatlands which supported the largest Marsh Cinquefoil populations. Use of some other unidentified larval host is likely in this region, possibly Cranberry (*Vaccinium oxycoccus* L.).

Lycaena epixanthe Boisduval & LeConte

This species was located at 5 Ashland, 11 Bayfield, 4 Douglas, and 3 Iron County peatlands. While occurring in all peatland types, populations were always restricted to wet, open *Sphagnum* mats with abundant Cranberry. Most muskeg and kettlehole populations were located on floating *Sphagnum* lawns immediately adjacent to bog lakes or next to roadsides where drainage had been impeded. In coastal peatlands it was restricted to *Sphagnum* islands within more eutrophic *Carex lasiocarpa* mats. At only one site were more than 25 individuals observed.

NYMPHALIDAE

Clossiana eunomia dawsoni (Barnes & McDunnough)

This taxon was located at 17 Bayfield, 15 Douglas, and 2 Iron County peatlands. Populations were observed from all peatland types. Although frequent in the western section of the study region, it was not observed on seemingly appropriate sites ranging from eastern Bayfield to central Iron County. Fewer than 5 individuals were noted at most stations. Individuals were largely seen on very wet *Sphagnum* islands or floating mats supporting a dense growth of Cranberry and Pitcherplant (*Sarracenia purpurea* L.). Oviposition on Cranberry was observed in 1995 in northeastern Wisconsin.

Cranberry has been identified as the larval host for eastern Canadian populations (Laplante 1985). Adults were frequently seen at site margins nectaring on Labrador Tea (*Ledum groenlandicum* Oeder.).

Clossiana freija (Thunberg)

This species was limited to 9 Douglas and 3 Iron County muskeg sites. Individuals were most frequently observed in dry Heath—*Carex oligosperma* openings, usually near site centers. These observations counter Opler and Krizek (1984) who state this species prefers bog margins. Individuals rapidly flew at or just above the cover of dead, matted Sedge leaves. Favored roosting sites appeared to be low, Sphagnous areas which were protected from the wind by the previous year's dead Sedge growth. In June of 1997 oviposition was noted on Cranberry in northeastern Wisconsin.

Clossiana frigga saga (Staudinger)

This taxon was only observed on single muskeg sites in Douglas and Ashland counties. Both were large and supported colonies of Bog Birch (*Betula pumila* L.) and Bog Willow (*Salix pedicellaris* Pursh.). Adults had an extremely rapid flight, and roosted on various low shrubs. Although Bog Birch has been listed as the host plant in northern Michigan (Opler and Krizek 1984), adults exhibited a much stronger association with Bog Willow, and were always limited to its immediate vicinity. Shrub willows have been noted as the host for *C. frigga saga* in Alberta (Opler and Krizek 1984).

Clossiana titania (Esper)

This species was limited to 6 muskeg sites in western Douglas County. All of these had extensive dry Heath—*Carex oligosperma* openings supporting *Clossiana freija* populations. Adults were only rarely seen within sites, however, and were most often observed nectaring and mating up to ½-mile from sites along upland openings and roadsides. Roadsides may serve as migration corridors, as individuals frequently patrolled these habitats. Oviposition plants and larval hosts have not yet been noted.

SATYRIDAE

Coenonympha inornata Edwards

This species was observed at 1 Ashland, 5 Bayfield, and 3 Douglas county peatland sites. It has also been located from at least 10 additional upland stations in the study region, including old fields and sand barrens. Peatlands harboring this species all possessed large, Sedge-dominated openings. Individuals were often scattered and rare within sites. Nectaring and oviposition were not noted for any of these populations.

Erebia discoidalis (Kirby)

This species was only located from single muskeg sites in Ashland and Douglas counties, with only single individuals being noted at each site. Both locations have extensive *Carex oligosperma* and *Eriophorum spissum* meadows. Individuals from this region, as well as those from northeastern Wisconsin, appear to most frequently patrol the margins of these openings. Oviposition and nectaring has not been observed.

Oeneis jutta (Hübner)

This species was observed from 4 Ashland, 4 Bayfield, 8 Douglas, and 2 Iron county peatland sites. Populations were most frequently encountered in muskegs, but were absent from coastal sites. Kettlehole populations were limited to sites possessing well developed Black Spruce groves. Rarely were more than 10 individuals observed within a single site. Contrary to Masters and Sorenson (1969), individuals did not favor bog edges, but were rather encountered throughout sites in Black Spruce groves adjacent to *Eriophorum spissum* openings. Individuals roosted on small Spruce branches with wings folded and were well camouflaged. When flushed, their flight was rapid and quick, and usually limited to the extent of the nearest opening. Nectaring was observed on Labrador Tea. Oviposition has not been witnessed.

DISCUSSION

Faunas of the three peatland types. Muskeg sites physically differed from other peatlands in their larger size, and their drier and presumably more nutrient poor soils. The wettest microsites on these habitats were limited to moats at site margins and to floating mats at the edge of bog lakes. Five taxa (*Clossiana freija, Clossiana frigga saga, Clossiana titania, Erebia discoidalis, Lycaena dorcas*) were restricted to muskegs. Two of these (*Clossiana freija, Lycaena dorcas*) were among the more frequently encountered muskeg taxa. The number of taxa observed per site was significantly greater than in other peatland types. This difference is apparently related to the larger average size of muskegs, as no significant differences were observed in richness when habitat size was limited to the range of overlap between the three peatland types. This conclusion is also supported by the statistically similar species-area relationships found between muskeg and kettlehole sites. However, the relationship between site area and species richness is undoubtedly related to more than simple area-sensitivity of the species concerned. As all species which are limited to muskegs are restricted to dry Heath-Sedge meadows, the lack of this microhabitat from smaller peatlands, rather than habitat size, *per se*, may be the actual factor limiting their occurrence.

Kettlehole sites were generally smaller and wetter than muskegs. Plant communities varied greatly between sites, ranging from acid Leatherleaf mats to inundated Sedge meadows and floating *Sphagnum* lawns. No taxa were restricted to this peatland type. While the two most frequent taxa are shared between kettleholes and muskegs (*Clossiana eunomia dawsonii, Incisalia augustinus*), the third most frequent kettlehole taxon (*Lycaena epixanthe*) was only the sixth most frequent muskeg taxon. Species richness of kettlehole sites was half that observed from muskegs.

Coastal peatlands were typically dominated by open tamarack groves and opening meadows of *Carex lasiocarpa* and *Carex lacustris* Willd. These sites also harbored a number of relative calciphiles such as *Triglochin maritima* L., *Salix candida* Flügge, and *Scirpus hudsonianus* (Michx.) Fern. *Sphagnum*-dominated islands or ridges set above the Sedge turf were the only microhabitats within coastal sites which supported acidophilic plants (like Cranberry) and peatland-obligate butterfly populations. The dominant obligate butterfly of coastal peatlands (*Lycaena epixanthe*) was much less frequent in the other habitats. However, coastal peatlands harbored the fewest total taxa, and had the fewest average taxa per site of all peatland types sampled. Additionally, coastal peatlands were the only type to not demonstrate a significant species-area relationship.

Within-site distribution of peatland taxa. Most published reports on the within-site distribution of the surveyed taxa (e.g., Masters and Sorenson 1969, Masters 1971a, 1971b, Opler and Krizek 1984) suggest that peatland margins are preferred by adults. This was not found to be the case during this study.

In muskegs, *Coenonympha inornata, Clossiana freija, Erebia discoidalis, Incisalia augustinus* and *Lycaena dorcas* adults were most often found in open *Carex oligosperma* meadows in site centers. *Clossiana frigga saga* was always found in proximity to its host plant, Bog Willow, which can occur from the center to margin of sites. *Oeneis jutta* was usually found flying within or at the periphery of Black Spruce groves throughout sites. Although apparently requiring *Carex oligosperma* meadows for larval life stages, adult *Clossiana titania* were mostly found adjacent to sites in upland borders possessing abundant nectar sources. Only *Clossiana eunomia dawsonii* and *Lycaena epixanthe* were reliably encountered at site margins, as their preferred habitat (floating *Sphagnum* mats) develop on moats. However, these two species were also commonly found on floating mats surrounding lakes in site centers.

In kettleholes, peatland butterflies (particularly *Clossiana eunomia dawsonii* and *Lycaena epixanthe*) favored *Sphagnum* lawns surrounding or islands within central lakes. *Oeneis jutta* adults were observed flying only in proximity of Black Spruce groves, which were limited to dry areas within the largest sites.

In coastal sites, all peatland taxa were restricted to isolated *Sphagnum* ridges and islands. The lack of correlation between area covered by this microhabitat vs. total site size (some large sites possess fewer *Sphagnum* patches than are present in smaller sites) may help explain the lack of observed relationship between species richness and total habitat size in this peatland type. A more accurate assessment of species-area relationships in coastal peatlands will probably require estimation of area covered by *Sphagnum* islands within each site.

Biogeographic relationships of the peatland faunas. Four of the peatland taxa (*Clossiana eunomia dawsonii, Coenonympha inornata, Incisalia augustinus,* and *Lycaena epixanthe*) were common to all peatland types. These taxa have boreal, western, and northeastern ranges respectively (Scott 1986). *Oeneis jutta*, found in both muskeg and kettlehole peatland sites, also has a boreal range (Scott 1986). The remaining five taxa (*Clossiana freija, Clossiana frigga saga, Clossiana titania, Erebia discoidalis, Lycaena dorcas*), all restricted to muskeg sites, range to northern Alaska and the high arctic islands of Canada (Scott 1986). All five of these species appear to favor dry, open Sedge-Heath meadows, which often constitute a large proportion of muskeg sites. The limitation of these arctic-boreal species to this microhabitat may indicate that muskeg Sedge-Heath meadows, from a lepidopteran point of view, may represent the closest analogue to tundra and taiga environments in northern Wisconsin.

From these analyses it is clear that all peatland areas in northwestern Wisconsin are not equal in relation to their butterfly faunas. Muskeg peatlands possess a significantly different fauna from kettlehole and coastal sites, and harbor twice the total number of taxa, as well as up to three times the number of taxa per site as compared to the remaining peatland types. The muskeg fauna is also significantly enriched in arctic-boreal taxa. These results suggest that a multiplicity of peatland ecosystems in Wisconsin should be recognized to help us better characterize the biological diversity of these sites.

ACKNOWLEDGMENTS

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LITERATURE CITED

Carpenter, Q.J. 1990. *Hydrology and Vegetation on a Calcareous Peat Mound Fen in Southeastern Wisconsin.* Masters Thesis, University of Wisconsin, Madison.

Crum, H. 1992. *A focus on peatlands and peat mosses.* University of Michigan Press, Ann Arbor.

Curtis, J.T. 1959. *The Vegetation of Wisconsin.* U. Wisconsin Press, Madison. 657 pp.

Ebner, J.A. 1970. *Butterflies of Wisconsin.* Milwaukee Public Museum Popular Science Handbook #12. 205 pp.

Ferge, L.A. and R.M. Kuehn. 1976. First records of *Boloria frigga* (Nymphalidae) in Wisconsin. *J. Lepid. Soc.* 30:233–234.

Fernald, M.L. 1950. *Gray's Manual of Botany, Eighth Edition.* American Book Company, New York. 1632 pp.

Glaser, P.H. 1987. *The ecology of boreal peatlands of northern Minnesota: a community profile.* U.S.D.I., Fish and Wildlife Service Biological Report 85(7.14).

Judziewicz, E.J. and R.G. Koch. 1993. Flora and vegetation of the Apostle Islands National Lakeshore and Madeline Island, Ashland and Bayfield counties, Wisconsin. *Michigan Botanist*. 32:43–189.

Kleinbaum, D.G., Kupper, L.L., and K.E. Muller. 1988. *Applied regression analysis and other multivariate methods.* PWS-Kent Publishing Company, Boston. 718 pp.

Laplante, J.P. 1985. *Papillions et Chenilles du Québec et de l'est du Canada.* Editions France-Amérique, Montréal. 280 pp.

Masters, J.H. 1971a. Ecological and distributional notes on *Erebia discoidalis* (Satyridae) in the north central states. *J. Res. Lepid.* 9:11–16.

Masters, J.H. 1971b. First records of *Boloria eunomia* (Nymphalidae) in Wisconsin. *J. Lepid. Soc.* 25:149.

Masters, J.H. 1972. Critical comments on James A. Ebner's "Butterflies of Wisconsin." *in:* Keuhn, R.M. and J.H. Masters (eds), *Wisconsin Butterflies*, Mid-Continent Lepididoptera Series #59.

Masters, J.H. and J.T. Sorenson. 1969. Field observations on forest *Oeneis* (Saytridae). *J. Lepid.* Soc. 23:155–161.

Newcomb, W.W. 1910. *Chrysophanus dorcas* Kirby, and related species in the upper peninsula of Michigan. *Canadian Entomologist.* 5:153–158.

Opler, P.A. and G.O. Krizek. 1984. *Butterflies East of the Great Plains*. Johns Hopkins University Press, Baltimore. 294 pp.

Opler, P.A. and V. Malikul. 1992. *A Field Guide to Eastern Butterflies*. Houghton Mifflin Company, New York. 396 pp.

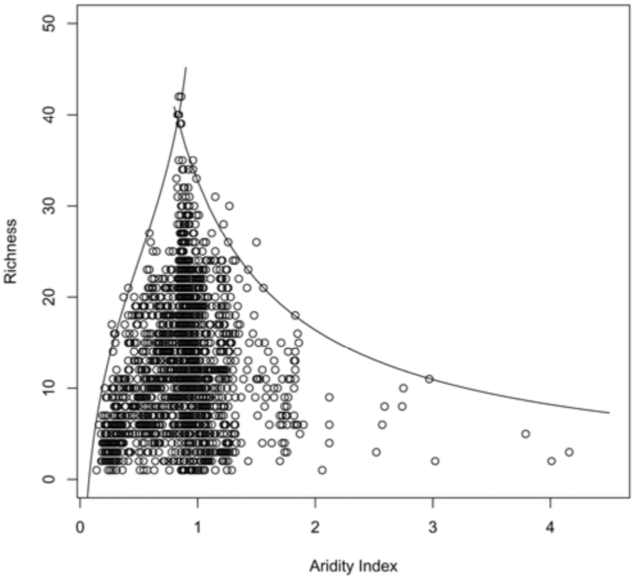
Reed, D.M. 1985. *Composition and Distribution of Calcareous Fens in Relation to Environmental Conditions in Southeastern Wisconsin*. Masters Thesis, University of Wisconsin at Milwaukee.

Scott, J.A. 1986. *The Butterflies of North America*. Stanford University Press, Stanford, California. 583 pp.

Zar, J.H. 1984. *Biostatistical Analysis.* Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Section II: Population and Community Ecology

A vital component of understanding ecological systems is determining the factors controlling species abundance, range and community composition at local scales. I have conducted such work on vascular plants, lepidoptera, and terrestrial gastropods. The focus for many of these studies is determination of the local environmental factors that most strongly regulate occurrence and composition patterns, especially for regionally rare taxa at or near their geographic range limits. Often these studies have employed multivariate statistical techniques such as multidimensional scaling ordination and model-based cluster analysis. I have also been involved in determining the age structure of cliff-face tree populations (including millennium-aged red and white cedars) along the Niagaran Escarpment in the Great Lakes region. These types of studies not only help focus future biological surveys, but also help determine optimum conservation strategies. They also allow for large-scale comparisons of the factors influencing range limits by allowing for comparison of distribution and abundance drivers across a species distribution.



Alpha-diversity (community species richness) vs. Aridity Index (yearly precipitation/yearly potential evapotranspiration) for North American land snails. The upper limit was determined using quantile regression at tau=0.99. For the domain AI<0.85 the best fit two parameter model is a modified logit function; for AI>0.85 it is a power-law function.

Using my community biodiversity database which currently represents 1823 sites, ~600 species (½ of the continental fauna) and ¾ million individuals ranging from Prudhoe Bay to San Diego east to Labrador and Key West (all personally sampled using uniform protocols) I have begun to investigate continental α-diversity. Two unexpected patterns emerge: First, site richness does not monotonically increase towards the tropics, with a local maximum generally occurring between 35°-45° N. Thus, central Appalachian and Ozark sites tend to support more species than those to their immediate south. Second, a strong linear and almost order of magnitude increase is noted from west to east between 30°-40° N, with a similar though weaker (roughly 60%) increase from 40°-50° N. Because regional species pools are roughly similar in size, it is likely that these differences are rooted in contemporaneous ecological process rather than environmental and/or evolutionary history. The upper limit of α-diversity in fact does appear to be strongly influenced by current climate, in particular Aridity Index (AI), peaking at values around 1, which occurs when annual precipitation = annual potential evaportranspiration. This result can be related back to land snail physiology, which demands both water to make mucus required for movement and Ca for shell construction. At low AI, land snails will be stressed by drought-induced inactivity, while at high AI they will be stressed by low [Ca] caused by leaching via excess precipitation. Given that land snail physiology is uniform across the biosphere, similar relationships must exist elsewhere in the globe. Initial analysis of European and New Zealand

land snail communities suggests that this pattern does represent a general global expectation. Additional work is also underway to investigate this relationship in east and southeast Asia, Australia, Africa, and the Neotropics. This work is being supported in part by grants from the National Park Service and Texas Parks and Wildlife.

Representative Publications
[number of citations as of October 27, 2017]

Růžička, V., M. Zacharda, L. Němcová, P. Šmilauer &. **J.C. Nekola**. 2012. Periglacial microclimate in low altitude scree slopes supports relict biodiversity. *Journal of Natural History.* 46:2145-2157. **[23]**

McClain, C.R., **J.C. Nekola**, L. Kuhnz, P.N. Slattery & J.P. Barry. 2011. Local-Scale Faunal Turnover on the Deep Pacific Seafloor. *Marine Ecology Progress Series*. 422:193-200. **[15]**

Nekola, J.C. 2010. Acidophilic terrestrial gastropod communities of North America. *Journal of Molluscan Studies*. 76:144-156. **[29]**

Stanisic, J, R.A.D. Cameron, B.M. Pokryszko & **J.C. Nekola**. 2007. Forest snail faunas from S.E. Queensland and N.E. New South Wales (Australia): Patterns of local and regional richness and differentiation. *Malacologia*. 49:445-462. **[26]**

Nekola, J.C. 2004. Vascular plant composition gradients within and between Iowa fens. *Journal of Vegetation Science.* 15:771-780. **[57]**

Nekola, J.C. 2003. Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. *Diversity and Distribution.* 9:55-71. **[52]**

Nekola, J.C. 2001. Distribution and ecology of *Vertigo cristata* (Sterki, 1919) in the western Great Lakes region. *American Malacological Bulletin.* 16:47-52. **[8]**

Nekola, J.C. & P.A. Massart. 2001. Distribution and ecology of *Vertigo nylanderi* Sterki, 1909 in the western Great Lakes region. *American Malacological Bulletin*. 16:53-60. **[5]**

Larson, D.W., U. Mattes-Sears, J.A. Gerrath, N.W.K. Larson, J.M. Gerrath, **J.C. Nekola**, G.L. Walker, S. Porembski & A. Charlton. 2000. Evidence for the widespread occurrence of ancient forests on cliffs. *Journal of Biogeography.* 27:319-331. **[42]**

Nekola, J.C. 1999. Terrestrial gastropod richness of carbonate cliff and associated habitats in the Great Lakes region of North America. *Malacologia.* 41:231-252. **[36]**

Nekola, J.C. & T.A. Smith. 1999. Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. *Malacologia.* 41:253-269. **[55]**

Larson, D.W., U. Mattes-Sears, J.A. Gerrath, J.M. Gerrath, **J.C. Nekola**, G.L. Walker, S. Porembski, A. Charlton & N.W.K. Larson. 1999. Ancient stunted forests on cliffs. *Nature.* 398:382-383. **[40]**

ACIDOPHILIC TERRESTRIAL GASTROPOD COMMUNITIES OF NORTH AMERICA

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ABSTRACT

Habitats with soil pH < 4 and Ca < 100 ppm, such as pocosins, *Sphagnum* bogs and heathlands, would appear inimical to land-snail biodiversity. Nevertheless, a survey of 1,356 sites, *c.* 1/2 million individuals and over 240 species (*c.* 1/5 of the continental fauna) across North America shows that *c.* 10% of species appear to favour such highly or moderately acidic sites, spread from subtropical forests of the Gulf of Mexico coast to the arctic tundra. Nonmetric multidimensional scaling ordination of faunas from 292 sites that support at least five co-occurring species documents that the principal axis of compositional variation in highly and moderately acidic habitats is significantly ($P < 0.0005$) correlated with latitude, while the second axis is significantly ($P < 0.0005$) correlated with moisture level. Composition was found to vary continuously along both axes, implying that discrete acidophilic communities are not present. While highly and moderately acidic sites were shown to have significantly ($P < 0.000000005$) lower richness and abundance compared with neutral/calcareous habitats, even the most acidic sites still typically supported 5–10 species. Abundance distributions in highly acidic habitats were found to be more uneven those of neutral/calcareous sites. The greater richness of the North American acidophilic land snail fauna compared with that in Europe has allowed communities to display replacement-driven compositional turnover. These results demonstrate that it is vitally important for biodiversity surveys of North American land snails not to ignore acidic habitats, because they harbour an important and surprisingly diverse fauna.

INTRODUCTION

It is well established that terrestrial gastropod communities in lime-rich habitats such as carbonate bedrock outcrops, fens, chalk grasslands and rich upland and lowland forests often support abundant and diverse land-snail communities (e.g. Boycott, 1934; Burch, 1962; Kerney & Cameron, 1979; Stanisic, 1997; Barker & Mayhill, 1999; Nekola, 1999; Schilthuizen, 2004; Horsák, 2005). In fact, one of the principle global trends identified in land-snail ecology is the strong positive correlation between individual abundance, species richness and the pH of the organic litter in which land-snail communities reside (Valovirta, 1968; Wäreborn, 1970; Waldén, 1981; Outeiro, Agüera & Parejo, 1993; Barker & Mayhill, 1999; Nekola & Smith, 1999; Hermida, Ondina & Rodreiguez, 2000; Pokryszko & Cameron, 2005; Horsák, 2006). This is not surprising given the high metabolic calcium demands of land snails not only for shell generation but also for egg production (Wäreborn, 1970; Gärdenfors, 1992). Across the entire northwestern European fauna of about 300 species, only five (*Columella aspera*, *Vertigo ronnebyensis*, *Vertigo lilljeborgi*, *Zonitoides excavatus* and *Zoogenetes harpa*) have been noted to favour acidic habitats (Boycott, 1934; Kerney & Cameron, 1979). Highly acidic habitats, such as *Sphagnum* bogs, heathlands and pine forest have thus generally been regarded as unfavourable for high land-snail biodiversity (Karlin, 1961; Kerney & Cameron, 1979; Horsák & Hájek, 2003).

No strongly acidophilic/calcifugic land-snail fauna had previously been reported from North America (Pilsbry, 1948; Hubricht, 1985) when *Vertigo malleata* was described and shown to be limited to ombotrophic peatlands of the Atlantic coastal plain (Coles & Nekola, 2007). These sites possess soils with organic litter pH ranging from 3.5 to 4.0 and Ca concentrations of only 25–100 ppm (Woodwell, 1958, Richardson, 1983). An additional 35 co-occurring species, representing about one-fifth of the entire North American Atlantic coastal plain fauna, were noted from these and adjacent upland pine-flatwood sites, which have soil pH ranging from 3.5 to 4.5 and Ca ppm values of 20–500 (Binkley *et al.*, 1992). Some of the species observed in these habitats, such as *Triodopsis soelneri* and *Vertigo alabamensis*, are thought to be among the continent's rarest species (Hubricht, 1985; NatureServe, 2009).

Does this apparent acidophilic land-snail fauna from the Atlantic seaboard represent an idiosyncratic outlier, or do similar faunas occur across North America? How many species should be considered acidophilic/calcifugic within the continental fauna? What major gradients in community composition can be identified, and with which environmental variables do these correlate? How does community richness and abundance vary between base-rich and base-poor habitats across the major land-snail habitat types? To provide a better understanding of the community ecology of acidophilic land-snail communities within North America these issues are addressed in the present paper.

MATERIAL AND METHODS

Study sites

Land-snail faunas were analysed from 1,356 sites ranging from the Alaskan North Slope and southern California coast eastwards to central Quebec, and the Atlantic seaboard from Maine to Georgia (Fig. 1). Matrix vegetation varies from tundra and taiga in the north, to tallgrass prairie in the Midwest, to mixed deciduous-conifer forest in the southwest and to mixed boreal-hardwood, deciduous and evergreen subtropical forest in the east and south (Barbour & Billings, 1988). Using the principal land-snail community types identified by Nekola (2003), this sample includes 377 rock outcrops,

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Figure 1. Location of all 1,356 sampling sites. Black circles represent highly or moderately acidic habitats; open circles represent neutral/calcareous stations.

357 upland forests, 286 lowland forests, 114 upland grasslands and 222 lowland grasslands.

Field methods

Documentation of terrestrial gastropod faunas from representative 100–1,000 m^2 areas within sites was accomplished by hand collection of larger shells and litter sampling for smaller taxa. Particular focus was placed on the latter approach as it provides the most complete assessment of site faunas (Oggier, Zschokke & Baur, 1998; Cameron & Pokryszko, 2005). As suggested by Emberton, Pearce & Randalana (1996), collections were made at places of high micromollusc density such as loosely compacted leaf litter lying on top of highly compacted damp mineral soil or humus. Approximately 500 ml of sieved litter ranging from 0.425 to 9.5 mm in minimum particle size was retrieved from each site, either by field sieving or collection of *c.* 4 l of unsorted leaf litter. These unsorted bagged samples were slowly and completely dried with the *c.* 500 ml of sorted litter extracted from each sample in the laboratory by use of careful but vigorous water disaggregation. A half litre of sieved litter was set as the sample goal, as this volume typically captured 10 times the number of individuals as species, which is advocated by Cameron & Pokryszko (2005) for accurate documentation of land-snail community composition.

The latitude–longitude position of each site was determined using either USGS 7.5 min topographic maps or a hand-held GPS. Each site was scored in one of the five principal land-snail habitat categories identified by Nekola (2003). Sites were also scored along a moisture gradient from 1 (dry vertical rock outcrops and xeric uplands) to 5 (completely saturated vegetation mats). Scores of 2 represented dry-mesic uplands, 3 represented mesic sites and 4 lowland sites with nearly saturated soils.

The soil acidity of each site was assessed by observation of exposed bedrock, vascular plant and bryophyte cover. Bryophyte composition was particularly noted as this group serves as one of the best bio-indicators of soil-water solution acidity (Vitt & Chee, 1990). Sites were categorized as 'highly acidic' when exposed bedrock consisted of silica sand, shale, quartzite, schist, gneiss or felsic igneous rock, when vascular plant cover was dominated by pines and/or oaks, the shrub layer was limited to various heaths, *Myrica* and/or *Ilex*, and when bryophytes were limited to acidophilic genera such as *Leucobryum*, *Polytrichum* and *Sphagnum* (Crum & Anderson, 1981). Sites were categorized as 'moderately acidic' when exposed bedrock consisted of $CaCO_3$-cemented sandstone or intermediate to intermediate-felsic igneous rock or when vascular plant and bryophyte cover included not only acidophilic taxa but also more base-demanding genera such as *Climacium*, *Hypnum*, *Mnium*, *Rhodobryum*, *Rhytididelphus* and *Thuidium* (Crum & Anderson, 1981). Sites were characterized as 'neutral or calcareous' when exposed bedrock consisted of carbonates or mafic/ultramafic igneous rock and/or when acidophilic vascular plants and bryophytes were absent.

Laboratory procedures

Retained leaf litter fractions were passed through a standard sieve series [ASTME 3/8" (9.5 mm), #10 (2.0 mm), #20 (0.85 mm) and #40 (0.425 mm) mesh screens], and then hand picked against a neutral-brown background. All shells and shell fragments were removed, and assigned to species (or subspecies) using the author's reference collection. The total numbers of shells per species per site were recorded, as were the number of unassignable immature individuals and fragmentary shells. Nomenclature is based principally on Hubricht (1985), with updates by Turgeon *et al.* (1998), Nekola (2004) and Nekola & Coles (in press). Authors and dates for each species are given in Table 1.

Statistical procedures

Occurrences for all species encountered were analysed in terms of their presence/absence in highly acidic, moderately acidic, or neutral/calcareous soils. The species limited only to highly acidic and/or moderately acidic sites were identified, as well as those species limited to neutral/calcareous sites. Additionally, species found across the entire base-status spectrum were enumerated.

The impact of base-status on population size was documented by first recording the observed population sizes for each species across all sites. These abundances were then grouped by their soil acidity category, with statistical difference in abundances between these groups being calculated using the nonparametric Kruskal–Wallis test. To provide appropriate statistical power to mitigate potential type-II errors, tests were limited to the 128 species with at least 10 total occurrences and 30 total individuals. A Bonferroni correction was used to modify the significance threshold of these tests to 0.05/128 or 0.00039.

Gradients in composition of acidic habitat land-snail communities were identified via global nonmetric multidimensional scaling (NMDS) using DECODA (Minchin, 1990). NMDS was used as it makes no assumptions regarding the underlying nature of distributions of species along compositional gradients. As such, NMDS is the most robust form of ordination for detection of ecological patterns (Minchin, 1987). To ordinate sites, a matrix of dissimilarity coefficients was calculated between all pairwise combinations of highly or moderately acidic sites with five or more species, using the Czekanowski (Bray–Curtis) index (Faith, Minchin & Belbin, 1987) on species abundance data which had been doubly standardized, first to make all species maxima = 1, and then to equalize the total number of individuals per site. All species (including the most rarely encountered) were considered. NMDS in one through four dimensions was then performed, with 200

Table 1. Calcifuge/calcicole status of species, based on their presence or absence across the soil acidity spectrum.

Occurring only in highly acidic sites:
Daedalochila leporina (Gould, 1848)
Glyphyalinia n. sp.
Mesomphix perlaevis (Pilsbry, 1900)
Neohelix divesta (Gould, 1851)
Neohelix solemi Emberton, 1988
Triodopsis soelneri (J.B. Henderson, 1907)
Vertigo oralis Sterki, 1898

Occurring only in moderately acidic sites:
Lobosculum pustula (Férussac, 1822)
Pristiloma arcticum (Lehnert, 1884)

Occurring only in highly or moderately acidic sites:
Glyphyalinia luticola Hubricht, 1966
Paravitrea petrophila (Bland, 1883)
Triodopsis juxtidens (Pilsbry, 1894)
Vertigo alabamensis Clapp, 1915
Vertigo malleata Coles & Nekola, 2007

Occurring in both acidic and neutral/calcareous habitats:
Anguispira alternata (Say, 1817)
Anguispira fergusoni (Bland, 1861)
Carychium exiguum (Say, 1822)
Carychium exile H.C. Lea, 1842
Carychium mexicanum Pilsbry, 1891
Catinella avara (Say, 1824)
Cepaea hortensis (Müller, 1774)
Cochlicopa lubrica (Müller, 1774)
Cochlicopa lubricella (Porro, 1838)
Cochlicopa morseana (Doherty, 1878)
Columella columella alticola (Ingersoll, 1875)
Columella simplex (Gould, 1841)
Daedalochila dorfeuilliana (I. Lea, 1838)
Deroceras leave (Müller, 1774)
Discus catskillensis (Pilsbry, 1898)
Discus cronkhitei (Newcomb, 1865)
Discus patulus (Deshayes, 1830)
Discus patulus edentulus (Pilsbry, 1948)
Discus shimeki (Pilsbry, 1890)
Euchemotrema fraternum (Say, 1824)
Euchemotrema leai leai (A. Binney, 1840)
Euconulus alderi (Gray, 1840)
Euconulus chersinus (Say, 1821)
Euconulus dentatus (Sterki, 1893)
Euconulus fulvus (Müller, 1774)
Euconulus fulvus alaskensis (Pilsbry, 1899)
Euconulus polygyratus (Pilsbry, 1899)
Euconulus trochulus (Reinhardt, 1883)
Gastrocopta contracta (Say, 1822)
Gastrocopta holzingeri (Sterki, 1889)
Gastrocopta pentodon (Say, 1821)
Gastrocopta riparia Pilsbry, 1948
Gastrocopta rupicola (Say, 1821)
Gastrocopta tappaniana (C.B. Adams, 1842)
Glyphyalinia indentata (Say, 1823)
Glyphyalinia rhoadsi (Pilsbry, 1899)
Glyphyalinia solida (H.B. Baker, 1930)

Continued

Table 1. *Continued*

Glyphyalinia wheatleyi (Bland, 1883)
Guppya sterkii (Dall, 1888)
Haplotrema concavum (Say, 1821)
Hawaiia minuscula (A. Binney, 1840)
Helicodiscus inermis H.B. Baker, 1929
Helicodiscus notius Hubricht, 1962
Helicodiscus parallelus (Say, 1817)
Helicodiscus shimeki Hubricht, 1962
Hendersonia occulta (Say, 1831)
Inflectarius inflectus (Say, 1821)
Mesodon elevatus (Say, 1821)
Mesodon zaletus (A. Binney, 1837)
Mesomphix capnodes (W.G. Binney, 1857)
Mesomphix friabilis (W.G. Binney, 1857)
Mesomphix globosus (MacMillan, 1940)
Mesomphix subplanus (A. Binney, 1842)
Neohelix albolabris (Say, 1816)
Neohelix alleni (Wetherby in Sampson, 1883)
Nesovitrea binneyana (Morse, 1864)
Nesovitrea electrina (Gould, 1841)
Oxyloma retusa (I. Lea, 1834)
Paravitrea andrewsae (W.G. Binney, 1858)
Paravitrea lamellidens (Pilsbry, 1898)
Paravitrea multidentata (A. Binney, 1840)
Paravitrea significans (Bland, 1866)
Paravitrea simpsoni (Pilsbry, 1889)
Patera binneyanus (Pilsbry, 1899)
Patera perigraptus (Pilsbry, 1894)
Planogyra asteriscus (Morse, 1857)
Pomatiopsis lapidaria (Say, 1817)
Punctum blandianum Pilsbry, 1900
Punctum californicum Pilsbry, 1898
Punctum minutissimum (I. Lea, 1841)
Punctum n. sp.
Punctum randolphi (Dall, 1895)
Punctum vitreum H.B. Baker, 1930
Pupilla hebes (Ancey, 1881)
Pupilla muscorum (Linné, 1758)
Pupisoma dioscoricola (C.B. Adams, 1845)
Pupisoma macneilli (Clapp, 1918)
Stenotrema barbatum (Clapp, 1904)
Stenotrema labrosum (Bland, 1862)
Stenotrema stenotrema (Pfeiffer, 1819)
Stenotrema unciferum (Pilsbry, 1900)
Striatura exigua (Stimpson, 1847)
Striatura ferrea Morse, 1864
Striatura meridionalis (Pilsbry & Ferriss, 1906)
Striatura milium (Morse, 1859)
Strobilops aenea Pilsbry, 1926
Strobilops affinis Pilsbry, 1893
Strobilops labyrinthica (Say, 1817)
Strobilops texasiana Pilsbry & Ferriss, 1906
Succinea ovalis Say, 1817
Succinea strigata Pfeiffer, 1855
Trichia hispida (Linné, 1798)
Triodopsis hopetonensis (Shuttelworth, 1852)
Vallonia costata (Müller, 1774)

Continued

Table 1. *Continued*

Vallonia gracilicosta Reinhardt, 1883
Vallonia pulchella (Müller, 1774)
Ventridens brittsi Pilsbry, 1892
Ventridens cerinoideus (Anthony, 1865)
Ventridens intertextus (A. Binney, 1841)
Ventridens pilsbryi Hubricht, 1964
Vertigo AK 1
Vertigo AK 2
Vertigo AK 3
Vertigo AK 5
Vertigo arthuri (von Martens, 1884)
Vertigo bollesiana (Morse, 1865)
Vertigo coloradensis (Cockerell, 1891)
Vertigo columbiana Sterki, 1892
Vertigo cristata Sterki, 1919
Vertigo elatior Sterki, 1894
Vertigo aff. *genesii* (Gredler, 1865)
Vertigo gouldii (A. Binney, 1843)
Vertigo hannai Pilsbry, 1919
Vertigo hubrichti Pilsbry, 1934
Vertigo milium (Gould, 1840)
Vertigo modesta hoppii (Möller, 1842)
Vertigo modesta modesta (Say, 1824)
Vertigo modesta ultima Pilsbry, 1948
Vertigo nylanderi Sterki, 1909
Vertigo oscariana (Sterki, 1890)
Vertigo oughtoni Pilsbry, 1948
Vertigo ovata Say, 1822
Vertigo paradoxa Sterki, 1900
Vertigo perryi Sterki, 1905
Vertigo pygmaea (Draparnaud, 1801)
Vertigo rugosula Sterki, 1890
Vertigo ventricosa (Morse, 1865)
Vitrina alaskana Dall, 1905
Vitrina limpida Gould, 1850
Vitrinizonites latissimus (Lewis, 1875)
Zonitoides arboreus (Say, 1816)
Zonitoides nitidus (Müller, 1774)
Zoogenetes harpa (Say, 1824)

Occurring only in neutral/calcareous sites:
Allogona profunda (Say, 1821)
Anguispira kochi (Pfeiffer, 1845)
Anguispira strongylodes (Pfeiffer, 1854)
Angusipira jessica Kutchka, 1938
Appalachina sayana (Pilsbry, 1906)
Carychium clappi Hubricht, 1959
Carychium nannodes Clapp, 1905
Catinella exile (Leonard, 1972)
Catinella gelida (F.C. Baker, 1927)
Catinella vermeta (Say, 1829)
Catinella wandae (Webb, 1953)
Cepaea nemoralis (Linné, 1798)
Daedalochila bisontes Coles & Walsh, 2006
Daedalochila lithica (Hubricht, 1961)
Daedalochila peregrina (Rehder, 1932)
Discus macclintockii (F.C. Baker, 1928)

Continued

Table 1. *Continued*

Discus rotundatus (Müller, 1774)
Euchemotrema hubrichti (Pilsbry, 1940)
Euchemotrema leai aliciae (Pilsbry, 1893)
Gastrocopta abbreviata (Sterki, 1909)
Gastrocopta armifera (Say, 1821)
Gastrocopta corticaria (Say, 1816)
Gastrocopta cristata (Pilsbry & Vanatta, 1900)
Gastrocopta pellucida (Pfeiffer, 1841)
Gastrocopta procera (Gould, 1840)
Gastrocopta rogersensis Nekola & Coles, 2001
Gastrocopta similis (Sterki, 1909)
Gastrocopta sterkiana Pilsbry, 1912
Glyphyalinia caroliniensis (Cockerell, 1890)
Glyphyalinia cumberlandiana (Clapp, 1919)
Hawaiia n. sp.
Helicina orbiculata (Say, 1818)
Helicodiscus n. sp.
Helicodiscus roundyi (Morrison, 1935)
Helicodiscus singleyanus (Pilsbry, 1890)
Inflectarius edentatus (Sampson, 1889)
Inflectarius subpalliatus (Pilsbry, 1893)
Lamellaxis gracilis (Hutton, 1834)
Lobosculum pustuloides (Bland, 1851)
Mesodon clausus clausus (Say, 1821)
Mesodon normalis (Pilsbry, 1900)
Mesodon thyroidus (Say, 1816)
Mesomphix cupreus (Rafinesque, 1831)
Mesomphix inornatus (Say, 1821)
Mesomphix rugeli (W.G. Binney, 1879)
Microphysula cookei (Pilsbry, 1922)
Neohelix dentifera (A. Binney, 1837)
Neohelix major (A. Binney, 1837)
Oxychylus cellarius (Müller, 1774)
Oxychylus draparnaudi (Beck, 1837)
Oxyloma haydeni (W.G. Binney, 1858)
Oxyloma peoriensis (Wolf, in Walker, 1892)
Oxyloma verrilli Bland, 1865
Paravitrea AR 1
Paravitrea tridens Pilsbry, 1946
Patera clenchi (Rehder, 1932)
Patera pennsylvanicus (Green, 1827)
Pilsbryna quadrilamellata Slapcinsky & Coles, 2002
Polygyra cereolus (Muhlfeld, 1818)
Polygyra septemvolva Say, 1818
Pomatiopsis cincinnatiensis (I. Lea, 1840)
Punctum conspectum (Bland, 1865)
Punctum smithi Morrison, 1935
Pupoides albilabris (C.B. Adams, 1821)
Rabdotus dealbatus (Say, 1821)
Stenotrema altispira (Pilsbry, 1894)
Stenotrema hirsutum (Say, 1817)
Stenotrema pilsbryi (Ferriss, 1900)
Succinea indiana Pilsbry, 1905
Succinea putris (Linné, 1798)
Trichia striolata (Pfeiffer, 1828)
Triodopsis cragini Call, 1886
Triodopsis discoidea (Pilsbry, 1904)

Continued

Table 1. *Continued*

Triodopsis neglecta (Pilsbry, 1899)
Triodopsis obsoleta (Pilsbry, 1894)
Triodopsis tridentata (Say, 1816)
Triodopsis vulgata (Pilsbry, 1948)
Vallonia excentrica Sterki, 1893
Vallonia parvula Sterki, 1892
Vallonia perspectiva Sterki, 1892
Ventridens acerra (Lewis, 1870)
Ventridens ligera (Say, 1821)
Vertigo AK 4
Vertigo binneyana Sterki, 1890
Vertigo clappi Brooks & Hunt, 1936
Vertigo meramecensis Van Devender, 1979
Vertigo morsei Sterki, 1894
Vertigo parvula Sterki, 1890
Vertigo tridentata Wolf, 1870
Webbhelix multilineata (Say, 1821)
Xolotrema denotata (Férussac, 1821)
Xolotrema fosteri (F.C. Baker, 1932)
Zonitoides limatulus (W.G. Binney, 1840)

maximum iterations, a stress ratio stopping value of 0.9999 and a small stress stopping value of 0.01. Output was scaled in half-change units, so that an interpoint distance of 1.0 will correspond, on average, to a 50% turnover in species composition.

Because a given NMDS run may locate a local (rather than the global) stress minimum, multiple NMDS runs were conducted on a given set of data from different initial random starting points to assess the stability of an individual solution (Minchin, 1987). In this analysis, DECODA used a total of 10 random starting configurations. Solutions in each of the four dimensions were compared using a Procrustes transformation to identify those that were statistically identical. The number of unique solutions, and number of runs which fell into each, was then calculated across each dimension. The modal solution out of 10 runs was identified, and was considered to be a global optimum when it was achieved in at least 50% of starts.

Compositional variation across the diagram was documented by dividing it into regions whose boundaries were either 0.5 standard deviation above or below the ordination centroid along all major axes of variation. Within each of these regions, all taxa found within at least 25% of included sites were identified.

Environmental correlations with this diagram were determined by calculating in DECODA the maximum correlation vector for site latitude and moisture level. The significance of each was estimated through Monte-Carlo simulations using 1,000 replications.

Full two-way ANOVAs were used to test for differences in the central tendency of richness and log-transformed abundance across the three acidity levels and five major terrestrial gastropod habitat types. ANOVA was performed as richness and log-transformed abundance were essentially normally distributed across all three categories of habitat acidity. Even though log-transformation greatly alters the appearance of the species abundance distribution within sites, this technique is appropriate when comparisons of identically transformed data are made between sites (Nekola *et al.*, 2008). The patterns among habitat types and acidity levels were visualized using box plots.

Abundance distribution variation between highly acidic, moderately acidic and neutral/calcareous categories within each major habitat type was displayed using rank–frequency (dominance–diversity) plots. These were created by calculating the proportional abundance for each species within a given site. Abundances were then sorted from most to least abundant. The median proportional abundance for the most abundant species was then determined across all sites of a given base-status within that habitat type. This process was repeated for the second, third, fourth etc. to the least abundant species. These abundance values were plotted on a log-axis *vs* rank position. This process was repeated for all three base-status levels within a given habitat type.

RESULTS

Even though almost two-thirds of sites sampled in California and the Southwest occurred on highly felsic igneous outcrops, acidophilic vegetation was never noted, with vascular plants and bryophytes appearing essentially identical across the bedrock acidity spectrum. In addition, no differences were noted between the land-snail community compositions of these sites. This result is almost certainly due to the high rates of dryfall Ca inputs (Waring & Schlesinger, 1985) which have been estimated to range between 190 and 200 mg/m^2/year in southern California (Ellis, Verfaillie & Kummerow, 1983). Because of low leaching rates, at least 98% of soil Ca in the Southwest originates from atmospheric deposition (Capo & Chadwick, 1999), allowing ample base to be present in all soils, no matter what the parent material. For this reason, all 162 sites sampled in Arizona, California, Colorado and New Mexico have been eliminated from further analysis, because none actually represents acidophilic conditions, regardless of the underlying bedrock type.

Calcifuge/calcicole status

Of the 1,194 analysed sites outside of the Southwestern USA, land snails were observed from 1,188. Of these, 391 were observed to be highly or moderately acidic: 91 rock outcrops, 67 upland forests, 124 lowland forests, 22 upland grasslands and 87 lowland grasslands. In total, 241 species (*c.* 40% of the eastern and northern North American fauna and *c.* 20% of the entire North American fauna) and 486,153 identified individuals were encountered across these sites. Essentially all wide-ranging eastern and northern taxa were observed, with most of the unencountered species representing regional endemics, principally in the Polygyridae and Zonitidae (Hubricht, 1985).

Seven species only occurred in highly acidic habitats, two only in moderately acidic habitats and a remaining five only in either moderately or highly acidic habitats (Table 1). While 93 species were restricted to neutral/calcareous habitats, the remaining 134 were found both in neutral/calcareous and moderately/highly acidic sites.

Kruskal–Wallis analysis of abundances between highly acidic, moderately acidic and neutral/calcareous sites for the 128 species with at least 10 occurrences and 30 individuals (Table 2) documented 10 species with abundances that were significantly ($P < 0.00039$) greater in highly acidic sites, and an additional seven that significantly ($P < 0.00039$) favoured moderately acidic sites. One species tended ($0.05 < P < 0.00039$) to favour moderately acidic sites. A total of 34 species was shown to display no significant ($P > 0.05$) changes in abundance across the acidity spectrum. Of these, 23 had only between 10 and 30 total occurrences, making it probable that some of these nonsignificant test scores represent type-II errors. This is particularly likely for *Discus macclintockii*, *Hawaiia* n. sp. and *Oxyloma verrilli*, which had their twelve or fewer occurrences limited to neutral/calcareous habitats. Likewise, it seems

Table 2. Base-status preferences based upon Kruskal–Wallis analysis of site abundance.

Species	*P*-value
Species significantly favouring highly acidic sites:	
Euconulus chersinus	0.00000039
Glyphyalinia luticola	0
Glyphyalinia n. sp.	0
Glyphyalinia solida	0
Striatura meridionalis	0.00000009
Strobilops texasiana	0
Ventridens cerinoideus	0.00000002
Vertigo alabamensis	0
Vertigo malleata	0
Vertigo modesta hoppii	0.00004532
Species significantly favouring moderately acidic sites:	
Planogyra asteriscus	0.00000001
Striatura exigua	0.00000002
Striatura ferrea	0.00002965
Vertigo cristata	0
Vertigo perryi	0
Vertigo ventricosa	0
Zoogenetes harpa	0
Species tending to favour moderately acidic sites	
Vertigo nylanderi	0.02831
Species demonstrating no preference in base status of habitat ($\geq$30 occurrences):	
Cochlicopa morseana	0.1217
Euconulus fulvus alaskensis	0.9992
Glyphyalinia rhoadsi	0.2121
Pupilla hebes	0.08355
Striatura milium	0.06981
Succinea strigata	0.4538
Vertigo AK 2	0.906
Vertigo coloradensis	0.1796
Vertigo hannai	0.5831
Vertigo modesta modesta	0.1135
Vertigo ovata	0.3306
Species demonstrating no preference in base status of habitat ($<$30 occurrences):	
Discus macclintockii	0.08603
Euconulus dentatus	0.404
Euconulus trochulus	0.7056
Glyphyalinia wheatleyi	0.0512
Hawaiia n. sp.	0.08603
Helicodiscus inermis	0.0714
Helicodiscus notius	0.1385
Inflectarius inflectus	0.2089
Neohelix albolabris	0.0578
Oxychylus cellarius	0.08603
Oxyloma verrilli	0.05241
Paravitrea significans	0.1658
Pomatiopsis lapidaria	0.0666
Punctum blandianum	0.1177
Pupilla muscorum	0.3372
Strobilops aenea	0.508
Ventridens brittsi	0.9471
Vertigo AK 1	0.3169
Vertigo AK 3	0.1944
Vertigo AK 5	0.9488
Vertigo genesii	0.819
Vertigo modesta ultima	0.2797
Vertigo oscariana	0.2958
Species significantly favouring neutral/calcareous sites:	
Allogona profunda	0.00001154
Anguispira alternata	0
Carychium exiguum	0
Carychium exile	0
Catinella avara	0.00000003
Cochlicopa lubrica	0
Cochlicopa lubricella	0
Columella simplex	0
Deroceras laeve	0
Discus catskillensis	0.00000001
Discus cronkhitei	0.00000013
Euchemotrema fraternum	0
Euchemotrema leai leai	0
Euconulus alderi	0.0001001
Euconulus fulvus	0.00000592
Euconulus polygyratus	0
Gastrocopta armifera	0
Gastrocopta contracta	0
Gastrocopta corticaria	0
Gastrocopta holzingeri	0
Gastrocopta pentodon	0
Gastrocopta similis	0.00000013
Vallonia perspectiva	0
Vallonia pulchella	0.00000001
Vertigo arthuri	0.00000276
Vertigo bollesiana	0.00000102
Vertigo elatior	0
Vertigo gouldi	0
Gastrocopta tappaniana	0.00000005
Glyphyalinia indentata	0
Guppya sterkii	0.0001567
Haplotrema concavum	0.0001865
Hawaiia minuscula	0
Helicodiscus parallelus	0
Helicodiscus shimeki	0.0001685
Helicodiscus singleyanus	0.0001555
Hendersonia occulta	0
Nesovitrea binneyana	0
Nesovitrea electrina	0
Oxyloma retusa	0.00000399
Paravitrea multidentata	0.00000049
Punctum vitreum	0
Pupoides albilabris	0.00000021
Stenotrema barbatum	0.0001403
Strobilops affinis	0.00008082
Strobilops labyrinthica	0
Succinea ovalis	0.00008805
Vallonia costata	0
Vallonia gracilicosta	0
Vallonia parvula	0.0000716

Continued

Table 2. *Continued*

Species	*P*-value
Vertigo hubrichti	0
Vertigo milium	0
Vertigo paradoxa	0.00000027
Vertigo pygmaea	0.0001343
Vertigo tridentata	0
Zonitoides arboreus	0
Species tending to favour neutral/calcareous sites:	
Catinella exile	0.0005619
Catinella 'gelida'	0.000435
Catinella 'vermeta'	0.03188
Columella columella alticola	0.04251
Gastrocopta procera	0.002008
Gastrocopta rogersensis	0.00552
Mesodon clausus clausus	0.0007254
Mesodon thyroidus	0.004289
Neohelix alleni	0.002879
Oxyloma haydeni	0.02484
Punctum minutissimum	0.00181
Punctum n. sp.	0.007416
Triodopsis tridentata	0.0071
Webbhelix multilineata	0.00552
Vertigo meramecensis	0.001558
Vertigo morsei	0.002587
Vertigo oughtoni	0.02095
Vitrina limpida	0.001014
Xolotrema fosteri	0.04088
Zonitoides nitidus	0.001456

The significance threshold has been modified to $P \leq 0.00039$ based on a Bonferroni correction.

probable that with additional observations *Punctum blandianum* will be found strongly to favour acidic sites, as its population sizes are more than five times greater on highly acidic as compared to neutral/calcareous sites. The remaining 76 taxa either significantly ($P < 0.00039$) favoured (56 species) or tended ($0.05 < P < 0.00039$) to favour (20 species) neutral/calcareous sites.

Compositional gradients

Visual observation of the optimal NMDS result (the two-dimensional solution) using all 305 highly or moderately acidic sites with at least five observed species indicated a group of 13 outliers along Axis 1 that represented tundra or near-tundra sites in Alaska and northern Manitoba. To assist gradient interpretation, these sites were assigned to a unique compositional group, and then removed from analysis. NMDS of the remaining 292 sites in one dimension generated a minimum stress configuration of 0.2603, which was achieved from nine of 10 random starting configurations. Procrustes analysis showed that these solutions fell into only a single group. NMDS along two dimensions generated a minimum stress configuration of 0.1934, which was achieved from all 10 random starting configurations. Procrustes analysis showed that these solutions fell into three unique categories, of which one was achieved in six different starts. NMDS along three dimensions generated a minimum stress configuration of 0.1489, which was achieved from six of the 10 random starting configurations. Procrustes analysis showed that these minimum stress solutions fell into two unique groups, each achieved in three different starting configurations. NMDS along four dimensions generated a minimum stress configuration of 0.1220, which was achieved from nine of 10 random starting configurations. Procrustes analysis showed that each of these solutions was unique.

Based on these results the modal configuration from the two-dimensional NMDS was chosen as the most stable for depicting land-snail community composition trends (Fig. 2). Approximately two complete turnovers in species composition are indicated along the first axis, with a single complete turnover being noted along the second. Environmental biplot analysis (Fig. 3) demonstrates that the first axis strongly ($P < 0.0005$) correlates with site latitude, with a maximum observed correlation of $r = 0.8366$. The second axis strongly ($P < 0.0005$) correlates with water level, with a maximum observed correlation of $r = 0.6753$. Ordination region one is found in the upper left of the diagram, and principally represents low latitude wetlands such as pocosins and bay-head swamps. Twelve species were found to occur in at least 25% of these sites (Table 3). Ordination region two is found at the mid-left side of the diagram, and principally represents low latitude mesic sites such as pine forest, bay forest and heathlands. Nine species were found to occur in at least 25% of these sites. Ordination region three is found on the lower left side of the diagram, and principally represents low latitude xeric sites such as dry bedrock outcrops, talus slopes and heath balds. Nine species were found to occur in at least 25% of these sites. Ordination region four is in the upper-mid portion of the diagram, and principally represents mid-latitude wetlands such as sedge meadows, and swamps of tamarack, northern white cedar, willow, red maple and alder. Twenty-three species were found to occur in at least 25% of these sites. Ordination region five is found in the centre of the diagram, and principally represents mid-latitude mesic sites such as pine, hemlock and yellow birch forests as well as some mesic bedrock outcrops. Fourteen species were found to occur in at least 25% of these sites. Ordination region six is on the bottom margin of the diagram, and principally represents mid-latitude xeric sites such as exposed bedrock outcrops and dry upland forest. Fourteen species were found to occur in at least 25% of these sites. Ordination region seven is on the upper right of the diagram, and principally represents high-latitude wetlands such as cattail swamps, sedge meadows and *Sphagnum* bogs. Ten species were found to occur in at least 25% of these sites. Ordination region eight is on the right-centre margin of the diagram, and principally represents high-latitude mesic sites such as heathlands, spruce-fir forest and some mesic rock outcrops. Eleven species were found to occur in at least 25% of these sites. Ordination region nine is found on the lower right of the diagram, and principally represents high-latitude xeric sites such as exposed bedrock outcrops. Nine species were found in at least 25% of these sites. Lastly, ordination region 10 represents the outlier sites found along the middle of Axis 2 to the right of the ordination diagram. These sites represent tundra sites across the full extent of the moisture gradient, ranging from sedge meadows to exposed rock outcrops. Ten species were found in at least 25% of these sites.

Richness and abundance patterns

ANOVA of richness and abundance patterns between the three soil acidity classes within the five major land-snail habitat types demonstrate that soil acidity imposed a highly significant ($P < 0.000000005$) negative impact on both site richness and log-transformed abundance (Table 4). Median richness levels ranged from 4.5 to 10 species per site in highly acidic soils, increased to 7–15 in moderately acidic soils, and were 11.5–20 in neutral/calcareous sites (Fig. 4). Median total abundance

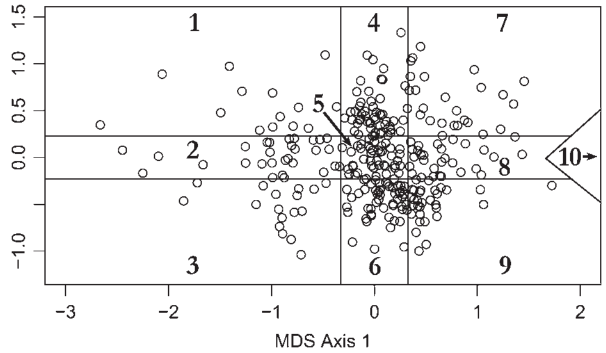

Figure 2. Optimum two-dimensional NMDS solution, showing locations of the 10 regions used to determine compositional changes.

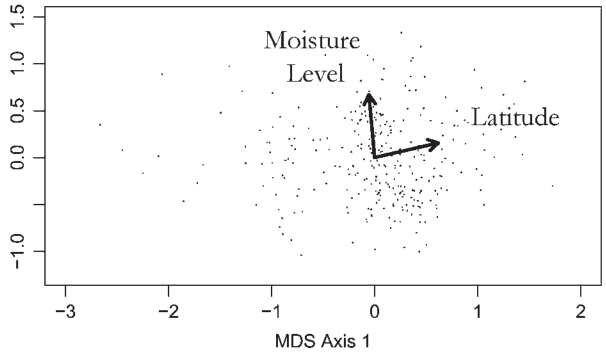

Figure 3. Environmental biplot diagram showing the vectors of maximum correlation for latitude and moisture levels.

ranged from 50.5 to 119.5 individuals in highly acidic soils to 57–292.5 in moderately acidic soils and 211–440 in neutral/calcareous sites (Fig. 4). Habitat type also had a highly significant ($P < 0.000000005$) impact on site richness, but only a marginally significant ($P = 0.04$) impact on log-transformed total abundance. Bedrock outcrop sites had the highest observed richness with a median score ranging from 10 to 20 species, followed by upland forests (8–15), lowland forests (6–15), lowland grasslands (5–12) and upland grasslands (4.5–11.5). While the interaction between habitat type and soil acidity significantly impacted site richness ($P = 0.001$), no effect on log-transformed abundance was noted ($P = 0.69$). The significant interaction appears due to the fact that richness of highly and moderately acidic bedrock outcrop sites was identical, as were the richness of moderately acidic and neutral/calcareous upland forests (Fig. 4).

Rank–abundance plots across all five habitat types demonstrate a clear tendency for highly acidic sites to have more uneven abundance distributions than for neutral/calcareous sites (Fig. 5), with the commonest species in highly acidic habitats tending to have a higher proportional median abundance and with scores rapidly decreasing to much smaller values for a given rank. In most cases, curves from moderately acidic sites were intermediate between highly acidic and neutral/calcareous sites. Exceptions to this were noted in lowland forest and upland grasslands, in which the curves for moderately acidic and neutral/calcareous sites were largely coincident.

DISCUSSION

The North American acidophilic land-snail fauna

These analyses clearly document that *Vertigo malleata* is not an idiosyncratic anomaly within the North American land-snail fauna. Almost two-thirds of all analysed northern and eastern North American species were found to occur at least occasionally in highly to moderately acidic habitats. Of these, 16 (*Daedalochila leporina*, *Euconulus chersinus*, *Glyphyalinia luticola*, *Glyphyalinia* n. sp., *Glyphyalinia solida*, *Mesomphix perlaevis*, *Neohelix divesta*, *Neohelix solemi*, *Striatura meridionalis*, *Strobilops texasiana*, *Triodopsis soelneri*, *Ventridens cerinoideus*, *Vertigo alabamensis*, *V. malleata*, *Vertigo modesta hoppii* and *Vertigo oralis*) only occurred or had statistically higher abundance in highly acidic sites. An additional 10 (*Lobosculum pustula*, *Planogyra asteriscus*, *Pristiloma arcticum*, *Striatura exigua*, *Striatura ferrea*, *Vertigo cristata*, *Vertigo nylanderi*, *Vertigo perryi*, *Vertigo ventricosa* and *Zoogenetes harpa*) only occurred or had statistically higher abundance in moderately acidic sites. *Paravitrea petrophila* and *Triodopsis juxtidens* were also only seen in moderately and highly acidic sites. Thus, about 12% of the sampled fauna exhibits clear signs of acidophilic/calcifugic affinities. Almost all of these taxa are wide-ranging, with only one (*Triodopsis solneri*) being a local endemic. While other presumed acidophiles (e.g. *Catinella oklahomarum*, *Inflectarius downieanus*, *Mesodon normalis*, *Neohelix dentifera*, *Praticolella bakeri*, *Praticolella jejuna*, *Praticolella lawae* and *Praticolella mobiliana*) have been reported previously (Hubricht, 1985), they have either not yet been encountered or have too few observed occurrences to draw firm conclusions regarding their preferred base status. The actual number of acidophilic/calcifugic land-snail species in North America is thus certainly higher than is reported here. It is therefore vitally important for North American land-snail biodiversity surveys not to ignore acidic habitats, because they harbour an important and surprisingly diverse fauna.

Acidophilic tendencies are not limited to a few closely related groups, with the taxa listed above representing at least eight families (Euconulidae, Gastrodontidae, Oxychilidae, Polygyridae, Pristolomatidae, Valloniidae and Vertiginidae of Bouchet *et al.*, 2005). With additional sampling, two more (Punctidae and Succineidae) will also likely be added to this list. Most of this fauna shares little phylogenetic overlap with the known European acid-tolerant fauna: only two of the above genera (*Vertigo* and *Zoogenetes*) possess acidophilic taxa in both the Old and New Worlds (Kerney & Cameron, 1979). Instead, most of the North American acidophilic fauna represents endemic families or genera, such as the Polygyridae (representing one-fifth of identified acidophilic species) and the gastrodontid genus *Striatura* (all species demonstrated acidophilic or generalist tendencies). Biogeographically, acidophilic species were found to range across the entire continent from semitropical forests of the Gulf Coast to arctic tundra on the Alaska North Slope. These factors all strongly suggest that the evolution of acidophilic traits has occurred *in situ* multiple times within North America.

A few clear analogues between the European and North American acidophilic faunas can be observed, however. For instance, *Vertigo ronnebyensis* not only shares a very similar shell with *V. cristata*, but also an apparent preference for acidic taiga soils (Kerney & Cameron, 1979). Additionally, *Vertigo lilljeborgi* not only shares roughly similar shell characteristics with *V. perryi*, but similar affinities with tussock-side sedge litter accumulations in acidic wet meadows. The Holarctic *Zoogenetes harpa* also appears to demonstrate acidophilic tendencies across its range. It remains unknown how close the evolutionary relationships between these taxa and populations may be, given that at least some supposed Holarctic land-snail species can be shown to be members of only distantly related clades based on their mitochondrial DNA sequences (Nekola, Coles & Bergthorsson, in press).

Table 3. Ordered matrix of species frequency within each of the 10 identified NMDS ordination regions, with the reported number representing the per cent of sites within that region which supported populations of that given species.

Species	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6	Region 7	Region 8	Region 9	Region 10
Vertigo malleata	64.3	41.4								
Strobilops texasiana	57.1	55.2								
Punctum minutissimum	57.1	82.8	35.3	86.5	88.4	65.4				
Gastrocopta pentodon	50.0	62.1	70.6		27.9					
Vertigo milium	35.7									
Striatura milium	35.7	34.5		78.9	95.4	84.6				
Striatura meridionalis	35.7	48.3	76.4							
Euconulus chersinus	35.7									
Gastrocopta tappaniana	35.7			80.8			36.0			
Glyphyalinia solida	35.7									
Hawaiia minuscula	35.7									
Gastrocopta contracta	28.6									
Zonitoides arboreus		34.5	58.8	44.2	53.5	88.5		51.7	74.2	
Vertigo alabamensis		31.0								
Glyphyalinia indentata		27.6	47.1							
Columella simplex			29.4	80.8	72.1	36.5	28.0	51.7		
Haplotrema concavum			29.4							
Helicodiscus parallelus			29.4		27.9					
Guppya sterkii			29.4							
Nesovitrea electrina				92.3	32.6		80.0	58.6		
Striatura exigua				78.9	65.1	51.9		27.6	29.0	
Carychium exiguum				71.2						
Strobilops labyrinthica				67.3	81.4	42.3				
Euconulus fulvus				67.3	79.1	36.5	48.0	93.1	71.0	
Euconulus alderi				65.4			32.0			
Vertigo cristata				59.6	74.4	67.3		72.4	80.7	
Vertigo nylanderi				51.9						
Vertigo ventricosa				50.0			28.0			
Nesovitrea binneyana				50.0	79.1	71.2	32.0	55.2	74.2	
Planogyra asteriscus				46.2	32.6					
Striatura ferrea				34.6	41.9			27.6		
Discus catskillensis				32.7	65.1	76.9			74.2	
Vertigo elatior				32.7						
Punctum n. sp.				30.8						
Succinea ovalis				30.8						
Helicodiscus shimeki				30.8	39.5	36.5				
Carychium exile				26.9						
Vertigo bollesiana					34.9					
Zoogenetes harpa						44.2		48.3	38.7	
Vertigo paradoxa						38.5			38.7	
Anguispira alternata						26.9				
Discus cronkhitei							40.0	51.7	38.7	
Vertigo perryi							32.0			
Vertigo modesta modesta							28.0			69.2
Vitrina limpida								27.6		
Euconulus fulvus alaskensis										76.9
Vertigo modesta hoppii										76.9
Vertigo AK 2										61.5
Vertigo hannai										46.2
Succinea strigata										46.2
Columella columella alticola										38.5
Pupilla hebes										38.5
Vertigo modesta ultima										38.5
Vertigo genesii										30.8

Only species with a frequency of at least 25% within a region are listed.

Acidic land-snail habitats

Acidophilic land-snail faunas were observed in a number of habitat types across the continent. In the south, some of the most diverse assemblages occurred in ombotrophic pocosin peatlands, bayhead seepage swamps, Atlantic white cedar forests, pine-wiregrass savanna, pine barrens, heath balds and upland oak woods. To the north, other important reservoirs for acidophilic land-snail diversity included *Sphagnum* bogs, swamps of base-poor cattail, sedge, northern white cedar, red maple, balsam fir and tamarack, wooded igneous rock outcrops and base-poor upland forests. Acidophilic land snails were also abundantly found across North America in base-poor taiga and acidic tundra over base-poor rock such as sandstone, quartzite and gneiss.

It is astonishing not only that land-snail communities exist on such sites, but also that many of the included species possess large populations (up to 2,000/m^2; Coles & Nekola, 2007) and strongly calcified shells (e.g. *S. texasiana*, *V. alabamensis*). Because of the very small Ca pools in such habitats (Binkley *et al.*, 1992), it is clear that these populations must be successfully capturing Ca that is fluxing rapidly through the environment. Ca sources in these sites are undoubtedly various organically derived Ca salts, including Ca citrate and Ca oxalate (Wäreborn, 1970), which are leached from various tree and shrub species such as aspen, dogwood or cedar (Karlin, 1961; Nation, 2007). Because of the high densities of individuals observed in their litter accumulations, it appears that heaths such as *Chamaedaphne*, *Gaylussacia*, *Lyonia*, *Kalmia*, *Vaccinium* and *Zenobia*, and other shrubs such as *Ilex*, *Gordonia*, *Magnolia* and *Myrica*, must also be important Ca sources. No matter the source, all acidophilic land snails must have evolved highly efficient Ca-pumps that are able to move ions counter to very strong osmotic gradients. If these pumps require low Ca concentrations or pH for proper functioning, it might provide a metabolic explanation for the calcifugic behaviour of some species.

Because of the very high soil acidity at many of these sites (e.g. pH < 4; Woodwell, 1958; Binkley *et al.*, 1992), the shells of many acidophilic snails are being actively dissolved even on living individuals. For instance, it is difficult to find living *V. malleata* or *V. alabamensis* individuals that do not possess at least one shell ulceration. Incipient ulcers can be seen in the individuals figured by Coles & Nekola (2007) as opaque white patches on otherwise translucent shells. Shell erosion is so rapid in these habitats that no adult shells of the seasonally active *V. alabamensis* could be found during autumn sampling, even on sites that supported colonies of >200 individuals/m^2 in spring (Nekola & Coles, in press).

Table 4. Summary statistics for ANOVA on the impacts of soil acidity and habitat type on community richness and log-transformed individual abundance.

Predictor variable	df	Sum-of-squares	Mean squares	*F*-value	*P*
A. Site richness					
Habitat type	4	10,181	2,545	86.459	<0.000000005
Soil acidity	2	11,602	5,801	197.064	<0.000000005
Habitat type * soil acidity	1	302	302	10.260	0.001396
B. Log-transformed total abundance					
Habitat type	4	17.97	4.5	2.5178	0.03981
Soil acidity	2	451.26	225.6	126.4315	<0.000000005
Habitat type * soil acidity		0.28	0.3	0.1596	0.68959

Acidophilic land-snail community composition gradients

The dispersion of sites across the optimal two-dimensional NMDS ordination diagram is continuous along both axes, implying that there are no hard compositional breaks within the fauna. This can be readily seen in the continuous variation exhibited in pineland and ombotrophic bog faunas along the Atlantic seaboard, with sites in the New Jersey Pine Barrens being intermediate between eastern Maine raised bogs and Carolina pocosins (Coles & Nekola, 2007). Similar transitions can be found between Atlantic coastal plain and mixed-deciduous forest faunas in central Massachusetts and southern Maine, between mixed-deciduous and taiga faunas along the Cote Nord in eastern Quebec and the western shore of Lake Superior, and between taiga and tundra faunas in the Alaskan interior, at Churchill, Manitoba, and in central Quebec.

Analysis of environmental covariates identifies essentially the same organizing factors as have been previously shown in calcareous sites in the Great Lakes region (Nekola, 2003):

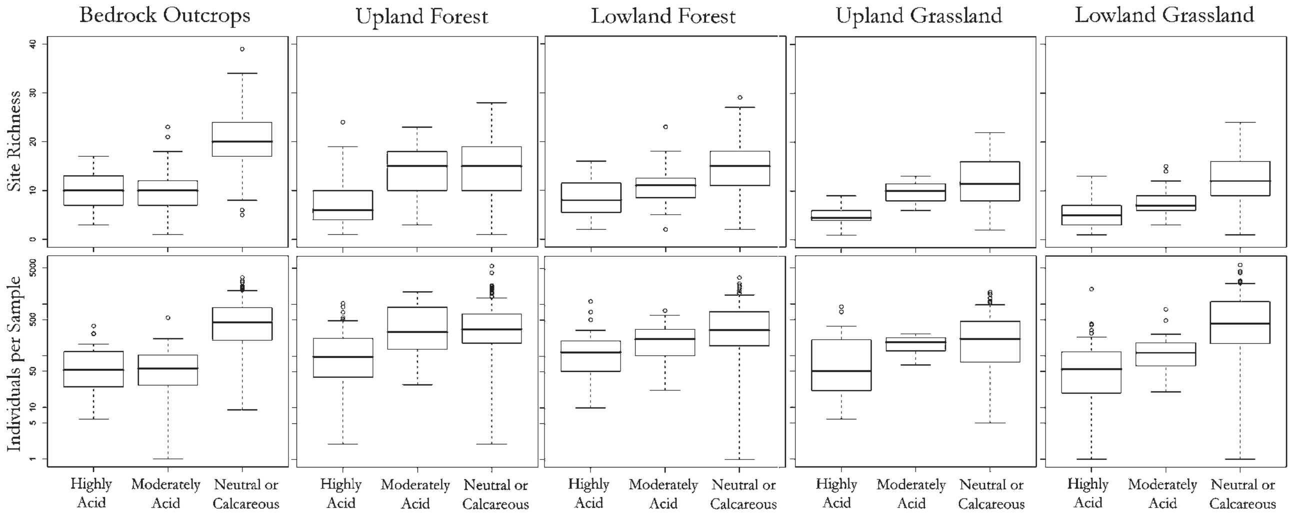

Figure 4. Box-plot diagrams demonstrating the impact of habitat type and soil acidity on site richness (top) and log-transformed site abundance (bottom).

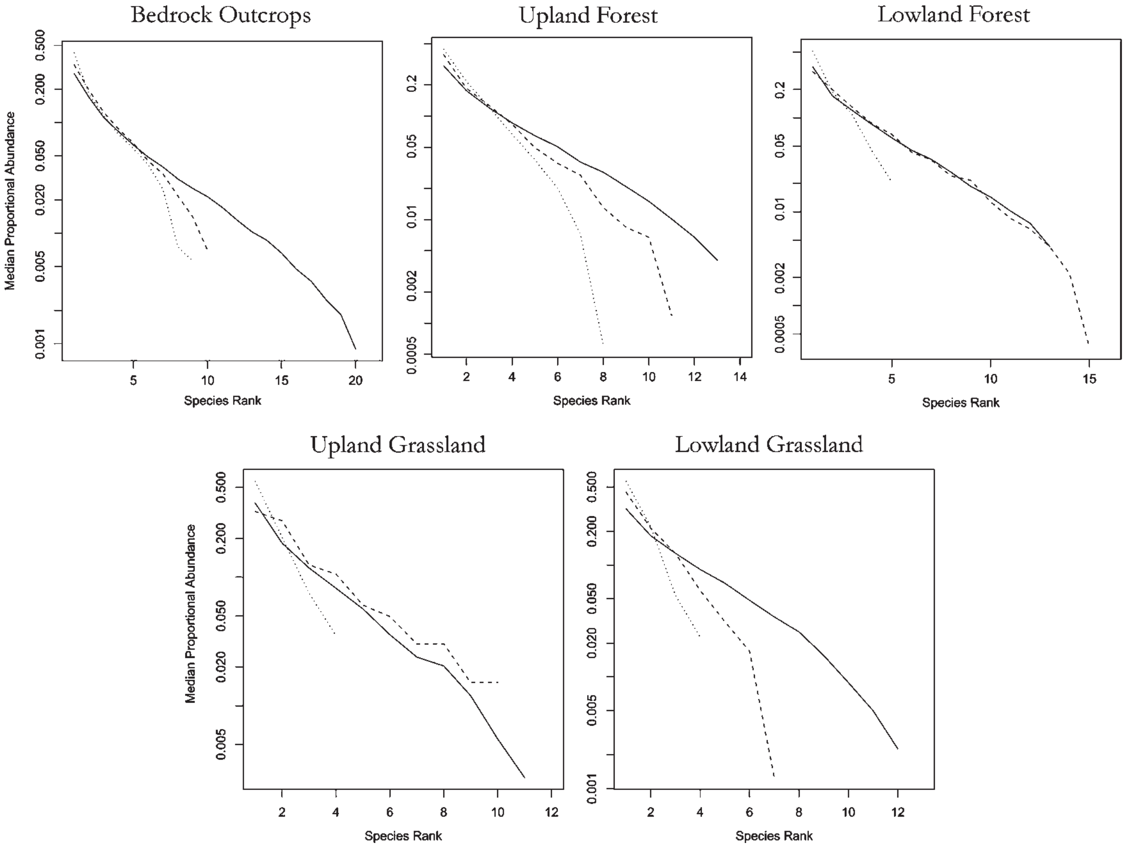

Figure 5. Rank–abundance (a.k.a. dominance–diversity) plots for median proportional abundance across all highly acidic (dotted line), moderately acidic (dashed line) and neutral/calcareous (solid line) sites within a given major habitat type.

latitude was most strongly correlated with the first axis, while water level was strongly related to the second. As a result, it appears that at a continental scale acidophilic faunas respond in similar ways to the same environmental variables as do calciphilic faunas. Although found to be very important in base-rich communities, the impact of soil surface architecture was not documented in the current analysis, because thick organic litter accumulations (e.g. 'duff soils') were present on essentially all sites. However, acidic soils did tend towards turf-style architecture with increasing water levels.

Diversity patterns

While faunas of acidic habitats were both more depauperate in species and individuals than those of neutral/calcareous sites, median richness fell by no more than half, while abundance fell by no more than an order of magnitude. Median richness of even the most acidic sites ranged up to 10 species. This contrasts with patterns observed in Europe, where moderately acidic sites may often harbour as many species as typical base-rich sites (Bishop, 1977, 1980; Tattersfield, 1990; Cameron & Greenwood, 1991), and the most acidic sites typically have maximum diversity levels of <10 (Kerney & Cameron, 1979).

As in Europe (Cameron & Pokryszko, 2005), faunas were found to become increasingly uneven in their abundance distributions with increasing soil acidity. Acidic site faunas thus tend to be dominated by a relatively few common species, with the remainder being rare. This pattern is common among a large number of high-stress communities (Whittaker, 1975). The steepness of the rank–abundance curve on acidic sites also indicates that adequate documentation of site faunas may require extra field collection effort as compared to sites with higher base status (Cameron & Pokryszko, 2005).

Acidophilic land-snail communities in a global perspective

This documentation of acidophilic land-snail faunas is not without precedent. Bishop (1977), Tattersfield (1990) and Cameron & Greenwood (1991) have reported on land-snail community patterns from acidic sites in southwestern Ireland, the English Pennines and Scottish Highlands, respectively. Valovirta (1968), Wäreborn (1970), Waldén (1981), Gärdenfors (1992) and Mänd, Ehlvest & Kristaja (2001) have documented acidophilic land-snail faunas in Scandinavia and the Baltic Republics. Agócsy (1968) and Štamol (1991) have documented acidophilic land-snail faunas from eastern Europe, while Bishop (1980) also demonstrated the existence of such faunas in Italy. The existence of a low-elevation acidophilic fauna from the North Island of New Zealand is also suggested by the work of Barker & Mayhill (1999). The species found on these sites can make up a not-inconsequential fraction of their respective regional faunas: Boycott (1934) reported roughly half of the British land-snail fauna to be 'indifferent to lime', occurring freely in both acidic and calcareous sites, while Bishop (1977) reported that about 40% of all Irish land snails occur in acidic woodlands.

What makes the North American fauna outstanding, however, is the presence of so many clearly acidophilic/calcifugic species. While these make up an estimated 10% of the sampled northern and eastern North American fauna, Boycott (1934) could only identify one such species from Britain. Even with updating by Kerney & Cameron (1979), it is clear that perhaps 1% or less of the northwestern European land-snail fauna can be considered acidophilic. This has profound implications in terms of composition gradients. First, the lack of acid-preferring species allows for considerable stochastic compositional variation between adjacent European acidic sites (Cameron & Pokryszko, 2005). In North America, however, the presence of acidophilic species allows for much greater consistency in site composition: the standard deviations of Axis 1 and Axis 2 scores for Carolina pocosins were only 0.36 and 0.25, respectively (implying *c.* 82-87% similarity), 0.26 along both Axis 1 and 2 for New England conifer swamps (*c.* 87% similarity), and 0.20 and 0.19 (*c.* 90% similarity) for western Lake Superior igneous outcrop sites.

Acidic-habitat faunas throughout Europe also tend to be characterized by a suite of ubiquitous species which occur across the entire base-status gradient. The major compositional change with increasing base-status is the continuous addition of increasingly calciphilic species (Valovirta, 1968; Waldén, 1981; Cameron & Greenwood, 1991; Horsák & Hájek, 2003) until a few taxa drop out at the sites of highest base-status (Horsák, 2006). Among European studies, only Agócsy (1968) did not recognize this pattern, instead noting that about 60% of acidic-habitat snails were restricted to these sites, whereas there was only 20% similarity between the faunas of adjacent acidic and calcareous habitats. European land-snail community compositions can thus be generally characterized as being nested along a base-status axis. Although also suggested from coastal British Columbia forests by Cameron (1986), this pattern appears not to be typical for the rest of North America. Rather, acidophilic faunas are made not only of species ‘indifferent’ to lime, but also a group of species (*c.* 20% of site faunas) that actually favour highly or moderately acidic sites. As a result, replacement-driven turnover in species occurrence can be seen along the base-status axis across much of North America.

An important question that remains unanswered, however, is why North America and Europe differ so much in their frequency of acidophilic land-snail species. Given the apparently frequent presence of acidophiles in land-snail faunas of West Africa (De Winter & Gittenberger, 1998) and Borneo (Schilthuizen & Rutjes, 2001), it seems possible that a productive line of inquiry may be directed at determining why Europe has an unusually depauperate fauna, as opposed to concentrating on why that of North America appears strangely enriched.

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REFERENCES

AGÓCSY, P. 1968. Data to quantitative conditions in the mollusk faunas of two different substrates in central Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae*, **14**: 1–6.

BARBOUR, M.G. & BILLINGS, W.D. 1988. *North American terrestrial vegetation*. Cambridge University Press, New York.

BARKER, G.M. & MAYHILL, P.C. 1999. Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru Ecological District, northeastern New Zealand. *Journal of Biogeography*, **26**: 215–238.

BINKLEY, D., RICHTER, D., DAVID, M.B. & CALDWELL, B. 1992. Soil chemistry in a Loblolly/Longleaf Pine forest with interval burning. *Ecological Applications*, **2**: 157–164.

BISHOP, M.J. 1977. The Mollusca of acid woodland in west Cork and Kerry. *Proceedings of the Royal Irish Academy, Section B*, **77**: 227–244.

BISHOP, M.J. 1980. The Mollusca of acid woodland in the Italian province of Novara. *Journal of Conchology*, **30**: 181–188.

BOUCHET, P., ROCROI, J.-P., FRÝDA, J., HAUSDORF, B., PONDER, W., VALDÉS, Á. & WARÉN, A. 2005. Classification and nomenclator of gastropod families. *Malacologia*, **47**: 1–397.

BOYCOTT, A.E. 1934. The habitats of land Mollusca in Britain. *Journal of Ecology*, **22**: 1–38.

BURCH, J.B. 1962. *The Eastern land snails*. W. C. Brown Co., Dubuque, Iowa.

CAMERON, R.A.D. 1986. Environment and diversities of forest snail faunas from coastal British Columbia. *Malacologia*, **27**: 341–355.

CAMERON, R.A.D & GREENWOOD, J.J.D. 1991. Some montane and forest molluscan faunas from eastern Scotland: effects of altitude, disturbance and isolation. In: *Proceedings of the Tenth International Molluscan Congress, Tübingen, 1989* (C. Meier-Brook, ed.), pp. 437–442. Unitas Malacologica, Tübingen.

CAMERON, R.A.D. & POKRYSZKO, B.M. 2005. Estimating the species richness and composition of land mollusc communities. *Journal of Conchology*, **38**: 529–547.

CAPO, R.C. & CHADWICK, O.A. 1999. Sources of strontium and calcium in desert soil and calcrete. *Earth and Planetary Science Letters*, **170**: 61–72.

COLES, B.F. & NEKOLA, J.C. 2007. *Vertigo malleata*, a new extreme calcifuge land snail from the Atlantic and Gulf coastal plains of the U.S.A. (Gastropoda, Vertiginidae). *Nautilus*, **121**: 17–28.

CRUM, H.A. & ANDERSON, L.E. 1981. *Mosses of eastern North America*. Columbia University Press, New York.

DE WINTER, A.J. & GITTENBERGER, E. 1998. The terrestrial gastropod fauna of a square kilometer patch of rainforest in southwestern Cameroon: high species richness, low abundance, and seasonal fluctuations. *Malacologia*, **40**: 231–250.

ELLIS, B.A., VERFAILLIE, J.R. & KUMMEROW, J. 1983. Nutrient gain from wet and dry atmospheric deposition and rainfall acidity in southern California chaparral. *Oecologica*, **60**: 118–121.

EMBERTON, K.C., PEARCE, T.A. & RANDALANA, R. 1996. Quantitatively sampling land-snail species richness in Madagascan rainforests. *Malacologia*, **38**: 203–212.

FAITH, D.P., MINCHIN, P.R. & BELBIN, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, **69**: 57–68.

GÄRDENFORS, U. 1992. Effects of artificial liming on land snail populations. *Journal of Applied Ecology*, **29**: 50–54.

HERMIDA, J., ONDINA, M.P. & RODREIGUEZ, T. 2000. The relative importance of edaphic factors on the distribution of some terrestrial gastropod species: autecological and synecological approaches. *Acta Zoologica Scientiarum Hungaricae*, **46**: 265–274.

HORSÁK, M. 2005. Molluscs. In: *Ecology and palaeoecology of spring fens of the west Carpathians* (A. Poulíčkova, M. Hájek & K. Rybníček, eds), pp. 197–208. Olomouc, Czech Republic.

HORSÁK, M. 2006. Mollusc community patterns and species response curves along a mineral richness gradient: a case study of fens. *Journal of Biogeography*, **33**: 98–107.

HORSÁK, M. & HÁJEK, M. 2003. Composition and species richness of molluscan communities in relation to vegetation and water chemistry in the western Carpathian spring fens: the poor-rich gradient. *Journal of Molluscan Studies*, **69**: 349–357.

HUBRICHT, L. 1985. The distributions of the native land mollusks of the eastern United States. *Fieldiana*, new series, **24**: 1–191.

KARLIN, E.J. 1961. Ecological relationships between vegetation and the distribution of land snails in Montana, Colorado and New Mexico. *American Midland Naturalist*, **65**: 60–66.

KERNEY, M.P. & CAMERON, R.A.D. 1979. *Field guide to the land snails of the British Isles and northwestern Europe*. Collins Press, London.

MÄND, R., EHLVEST, A. & KRISTAJA, P. 2001. Land snails in an afforested oil-shale mining area. *Proceedings of the Estonian Academy of Science: Biology and Ecology*, **50**: 37–41.

MINCHIN, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, **69**: 89–108.

MINCHIN, P.R. 1990. *DECODA software*. Australian National University, Canberra, Australia.

NATION, T.H. 2007. The influence of flowering dogwood (*Cornus florida*) on land snail diversity in a southern mixed hardwood forest. *American Midland Naturalist*, **157**: 137–148.

NATURESERVE. 2009. *NatureServe Explorer: an online encyclopedia of life*. Version 7.0. NatureServe, Arlington, Virginia. http://www.natureserve.org/explorer. (accessed 5 September 2009).

NEKOLA, J.C. 1999. Terrestrial gastropod richness of carbonate cliff and associated habitats in the Great Lakes region of North America. *Malacologia*, **41**: 231–252.

NEKOLA, J.C. 2003. Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. *Diversity and Distribution*, **9**: 55–71.

NEKOLA, J.C. 2004. Terrestrial gastropod fauna of northeastern Wisconsin and the southern Upper Peninsula of Michigan. *American Malacological Bulletin*, **18**: 21–44.

NEKOLA, J.C. & COLES, B.F. In press. Pupillid land snails of eastern North America. *American Malacological Bulletin*.

NEKOLA, J.C., COLES, B.F. & BERGTHORSSON, U. Evolutionary pattern and process in the *Vertigo gouldii* group of minute North American land snails. *Molecular Phylogenetics and Evolution*, **53**: 1010–1024.

NEKOLA, J.C., ŠIZLING, A.L., BOYER, A.G. & STORCH, D. 2008. Artifactions in the log-transformation of species abundance distributions. *Folia Geobotanica*, **43**: 259–468.

NEKOLA, J.C. & SMITH, T.A. 1999. Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. *Malacologia*, **41**: 253–269.

OGGIER, P., ZSCHOKKE, S. & BAUR, B. 1998. A comparison of three methods for assessing the gastropod community in dry grasslands. *Pedobiologia*, **42**: 348–357.

OUTEIRO, A., AGÜERA, D. & PAREJO, C. 1993. Use of ecological profiles and canonical correspondence analysis in a study of the relationship of terrestrial gastropods and environmental factors. *Journal of Conchology*, **34**: 365–375.

PILSBRY, H.A. 1948. *Land Mollusca of North America (north of Mexico)*. Academy of Natural Sciences of Philadelphia Monograph vol. 1(1) and 2(2).

POKRYSZKO, B.M. & CAMERON, R.A.D. 2005. Geographic variation in the composition and richness of forest land snail faunas in northern Europe. *Records of the Western Australian Museum*, Supplement, **68**: 115–132.

RICHARDSON, C.J. 1983. Pocosins: vanishing wastelands or valuable wetlands? *Bioscience*, **33**: 626–633.

SCHILTHUIZEN, M. 2004. Land snail conservation in Borneo: limestone outcrops act as arks. *Journal of Conchology, Special Publication*, **3**: 149–154.

SCHILTHUIZEN, M. & RUTJES, H.A. 2001. Land-snail diversity in a square kilometre of tropical forest in Sabah, Malaysian Borneo. *Journal of Molluscan Studies*, **67**: 417–423.

ŠTAMOL, V. 1991. Coenological study of snails (Mollusca: Gastropoda) in forest phytocoenoses of Medvednica mountain (NW Croatia, Yugoslavia). *Vegetatio*, **95**: 33–54.

STANISIC, J. 1997. An area of exceptional land snail diversity: the Macleay Valley, north-eastern New South Wales. *Memoirs of the Museum of Victoria*, **56**: 441–448.

TATTERSFIELD, P. 1990. Terrestrial mollusc faunas from some south Pennine woodlands. *Journal of Conchology*, **33**: 355–374.

TURGEON, D.D., QUINN, J.F., JR, BOGAN, A.E., COAN, E.V., HOCHBERG, F.G., LYONS, W.G., MIKKELSEN, P., NEVES, R.J., ROPER, C.F.E., ROSENBERG, G., ROTH, B., SCHELTEMA, A., THOMPSON, F.G., VECCHIONE, M. & WILLIAMS, J.D. 1998. *Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks*. Edn. 2. American Fisheries Society Special Publication vol. 26. Bethesda, Maryland.

VALOVIRTA, I. 1968. Land molluscs in relation to acidity on hyperite hills in central Finland. *Annales Zoologici Fennici*, **5**: 245–253.

VITT, D.H. & CHEE, W.L. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio*, **89**: 87–106.

WALDÉN, H.W. 1981. Communities and diversity of land molluscs in Scandinavian woodlands. I. high diversity communities in taluses and boulder slopes in SW Sweden. *Journal of Conchology*, **30**: 351–372.

WÄREBORN, I. 1970. Environmental factors influencing the distribution of land molluscs of an oligotrophic area in southern Sweden. *Oikos*, **21**: 285–291.

WARING, R.H. & SCHLESINGER, W.H. 1985. *Forest ecosystems: concepts and management*. Academic Press, New York.

WHITTAKER, R.H. 1975. *Communities and ecosystems*. MacMillan Publishing Co., New York.

WOODWELL, G.M. 1958. Factors controlling growth of Pond Pine seedlings in organic soils of the Carolinas. *Ecological Monographs*, **28**: 219–236.

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Vascular plant compositional gradients within and between Iowa fens

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Abstract

Question: What is the nature and relative importance of compositional gradients within- and between fens?

Location: Iowa, USA.

Methods: 506 0.5 m × 0.5 m quadrats were sampled from 31 fens across a 550 km extent. Presence/absence of all vascular plant taxa, plus the non-vascular genera *Sphagnum* and *Chara*, and values for 24 environmental variables were noted. Global Non-Metric Multidimensional Scaling and Monte Carlo tests were used to describe compositional variation and identify significant environmental co-variables. Model-based cluster analysis was used to identify the optimal number of groups supported by the data, while *k*-means clustering was used to assign each quadrat to a group. The number of occurrences (and frequency) of each species within each group was calculated. Two-dimensional 95% Gaussian confidence intervals, ANOVA, correlation coefficient homogeneity tests, log-linear modelling, and Fisher's exact tests were used to document patterns of compositional change.

Results: Two stable axes of variation were identified: the first being most closely correlated with soil pH, Mg, Ca, P, S, vegetation height, surface and –10 cm soil temperature, site area, perimeter, perimeter/area ratio, growing season, and air temperature, with the second being most correlated to soil moisture, N, disturbance level, % organic matter, hummock height, N-S coordinate, and precipitation. Individual sites harboured between 20-47% of total compositional variation, with 28% of Axis 1 and 55% of Axis 2 scores being contained within-sites. Five compositional regions were identified that differed in the proportion of calciphile and hydrophile species. Compositional groups differed significantly between geologic types.

Conclusions: While the principal axis of variation (corresponding to the rich-poor fen gradient) is present largely between sites, the second axis (corresponding to water level) is largely repeated within sites. Documentation and protection of vegetation patterns and species diversity within Iowa fens will thus require consideration of multiple sites across the landscape.

Keywords: Cluster analysis; Community ecology; Gradient analysis; Landscape pattern; Multidimensional scaling; North America; Peatland.

Nomenclature: Nekola (1994).

Introduction

To understand the full range of environmental factors influencing peatland vegetation, simultaneous documentation of both within- and between-site gradients must take place. Unfortunately, previous investigations have focused either on numerous (> 80) quadrats from individual sites (van der Valk 1975; Bernard et al. 1983; Stewart 1987; Singsaas 1989; Gerdol 1990; Glaser et al. 1990; Magnússon & Magnússon 1990; Mooney & O'Connell 1990; Wassen et al. 1990a; Stoynoff 1993; McCormac & Schneider 1994; Fojt & Harding 1995; Bowles et al. 1996; Choesin & Boerner 2000; Gunnarsson et al. 2000; Choesin & Boerner 2002; Southall et al. 2003), or on few (< 10) quadrats sampled from multiple sites in the landscape (Charman 1993; Johnson & Leopold 1994; Motzkin 1994; Slack 1994; Bergamini et al. 2001; Vanderpuye et al. 2002; Stammel et al. 2003). The following study considers the relative importance of compositional gradients within- and between-site fens based on moderate numbers (10-30) of quadrats sampled from multiple sites (31) across Iowa. These data will be used to address the following questions: 1. What are the major compositional gradients? 2. What environmental factors underlie these trends? 3. How much compositional variation is captured within vs. between sites?

Methods

Study region

Fens are peatland habitats with saturated (not inundated) soils whose source water has been enriched in nutrients by passage through the ground (Sjörs 1952). Fewer than 200 fens remain in the northeastern half of Iowa out of an original ca. 2400 pre-settlement sites (Nekola 1994). Extant examples are most common on the Iowan Erosional Surface and the northwestern margin of the Des Moines Lobe (Fig. 1). The Iowan Erosional Surface was formed through intense periglacial erosion during the Wisconsinan, while the Des Moines Lobe was formed ca. 14000-12000 yr ago during a final surge of Wisconsinan ice sheet following the onset of climatic warming (Prior 1991).

These fens can be broadly classified into five geological types, depending upon aquifer type (Thompson et al. 1992): glacial till, bedrock, eolian sand, fluvial sand, and former lake basins (pothole or oxbow lakes). While statistical differences exist in peat chemistry between these groups (e.g. percent organic matter, pH, P, Ca, and Mg), no more than 35% of observed variance is accounted for by them (Nekola 1994).

Study sites

In total 31 fens from 23 counties across a 550 km extent (Fig. 1) were selected for analysis based on their natural integrity and geographical location. Investigation was limited to high-quality, undisturbed sites that maximized geographic spread across the landscape. While an attempt was made to maintain at least 40 km separation, some very high-quality sites were selected even though they were more closely positioned. Selected fens represent all five major geologic groups (22 till, 4 basin, 2 bedrock, 2 eolian, and 1 fluvial) and range in size from 0.1 - 28.8 ha (Table 1).

Field methods

A total of 506 0.5 m × 0.5 m quadrats were sampled in June and July, 1989. While this quadrat size is smaller than some previous North American investigations (i.e. Motzkin 1994), it is consistent with many other peatland vegetation studies (e.g. Bellamy 1967; Singaas 1989; Magnússon & Magnússon 1990; Stoynoff 1993; Bowles et al. 1996). This grain size is adequate for ordination analysis as it captures an average of 12 co-occurring species, or ca. 15% of an individual site flora.

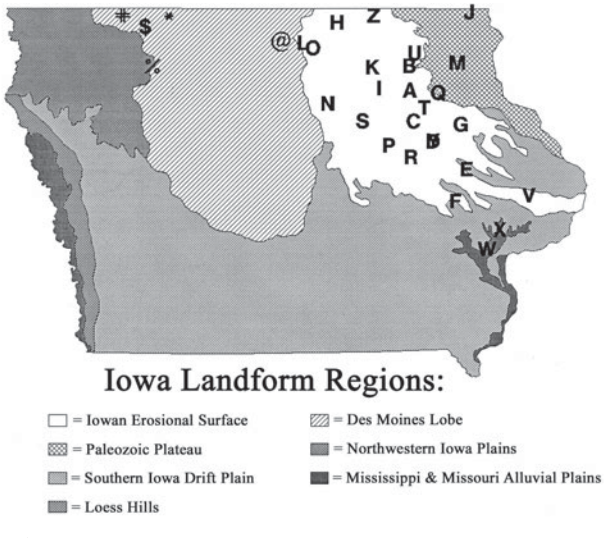

Fig. 1. Landform regions of Iowa with location of sampled fen sites. Site letter codes correspond to those in Table 1.

Sites were sampled at two intensity levels. One group (10 sites) was more intensively sampled at 30 quadrats per site. An effort was made to geographically stratify these across the landscape. At Mt. Auburn fen, only 26 quadrats were sampled due to weather conditions; 10 quadrats per site were recorded from the second group (21 sites). Only 7 and 5 quadrats were recorded from Rochester South and Rowley North, respectively, due to weather conditions.

Each site was divided into five concentric zones of equal width positioned from the centre to edge. While zone widths differed between sites, their moisture levels were similar. Stratified-random sampling was used to position quadrats within each zone. When this sampling protocol missed major vegetation types or rare species, additional quadrats were non-randomly placed to capture them. Such subjective placement was limited to less than 10 quadrats (< 2% of total).

All vascular plant species, plus *Sphagnum* and *Chara* spp., were noted from each quadrat. Surface and subsurface (–10 cm) soil temperature, vegetation height, and maximum hummock height were also recorded. Level of disturbance was noted using a subjective score ranging from 1 (least) to 3 (most). Site locations, perimeters and areas were calculated through digitization of USDA Soil Conservation Service county soil maps.

Soil chemistry

A 100-cm^3 soil sample was taken from the centre of each quadrat. These were transported in water-tight plastic bags and not allowed to come in contact with sulfur-rich paper products. Samples were either oven dried within eight hours of collection, or frozen for later drying. Following the methodologies of Dahnke (1988), percent organic matter, pH, NO_3-N, extractable P, exchangeable K, extractable SO_4-S, exchangeable Ca, and exchangeable Mg were determined by Minnesota Valley Testing Laboratory of Nevada, Iowa.

The percent water mass present in each wet sample was determined. However, because the water holding capacity of soils is positively correlated with organic matter content (Hudson 1994), many waterlogged but mineral-rich samples had lower water mass percentages than seemingly drier samples with higher organic matter levels. To help correct for this, soil moisture (*SM*) was calculated for each sample based on the following:

$$SM = W * (1 - O) \quad (1)$$

Table 1. List and locations for sampled fen sites, including their size, geologic type, sampled quadrats, and percent compositional overlap with all other sites.

County	Site name	Location	Size (ha)	Geologic type	Quadrats sampled	% overlap	Site code
Allamakee County	Clear Creek 1	91° 25' 28" W., 43° 27' 30" N.	1.3	Fluvial	11	80.4	J
Benton County	Mt. Auburn	92° 5' 59" W., 42° 14' 50" N.	28.8	Till	26	22.3	R
Black Hawk County	Hammond Road	92° 20' 36" W., 42° 20' 48" N.	1.6	Till	10	23.8	P
Bremer County	Brayton-Horsley	92° 6' 27" W., 42° 48' 35" N.	4.7	Till	30	35.7	A
	Bushing	92° 27' 1" W., 42° 49' 48" N.	2.0	Till	12	43.5	I
Buchanan County	Cutshall Access	92° 4' 17" W, 42° 32' 47" N.	4.0	Basin	10	46.6	C
	Rowley	91° 51' 7" W., 42° 22' 27" N.	2.2	Till	30	22.9	D
	Rowley North	91° 51' 5" W., 42° 22' 36" N.	0.3	Till	5	70.1	Y
Cedar County	Rochester South	91° 8' 12" W., 41° 36' 59" N.	0.3	Eolian	7	23.4	X
Cerro Gordo County	Buffalo Slough	93° 11' 54" W., 43° 10' 36" N.	12.6	Basin	30	36.6	O
	Neuhring	93° 18' 39" W., 43° 13' 3" N.	1.0	Till	10	45.8	L
Chickasaw County	Chickasaw 1	92° 31' 3" W., 43° 0' 33" N.	18.4	Till	10	65.9	K
	Kleiss	92° 6' 20" W., 43° 0' 58" N.	1.6	Till	10	28.8	B
Clay County	Gillett	95° 0' 52" W., 43° 0' 53" N.	3.1	Till	10	48.6	%
Clayton County	Postville	91° 34' 0" W., 43° 2' 3" N.	37.5	Till	10	84.7	M
Clinton County	Toronto 2	90° 48' 9" W., 41° 53' 49" N.	1.3	Eolian	30	87.0	V
Delaware County	Hawker	91° 32' 38" W., 42° 30' 47" N.	7.3	Till	30	45.6	G
Dickinson County	Silver Lake	95° 21' 55" W., 43° 26' 16" N.	2.6	Till	12	84.4	#
	Lower Gar Lake	95° 6' 34" W., 43° 20' 48" N.	3.3	Till	10	61.7	$
Emmet County	O'Brien	94° 50' 36" W., 43° 26' 16" N.	0.1	Till	10	31.5	*
Fayette County	Hunter Creek	91° 56' 50" W., 42° 39' 32" N.	0.9	Till	10	18.3	T
	Smithfield Township Hall	91° 47' 18" W., 42° 46' 57" N.	3.5	Till	30	21.2	Q
Franklin County	Maynes Creek	93° 1' 49" W., 42° 42' 24" N.	1.0	Bedrock	10	35.1	N
Grundy County	New Hartford	92° 38' 22" W., 42° 33' 16" N.	1.4	Till	10	34.7	S
Howard County	Staff Creek	92° 30' 34" W., 43° 26' 40" N.	2.4	Till	13	54.4	Z
Linn County	Matus	91° 29' 4" W., 42° 7' 57" N.	18.5	Till	30	55.9	E
	Western College	91° 37' 2" W., 41° 51' 56" N.	0.6	Till	10	31.9	F
Mitchell County	St. Ansgar	92° 55' 27" W, 43° 23' 21" N.	2.0	Bedrock	30	55.2	H
Muscatine County	Nichols	91° 16' 54" W., 41° 27' 24" N.	49.3	Basin	30	17.9	W
Palo Alto County	Dead Man's Lake	93° 33' 59" W., 43° 14' 57" N.	1.2	Basin	10	11.3	@
Winneshiek County	Jackson Juncton	92° 2' 52" W., 43° 7' 15" N.	1.4	Till	10	46.0	U

where W = percent water mass of wet soil sample; and O = percent organic mass of dry soil sample. When soil organic content is low SM remains close in value to the observed percent water mass. However, as soil organic matter content increases, SM will fall accordingly. Meaningful comparisons between sites were made possible by severe drought conditions that allowed differences to reflect differential groundwater seepage rates as opposed to timing of rainfall events.

Water chemistry was not measured for two principal reasons: First, as standing water was not present in all quadrats it could have been sampled only through the digging of pits that will cause significant alterations to water chemistry (Glaser et al. 1990). Second, soil chemistry is a much better correlate for vascular plant composition (Sjörs & Gunnarsson 2002) while water chemistry principally impacts bryophytes (Vitt & Chee 1990).

Climate analysis

Principal Components Analysis in conjunction with a varimax rotation was conducted on 30-yr mean values for 22 climate variables measured from 96 Iowa recording stations. Four major gradients, accounting for over 95% of the total climate variation, were identified: air temperature (correlated with Average Yearly, Summer, Fall, and Spring Temperatures, Heat Stress Days/Year, Heat Stress Degrees/Year, Heating Degree Days, Cooling Degree Days, Growing Degree Days), non-summer precipitation (correlated with Average Yearly, Winter, Spring and Fall Precipitation, Average Winter Temperature, Maximum 24-hr Precipitation), growing season (correlated with 32°, 30°, 28°, 26°, and 24° Growing Seasons, number of Freezing Days/Year), and average summer precipitation (Nekola 1994). PCA scores along each of these axes were determined for each recording station, with punctual kriging (Burgess & Webster 1980) being used to estimate site-specific values along each axis based upon the nearest 20 stations.

Statistical procedures

Ordination

Species lists from each quadrat were subjected to global non-metric multidimensional scaling (NMDS) using the DECODA software program (Minchin 1990).

NMDS was used as it is the most robust form of ordination for detection of ecological pattern (Minchin 1987). Using all species, a dissimilarity matrix was calculated using the Kulczynski index (Faith et al. 1987) for all pairwise combinations of sites. NMDS in one through four dimensions was then performed with 200 maximum iterations, a stress ratio stopping value of 0.999900, and a small stress stopping value of 0.010000. Output was scaled in half-change units.

Because a given NMDS run may locate a local (rather than the global) stress minimum, multiple NMDS runs starting from different initial random points must be compared to determine solution stability (Minchin 1987). For this ordination, DECODA used a total of 20 random starting configurations. Solutions in each of the four dimensions were compared using Procrustes transformations to identify those that were statistically distinct. The number of unique solutions, and runs that fell into each was then calculated across each of the four dimensions. The modal solution out of twenty runs was identified and was considered stable when it was achieved in at least 25% of starts.

Identification of compositional groups

Clustering was performed on the selected ordination output rather than raw data as the former are less susceptible to sampling or other inadvertent errors (Equihua 1990). Model-based cluster analysis (Banfield & Raftery 1992) was used to identify the number of groups most supported by the data. A sum-of-squares model was employed as it generates spherical clusters that will be of maximal compositional similarity. The approximate weight of evidence for k clusters (AWE_k) was calculated for $k = 1$ to $n–1$ clusters (where n = the total number of ordinated sites) via the *S*+ MCLUST algorithm (Anon. 1995); k-means iterative relocation (Hartigan 1975) was then used to assign each site to a cluster as it is also based on sum-of-squares criteria.

Ordination interpretation

The number of occurrences (and frequency) of each species within each k-means cluster was calculated. The 20 most frequent taxa, and rare taxa (see Nekola 1994) reaching modal frequency within each cluster, were then determined. Two-dimensional 95% Gaussian confidence intervals (Sokal & Rohlf 1981) were calculated for each site and used to estimate compositional overlap between sites. Quadrats from other sites were considered statistically similar in composition when they fell within a given site's 95% confidence ellipse. Quantification of Axis 1 and Axis 2 stand score variation between sites was accomplished via ANOVA and represented using box plots. The significance of differences in the variation accounted for between sites was estimated using a correlation coefficient homogeneity test (Sokal & Rohlf 1981).

The maximum correlation vectors for all environmental variables were calculated by DECODA and their significance estimated through Monte-Carlo tests. Variables were assigned into one of two groups: those that varied within sites (pH, NO_3-N, P, K, SO_4-S, Ca, Mg, % organic matter, vegetation height, hummock height, surface soil temperature, –10 cm soil temperature, disturbance level, soil moisture), and those that only varied between sites (N-S Coordinate, E-W Coordinate, Perimeter, Area, Perimeter/Area Ratio, Non-Summer Precipitation, Summer Precipitation, Growing Season, Air Temperature).

Significance of differences in frequency of each k-means cluster between the five geologic fen types was estimated via log-linear modelling. As predicted values were sparse (< 5) in more than one-fifth of cells (Zar 1984), Fisher's Exact test was used to identify those compositional clusters significantly favoured within each geologic group. Because the total number of quadrats sampled from glacial till sites exceeded 200, log-linear modelling was used to estimate significance for this group. The significance threshold for these analyses were adjusted to $p = 0.01$ using a Bonferroni correction.

Results

Site ordination

A total of 217 taxa (including *Sphagnum* and *Chara*) were identified (App. 1). NMDS demonstrated that in one dimension the most stable solution (minimum stress configuration = 0.3607) was achieved in 14 starts; in two dimensions the most stable solution (minimum stress configuration = 0.2467) was achieved in five starts; in three dimensions the most stable solution (minimum stress configuration = 0.1923) was achieved in two starts; and in four dimensions all starts provided different solutions (minimum stress configuration = 0.1594). The most stable two-dimensional solution was chosen for further analysis because it possessed a relatively low stress level while also being achieved in at least 25% of starts.

Visual observation of this solution demonstrated essentially constant variation across both axes (Fig. 2). One major outlier (from Silver Lake Fen and the lone quadrat located in a hypercalcarous water track) is present approximately 0.75 axis units to the right of the general distribution. This microhabitat is quite rare in Iowa, being limited to this and two adjacent sites.

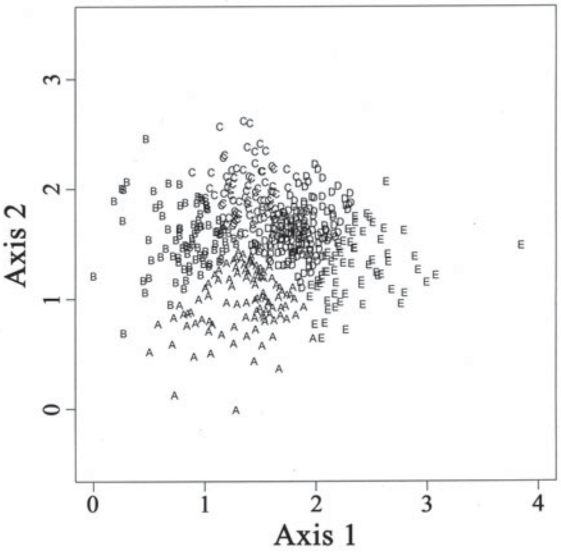

Fig. 2. NMDS ordination of 506 Iowa fen quadrats. Letters correspond to the compositional group that each quadrat was assigned via *k*-means clustering.

Compositional variation within and between sites

Considerable compositional overlap was noted between sites, ranging from 11.3% of all other quadrats (Dead Man's Lake) to 87% (Toronto 2), with a median of 43.5% (Table 1). These values are skewed slightly to the right, with the bulk ranging from 20 - 47%. ANOVA identified significant ($p < 0.0005$) partitioning of both Axis 1 and Axis 2 scores between sites. However, the amount of variance explained significantly ($p < 0.000005$) varies from 72% for Axis 1 to 45% for Axis 2 (Fig. 3).

Identification and description of compositional clusters

The maximum AWE_k score (2426.9) was achieved at 73 compositional clusters. As this represents too many groups for generalization of compositional trends, AWE_k scores from $k = 1$ to 15 were calculated, along with the percent increase in AWE_k from $k–1$ to k clusters. After six clusters, the percent increase in AWE_k fell below 10%, and decreased steadily to the 2.5% range by cluster 15. However, as the sixth k-means cluster contained only a single outlying quadrat (the Silver Lake fen water track), it was considered a statistical artifact with low inferential power. Each quadrat was thus assigned to one of five clusters.

Cluster A (100 quadrats) is located on the lower left of the ordination diagram (Fig. 2) and is dominated by plants such as *Campanula aparinoides, Impatiens capensis, Aster puniceus, Carex prairea*, and *Lycopus americanus* that demand high moisture levels but can tolerate non-calcareous conditions (Table 2). In this cluster 14 rare Iowa fen species reach their modal frequencies (Table 3) including *Aster junciformis, Berula erecta, Galium labradoricum, Menyanthes trifoliata, Salix pedicellaris* and *Solidago uliginosa*.

Cluster B (88 quadrats) is located in the upper left of the ordination diagram (Fig. 2) and is dominated by two ferns (*Thelypteris palustris* and *Onoclea sensibilis*) and other species such as *Polygonatum sagittatum* and *Triadenum fraseri* that can tolerate somewhat drier, non-calcareous conditions (Table 2). Four rare Iowa fen species/genera reach modal frequencies in this cluster (Table 3) including *Drosera rotundifolia, Potentilla palustris, Rubus pubescens, Sphagnum* spp. and *Triadenum fraseri*.

Cluster C (85 quadrats) is located in the upper centre of the ordination diagram (Fig. 2) and is dominated by typical sedge meadow species such as *Carex stricta, Aster puniceus, Thelypteris palustris, Pycnanthemum virginianum*, and *Solidago altissima* that require rich, moderately wet soils (Table 2). Only three rare Iowa fen plants (*Cypripedium parviflorum, Ophioglossum vulgatum, Viola pallens*) reach modal frequencies in this cluster (Table 3).

Cluster D (169 quadrats) is located to the lower right of Cluster C (Fig. 2). This cluster demarcates the most commonly encountered vegetation of Iowa fen mats, and is dominated by *Aster puniceus, Lycopus americanus, Muhlenbergia glomerata, Viola nephrophylla* and *Lysimachia quadriflora* (Table 2). *Carex* species are present but do not dominate, with the flora representing a wide mix of relatively low-statured forbs and graminoids. Nine rare Iowa fen plants reach modal frequencies in this cluster (Table 3) including such characteristic Midwestern USA fen taxa as *Betula pumila, Carex prairea, Cypripedium candidum, Salix candida, Solidago riddellii* and *Valeriana edulis*.

Cluster E (64 quadrats) is located in the centre-right of the ordination diagram (Fig. 2) and is dominated by species requiring both relatively high moisture levels and calcareous conditions such as *Muhlenbergia glomerata, Parnassia glauca, Eleocharis elliptica, Rhynchospora capillacea,* and *Lobelia kalmii* (Table 2). In cluster E 24 rare Iowa fen plants reach their modal frequencies in this cluster (Table 3) including *Carex sterilis, Eleocharis pauciflora, Juncus alpinus, Platanthera hyperborea, Rhynchospora capillacea, Scleria triglomerata, Spiranthes romanzoffiana, Triglochin maritimum, T. palustre* and *Utricularia minor*.

Table 2. Most frequent taxa (*n* = 20 or 21) in each of the five compositional clusters.

Cluster A (*n* = 100 quadrats)		Cluster B (*n* = 88)		Cluster C (*n* = 85)		Cluster D (*n* = 169)		Cluster E (*n* = 64)	
Species	Freq.	Species	Freq.	Species	Freq.	Species	Freq.	Species	Freq.
Campanula aparinoides	64.00%	*Thelypteris palustris*	93.18%	*Carex stricta*	82.35%	*Aster puniceus*	90.30%	*Muhlenbergia glomerata*	87.50%
Impatiens capensis	64.00%	*Impatiens capensis*	63.64%	*Aster puniceus*	82.35%	*Lycopus americanus*	88.48%	*Viola nephrophylla*	54.69%
Aster puniceus	61.00%	*Polygonum sagittatum*	61.36%	*Thelypteris palustris*	80.00%	*Muhlenbergia glomerata*	81.82%	*Lycopus americanus*	51.56%
Carex prairea	59.00%	*Aster puniceus*	50.00%	*Pycnanthemum virginianum*	51.77%	*Viola nephrophylla*	78.79%	*Parnassia glauca*	48.44%
Lycopus americanus	48.00%	*Onoclea sensibilis*	48.86%	*Solidago altissima*	50.59%	*Lysimachia quadriflora*	72.73%	*Carex prairea*	45.31%
Carex stricta	41.00%	*Triadenum fraseri*	44.32%	*Lycopus americanus*	45.88%	*Carex prairea*	66.67%	*Eleocharis elliptica*	42.19%
Pilea fontana	40.00%	*Carex stricta*	43.18%	*Campanula aparinoides*	41.18%	*Carex stricta*	63.64%	*Lysimachia quadriflora*	39.06%
Muhlenbergia glomerata	39.00%	*Campanula aparinoides*	42.05%	*Aster umbellatus*	36.47%	*Pycnanthemum virginianum*	60.61%	*Scirpus validus*	35.94%
Caltha palustris	34.00%	*Eupatorium maculatum*	31.82%	*Viola nephrophylla*	35.29%	*Carex interior*	44.24%	*Carex interior*	32.81%
Eupatorium maculatum	32.00%	*Typha latifolia*	31.82%	*Helianthus grosserratus*	34.12%	*Campanula aparinoides*	40.00%	*Rhynchospora capillacea*	32.81%
Lysimachia thyrsiflora	25.00%	*Lycopus americanus*	26.14%	*Onoclea sensibilis*	29.41%	*Thelypteris palustris*	38.18%	*Eupatorium perfoliatum*	31.25%
Cardamine bulbosa	24.00%	*Scutellaria galericulata*	23.86%	*Muhlenbergia glomerata*	23.53%	*Eleocharis elliptica*	35.15%	*Lobelia kalmii*	29.69%
Equisetum fluviatile	24.00%	*Pilea fontana*	21.59%	*Polygonum sagittatum*	22.35%	*Eupatorium maculatum*	34.55%	*Eupatorium maculatum*	28.12%
Viola nephrophylla	23.00%	*Boehmeria cylindrica*	21.59%	*Eupatorium maculatum*	18.82%	*Lythrum alatum*	30.91%	*Carex hystericina*	28.12%
Galium labradoricum	21.00%	Immature *Muhlenbergia*	20.45%	*Fragaria virginica*	17.65%	*Salix candida*	27.88%	*Aster umbellatus*	26.56%
Thelypteris palustris	19.00%	*Carex lacustris*	18.18%	*Geum aleppicum*	17.65%	*Lobelia siphilitica*	26.06%	*Carex stricta*	26.56%
Epilobium leptophyllum	19.00%	*Aster umbellatus*	15.91%	*Polemonium reptans*	16.47%	*Sphenopholis intermedia*	24.24%	*Juncus nodosus*	26.56%
Leerzia oryzoides	19.00%	*Carex lanuginosa*	12.50%	*Poa pratensis*	15.29%	*Aster umbellatus*	20.61%	*Glyceria striata*	25.00%
Typha latifolia	18.00%	*Bidens coronata*	12.50%	*Saxifraga pensylvanica*	15.29%	*Caltha palustris*	19.39%	*Scirpus americana*	23.44%
Sphenopholis intermedia	17.00%	*Leerzia oryzoides*	12.50%	*Carex interior*	14.12%	*Parnassia glauca*	19.39%	*Equisetum arvense*	20.31%
Polygonum sagittatum	17.00%			*Caltha palustris*	14.12%			*Scleria verticillata*	20.31%

Table 3. Rare taxa (as listed in Nekola 1994) reaching modal frequencies in each compositional cluster.

Cluster A
Angelica atropurpurea
Aster junciformis
Berula erecta
Carex rostrata
Cirsium muticum
Eleocharis smallii
Equisetum fluviatile
Galium labradoricum
Menyanthes trifoliata
Mimulus glabratus
Rumex orbiculatus
Salix pedicellaris
Solidago uliginosa

Cluster B
Drosera rotundifolia
Potentilla palustris
Rubus pubescens
Sphagnum spp.
Triadenum fraseri

Cluster C
Cypripedium parviflorum
Ophioglossum vulgatum
Viola pallens

Cluster D
Betula pumila
Bromus ciliatus
Carex prairea
Cypripedium candidum
Salix candida
Salix × *rubella*
Salix × *clarkei*
Solidago riddellii
Valeriana edulis

Cluster E
Carex granularis
Carex sartwellii
Carex tetanica
Carex sterilis
Chara spp.
Eleocharis elliptica
Eleocharis pauciflora
Eriophorum angustifolium
Gentiana crinita
Gentiana procera
Gerardia paupercula
Juncus alpinus
Juncus balticus
Liparis loeselii
Lobelia kalmii
Muhlenbergia glomerata
Parnassia glauca
Platanthera hyperborea
Rhynchospora capillacea
Scleria verticillata
Spiranthes romanzoffiana
Triglochin maritimum
Triglochin palustre
Utricularia minor

Analysis of environmental co-variables

All environmental variables except K ($p = 0.060$) and Average Summer Precipitation ($p = 0.067$) demonstrated significant correlation with the ordination diagram. Maximum r^2 values for significant variables ranged from 0.0246-0.3204. For those varying within sites, pH, -10 cm soil temperature, Mg, Ca, surface soil temperature, and S were most positively correlated with Axis 1 scores, while vegetation height and P were negatively correlated (Fig. 4). N, disturbance level, % organic matter, and hummock height were positively correlated with Axis 2 scores, while soil moisture was negatively correlated. Of the factors varying only between sites, site perimeter/area ratio was positively correlated with Axis 1 scores, while site area, air temperature, and site perimeter were negatively correlated. E-W coordinate location was positively correlated with Axis 1 but negatively correlated with Axis 2 scores, while precipitation, growing season,

Table 4. Contingency table analysis showing the number of quadrats within each of the five compositional clusters represented in each of the geologic fen types. Log-linear test statistic represents significance across entire table.

Cluster	Geologic fen type				
	Till	Bedrock	Fluvial	Basin	Eolian
A	41	10	4	37	8
B	40	0	0	37	11
C	62	2	0	5	16
D	144	21	2	1	1
E	51	7	5	0	1
Significance within each geologic type					
	< 0.00005	0.0017	0.2552	< 0.00005	0.0087

Log-linear model test statistic = 221.03; df = 16; $p < 0.0000005$.

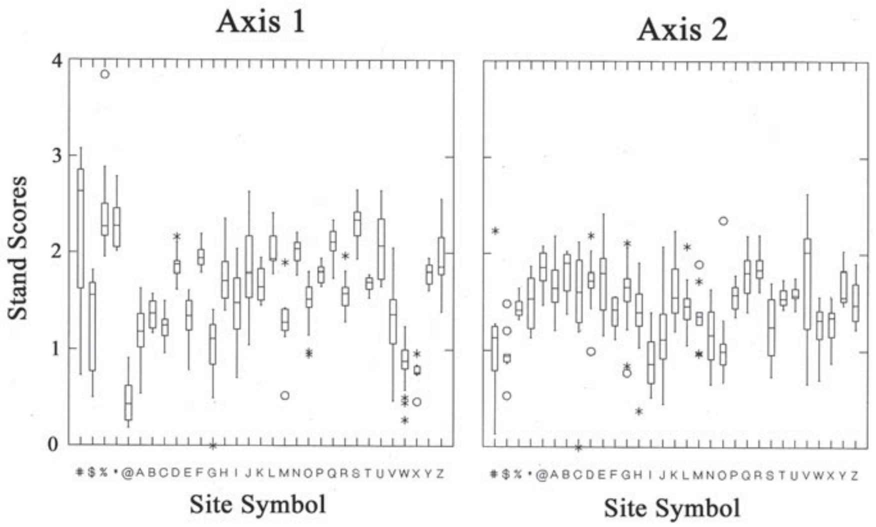

Fig. 3. Box plot of variation within each site along NMDS Axes 1 and 2. Site letter codes correspond to those in Table 1.

and N-S coordinate location were negatively correlated with Axis 1 but positively correlated with Axis 2.

The frequency of the five compositional clusters was found to significantly ($p < 0.0000005$) vary between the five geologic groups (Table 4). Glacial till sites were over-represented in Cluster D and under-represented in Clusters A and B ($p < 0.00005$). Bedrock outcrop sites were over-represented in Cluster D and underrepresented in Clusters B and C ($p = 0.0017$). Basin sites were over-represented in Clusters A and B and underrepresented in Clusters C, D, and E ($p < 0.00005$). Eolian Sand sites were over-represented in Clusters B and C and underrepresented in Clusters D and E ($p = 0.0087$). No significant patterns ($p = 0.2552$) were noted from the lone Fluvial Sand site sampled.

Discussion

Major compositional gradients

These analyses demonstrate two strong compositional gradients (3 and 2 half-change units) within Iowa fens. The principal axis varies from vegetation supporting few to many calciphiles, while the second axis varies from vegetation supporting few to many hydrophiles. The compositional clusters created to help interpret these patterns are not separated in ordination space, with quadrats from different clusters often being more similar to each other than they are to other quadrats within their own group.

The variation along Axis 1 is consistent with the

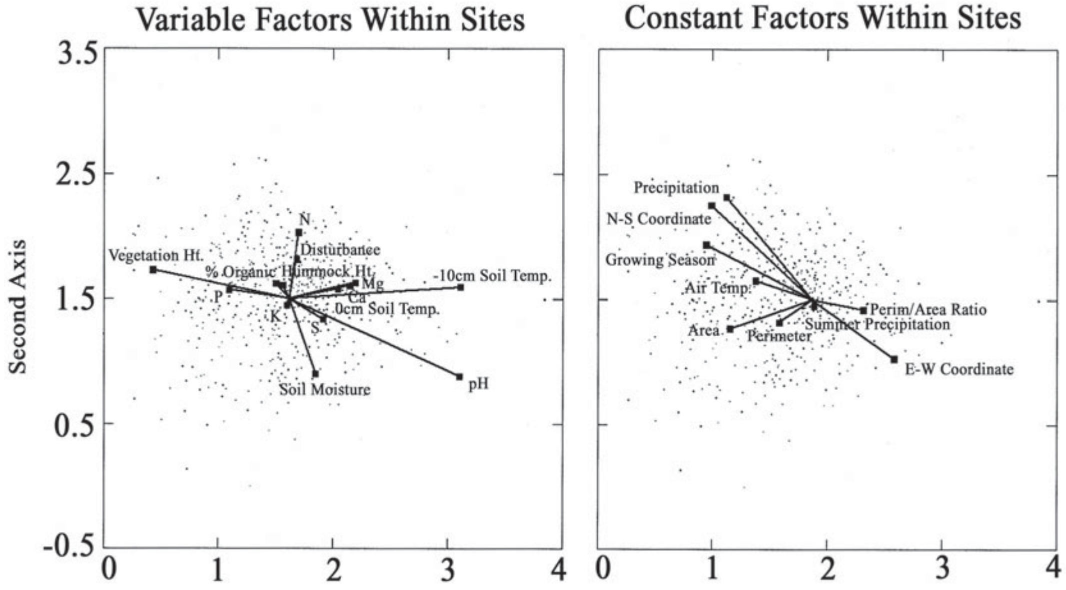

Fig. 4. Environmental variable biplots for the ordination diagram.

rich-poor fen gradient noted in most peatland landscapes, including Estonia (Masing 1982), Poland (Wassen et al. 1990a), the eastern Carpathians (Hájek 2002), Switzerland (Bergamini 2001), the southern Alps (Gerdol 1990), northwestern Europe (Sjörs 1952; Økland 1990; Sjörs & Gunnarsson 2002), Scotland (Charman 1993), boreal Canada (Vitt & Chee 1990), the northern USA (Glaser 1987; Glaser et al. 1981), northeastern USA (Motzkin 1994), and New Zealand (McQueen & Wilson 2000). Similarly, the wet-mesic gradient demonstrated along the Axis 2 has been previously documented from Illinois (Bowles et al. 1996), northern Minnesota (Glaser et al. 1990), Ohio (Stewart 1987), New York (Bernard et al. 1983), Scotland (Charman 1993), and Norway (Singsaas 1989) fens.

From a conservation perspective, the most important microsites for rare plants were those that had the highest soil moisture levels. Fourteen rare Iowa plants reached their modal frequencies in Cluster A (moderate pH and cation levels), while 25 rare species reached modal frequencies in Cluster E (high pH and cation levels). This pattern is consistent with previous investigations of Minnesota (Almendinger & Leete 1998a) and Suffolk, England (Fojt & Harding 1995) fens that have documented a positive correlation between soil water levels and rare plant richness.

Environmental co-variables

As for many other fen systems (e.g. Gerdol 1990; Vitt & Chee 1990; Wassen et al. 1990a; Charman 1993; Motzkin 1994; Fojt & Harding 1995; McQueen & Wilson 2000; Bergamini et al. 2001; Sjörs & Gunnarsson 2002) the principal axis of compositional variation was significantly correlated with pH, Ca, and Mg. The strong correlation of the principal axis with P, vegetation height, and soil temperature is likely due to the limited solubility of P compounds in areas with high soil/water pH and Ca (Bedford et al. 1999). This causes reduced primary production, fertility, and plant height in Minnesota (Almendinger & Leete 1998a), English (Boyer & Wheeler 1989), Italian alpine (Gerdol 1990) and Dutch (Verhoeven et al. 1990) fens. With increased penetration of solar energy to the ground, areas with less vegetation growth will also have higher soil temperatures. As low vegetation mats support the highest plant diversity and number of rare species in Iowa (twice the number of rare species occur in Cluster E vs. A) and other fen systems (Johnson & Leopold 1994; Wheeler & Shaw 1991; Jensen & Meyer 2001), maintenance of low available P levels will be important to fen conservation.

Previous research has also documented that soil moisture, N concentration, and disturbance level will influence fen vegetation. Water levels are one of the most commonly documented correlates with peatland vegetation gradients (Bernard et al. 1983; Stewart 1987; Økland 1989; Singsaas 1989; Glaser et al. 1990; Wassen et al. 1990a; Charman 1993; Bowles et al. 1996). Soil N has been shown to impact vegetation composition in Swiss montane (Bergamini et al. 2001) and Icelandic (Magnússon & Magnússon 1990) fens. Disturbance gradients also underlie some peatland vegetation patterns, with grazing being more intense on drier soils (Bowles et al. 1996). In Iceland these environmental factors are linked as fen sites subjected to higher grazing pressures also exhibit the highest soil N concentrations (Magnússon & Magnússon 1990).

Climate and geology may also significantly impact peatland ecology as increased precipitation and temperature lead to increased leaching rates and decreased soil Ca levels in boreal North America (Glaser 1992), Fennoscandia (Økland 1989), and Minnesota (Almendinger & Leete 1998a) fens. Similarly, in Iowa the frequency of calcareous microsites increase towards the northwest where precipitation and temperature are the lowest. A linkage between fen soil and aquifer chemistry has been previously demonstrated in Minnesota (Almendinger & Leete 1998b). Not surprisingly, Iowa sites originating from the most base-rich aquifers (e.g. bedrock, till) supported the richest fen vegetation. However, the linkage between site configuration (area, perimiter/area ratio) and vegetation has not been previously documented. While these could be related to edge-effects, they are more likely related to differential landscape positions for large (basins) vs. small (sideslope) sites, increasing the contribution of cation-rich groundwater in the latter.

Within- vs. between-site compositional gradients

While most individual sites capture between 25-50% of total observed compositional variation, this overlap was less evident along Axis 1 as compared to Axis 2. This result is to be expected as Axis 1 environmental co-variables are most strongly related to soil pH, Ca, Mg, and P, which will vary most between sites due to differences in aquifer chemistry (Almendinger & Leete 1998b), while Axis 2 scores are most strongly related to differences in soil water levels, which are largely repeated from the dry margins (lags) to wet centres of each site (Wassen et al. 1990b; Wassen & Barendregt 1992; Gerdol 1993). Thus, water levels vary more within vs. between New York fens (Slack 1994), while in nutrient levels vary more between vs. within Dutch fens (Verhoeven et al. 1990).

This differential within- and between-site variation along both axes has important consequences to the study and conservation of Iowa fens. To observe (and protect) the principal compositional gradient from poor-rich sites, multiple locations within the landscape must be considered. When only single sites are investigated or conserved, gradients associated with water levels gain importance. It is thus not surprising that as previous quantitative vegetation analysis of Midwestern fens have been limited to single or few sites (e.g. van der Valk 1975; Stewart 1987; Wilcox et al. 1986; Stoynoff 1993; McCormac & Schneider 1994; Bowles et al. 1996; Choesin & Boerner 2000) the poor-rich fen gradient has not been previously reported from this landscape. However, these single-site studies have generally documented the importance of water levels in determining vegetation pattern. Conservation prioritization simply based upon the number of rare species per site will likely lead to an over-representation of calcareous sites, as these areas support the greatest number of rare species. The rare species characteristic of poor and intermediate fens, though fewer in number, may thus be overlooked.

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References

Anon. 1995. *S-PLUS guide to statistical and mathematical analysis*. Version 3.3. Statistical Sciences, Seattle, WA, US.

Almendinger, J.E. & Leete, J.H. 1998a. Peat characteristics and groundwater geochemistry of calcareous fens in the Minnesota River basin, U.S.A. *Biogeochemistry* 43: 17-41.

Almendinger, J.E. & Leete, J.H. 1998b. Regional and local hydrology of calcareous fens in the Minnesota River basin, USA. *Wetlands* 18: 184-202.

Banfield, J.D. & Raftery, A.E. 1992. Model-based Gaussian and non-Gaussian clustering. *Biometrics* 49: 803-822.

Bedford, B.L, Walbridge, M.R. & Aldous, A. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. *Ecology* 80: 2151-2169.

Bellamy, D.J. 1967. *Ecological studies on some European mires*. Ph.D. Dissertation, University of London. London, UK.

Bergamini, A., Peintinger, M., Schmid, B. & Urmi, E. 2001. Effects of management and altitude on bryophyte species diversity and composition in montane calcareous fens. *Flora* 196: 180-193.

Bernard, J.M., Sieschab, F.K. & Gauch, H.G. Jr. 1983. Gradient analysis of the Byron-Bergen swamp, a rich fen in western New York. *Vegetatio* 53: 85-91.

Bowles, M., McBride, J., Stoynoff, N. & Johnson, K. 1996. Temporal changes in vegetation composition and structure in a fire-managed prairie fen. *Nat. Areas J.* 16(4): 275-288.

Boyer, M.L.H. & Wheeler, B.D. 1989. Vegetation patterns in spring-fen calcareous fens: calcite precipitation and constraints on fertility. *J. Ecol.* 77: 597-609.

Burgess, T.M. & Webster, R. 1980. Optimal interpolation and isarithmic mapping of soil properties. II. Block kriging. *J. Soil Sci.* 31: 333-341.

Charman, D.J. 1993. Patterned fens in Scotland: evidence from vegetation and water chemistry. *J. Veg. Sci.* 4: 543-552.

Choesin, D.V. & Boerner, R.E.J. 2000. Vegetation and ground water alkalinity of Betsch Fen, a remnant preiglacial fen in south central Ohio. *Castanea* 65: 193-206.

Choesin, D.V. & Boerner, R.E.J. 2002. Vegetation boundary detection: a comparison of two approaches applied to field data. *Plant Ecol.* 158: 85-96.

Dahnke, W.C. 1988. *Recommended chemical soil test procedures for the North-central Region*. North Dakota Agricultural Experiment Station, Bull. No. 499, North Dakota State University, Fargo, ND, US.

Equihua, M. 1990. Fuzzy clustering of ecological data. *J. Ecol.* 78: 519-534.

Faith, D.P., Minchin, P.R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57-68.

Fojt, W. & Harding, M. 1995. Thirty years of change in the vegetation communities of three valley mires in Suffolk, England. *J. Appl. Ecol.* 32: 561-577.

Gerdol, R. 1990. Vegetation patterns and nutrient status of two mixed mires in the southern Alps. *J. Veg. Sci.* 1: 663-668.

Gerdol, R. 1993. The vegetation of wetlands in the southern Carnian alps (Italy). *Gortania Atti del Museo Friuland di Storia Naturale* 15: 67-107.

Glaser, P.H. 1987. *The ecology of patterned boreal peatlands of northern Minnesota: a community profile*. USDI Fish and Wildlife Service, Biological Report 85 (7.14), Washington, DC, US.

Glaser, P.H. 1992. Raised bogs in eastern North America – regional controls for species richness and floristic assemblages. *J. Ecol.* 80: 535-554.

Glaser, P.H., Wheeler, G.A., Gorham, E. & Wright, H.E. 1981. The patterned mires of the Red Lake peatland, northern Minnesota: vegetation, water chemistry, and landforms. *J. Ecol.* 69: 575-599.

Glaser, P.H., Janssens, J.A. & Siegel, D.I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. *J. Ecol.* 78: 1021-1048.

Gunnarsson, U., Rydin, H. & Sjörs, H. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, central Sweden. *J. Veg. Sci.* 11: 277-286.

Hájek, M. 2002. The class *Scheuchzerio-Caricetea fuscae* in the western Carpathians: indirect gradient analysis, species groups and their relation to phytosociological classification. *Biologia* (Bratislava) 57: 461-469.

Hartigan, J.A. 1975. Clustering algorithms. John Wiley Press, New York, NY, US.

Hudson, B. 1994. Soil organic matter and available water capacity. *J. Soil Water Cons.* 49: 189-193.

Jensen, K. & Meyer, C. 2001. Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. *Plant Ecol.* 155: 169-181.

Johnson, A.M. & Leopold, D.J. 1994. Vascular plant species richness and rarity across a minerotrophic gradient in the wetlands of St. Lawrence County, New York, USA. *Biodivers. Conserv.* 3: 606-627.

Magnússon, B. & Magnússon, S.H. 1990. Studies in the grazing of a drained lowland fen in Iceland. I. The responses of the vegetation to livestock grazing. *Búvísindi* 4: 87-108.

Masing, V. 1982. The plant cover of Estonian bogs: a structural analysis. in: Masing, V. (ed.) *Peatland ecosystems*, pp. 50-92. Academy of Sciences of the Estonian S.S.R.Valgus, Tallinn, EE.

McCormac, J.S. & Schneider, G.J. 1994. Floristic diversity of a disturbed western Ohio fen. *Rhodora* 96: 327-353.

McQueen, A.A.M. & Wilson, J.B. 2000. Vegetation and environment of a New Zealand raised bog. *J. Veg. Sci.* 11: 547-554.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89-108.

Minchin, P.R. 1990. *DECODA software*. Australian National University, Canberra, AU.

Mooney, E.P. & O'Connell, M. 1990. The phytosociology and ecology of the aquatic and wetland plant communities of the lower Corrib basin, County Galway. *Proc. R. Irish Acad.* 90b: 57-97.

Motzkin, G. 1994. Calcareous fens of western New England and adjacent New York state. *Rhodora* 96: 44-68.

Nekola, J.C. 1994. The environment and vascular flora of northeastern Iowa fen communities. *Rhodora* 96: 121-169.

Økland, R.H. 1990. Regional variation in SE Fennoscandian mire vegetation. *Nord. J. Bot.* 10: 285-310.

Prior, J.C. 1991. *Landforms of Iowa*. University of Iowa Press, Iowa City, IA, US.

Singsaas, S. 1989. Classification and ordination of the mire vegetation of Stormyra near Tynset, S Norway. *Nord. J. Bot.* 9: 413-423.

Sjörs, H. 1952. On the relation between vegetation and electrolytes in North Swedish mire waters. *Oikos* 2: 241-258.

Sjörs, H. & Gunnarsson, U. 2002. Calcium and pH in north and central Swedish mires. *J. Ecol.* 90: 650-657.

Slack, N.G. 1994. Can one tell the mire type from the Bryophytes alone? *J. Hattori Bot. Lab.* 75: 149-159.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. W.H. Freeman and Co., San Francisco, CA, US.

Southall, E.J., Dale, M.P. & Kent, M. 2003. Floristic variation and willow carr development within a southwest England wetland. *Appl. Veg. Sci.* 6: 63-72.

Stammel, B., Kiehl, K. & Pfadenhauer, J. 2003. Alternative management on fens: Response of vegetation to grazing and mowing. *Appl. Veg. Sci.* 6: 245-254.

Stewart, D.J. 1987. *The vegetation and flora of Gott fen (Ohio), with a comparison of community classifications*. M.Sc. Thesis, Miami University, Oxford, OH, US.

Stoynoff, N.A. 1993. A quantitative analysis of the vegetation of Bluff Spring Fen Nature Preserve. *Trans. Illinois Acad. Sci.* 86: 93-110.

Thompson, C.A., Bettis, E.A. III & Baker, R.G. 1992. Geology of Iowa fens. *J. Iowa Acad. Sci.* 99: 53-59.

van der Valk, A.G. 1975. Floristic composition and structure of a fen in northwest Iowa. *Proc. Iowa Acad. Sci.* 82: 113-118.

Vanderpuye, A.W., Elvebakk, A. & Nilsen, L. 2002. Plant communities along environmental gradients of high-arctic mires in Sassendalen, Svalbard. *J. Veg. Sci.* 13: 875-884.

Verhoeven, J.T.A., Maltby, E. & Schmitz, M.B. 1990. Nitrogen and Phosphorus mineralization in fens and bogs. *J. Ecol.* 78: 713-726.

Vitt, D.H. & Chee, W.L. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89: 87-106.

Wassen, M.J. & Barendregt, A. 1992. Topographic position and water chemistry of fens in a Dutch river plain. *J. Veg. Sci.* 3: 447-456.

Wassen, M.J., Barendregt, A., Palczynski, A., de Smidt, J.T. & de Mars, H. 1990a. The relationship between fen vegetation gradients, groundwater flow and flooding in an undrained valley mire at Biebrza, Poland. *J. Ecol.* 78: 1106-1122.

Wassen, M.J., Barendregt, A., Schot, P.P. & Beltman, B. 1990b. Dependency of local mesotrophic fens on a regional groundwater flow system in a poldered river plain in the Netherlands. *Landscape Ecol.* 5: 21-38.

Wheeler, B.D. & Shaw, S.C. 1991. Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. *J. Ecol.* 79: 285-301.

Wilcox, D.A., Shedlock, R.J. & Hendrickson, W.H. 1986. Hydrology, water chemistry, and ecological relations in the raised mound of Cowles Bog. *J. Ecol.* 74: 103-117.

Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, NJ, US.

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BIODIVERSITY RESEARCH

Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America

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Abstract: Previous ordination studies of land snail community composition have been limited to four or fewer habitat types from sites separated by no more than 300 km. To investigate the nature of large-scale patterns, North American land snail assemblages at 421 sites, representing 26 habitat types and covering a 1400 × 800 km area, were ordinated using global, nonmetric multi-dimensional scaling (NMDS). These data were then subjected to model-based cluster analysis and kmeans clustering to identify the main compositional groups and most important environmental covariables. Six primary compositional groups were identified. Three of these largely represent upland forest and rock outcrop sites, while the remaining largely represent either lowland forest, lowland grassland or upland grassland habitats. The geographical location and moisture level of sites also influences community composition. A strong compositional difference exists between sites having duff vs. turf soil surface layers. Only 8% of sites were improperly classified when soil surface architecture was used as the sole predictor variable. Fully 43% of taxa exhibited significant preferences towards one of these surface types, while only 15% of relatively common (10 + occurrence) taxa showed no preferences. Twelve groups of closely related taxa within the same genus had members that favoured different surface types, indicating that differential selection pressures have existed over evolutionary time scales. While turf faunas appeared unaffected by anthropogenic disturbance, duff faunas were strongly impacted, suggesting that their conservation will require protection of soil surface architecture.

Key words. Cluster analysis, community ecology, conservation biology, landscape pattern, multi-dimensional scaling, North America, soil architecture, terrestrial gastropods.

INTRODUCTION

Land snails are regarded typically as generalist herbivores, fungivores and detritivores (Burch & Pearce, 1990) that exhibit weak levels of intraspecific competition (Cain, 1983; Cowie & Jones, 1987; Smallridge & Kirby, 1988; Barker & Mayhill, 1999). As land snail communities can consume less than 0.5% of annual litter input per year (Mason, 1970), some speculate that few resources, beyond $CaCO_3$ (Boycott, 1934) and appropriate resting site availability (Pearce, 1997), will limit distribution. This concept is supported by high levels of microsympatry in land snail communities, where 13–35 (representing up to 50% of the regional fauna) co-occurring taxa can be found at < 1 m^2 grains (Schmid, 1966; Cameron & Morgan-Huws, 1975; Nekola & Smith, 1999; Cameron, 2002).

However, at landscape scales, land snail population size and faunistic composition has been suggested to vary with habitat and vegetation types (e.g. Burch, 1956; Wäreborn, 1970; Van Es & Boag, 1981; Young & Evans, 1991; Stamol, 1991; Stamol, 1993; Ports, 1996; Theler, 1997; Nekola, 2002). Habitat preferences for individual species have also been discussed (without supporting empirical data) at subcontinental scales

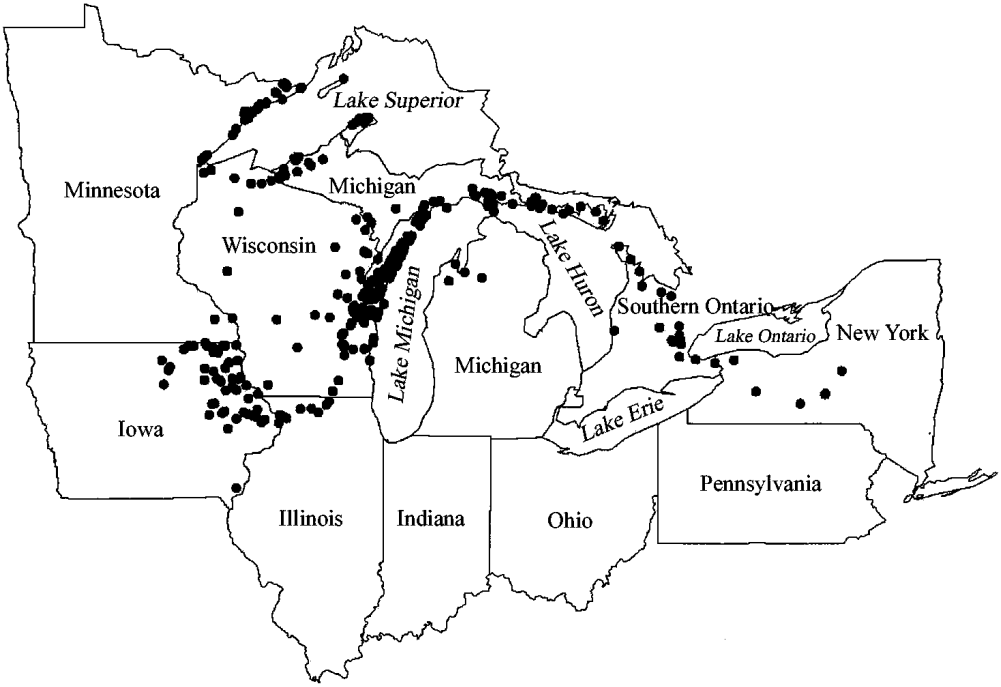

Fig. 1 Map of the study region showing the location of the 443 sample sites.

in both western Europe (Kerney & Cameron, 1979) and eastern North America (Hubricht, 1985).

Ordination techniques have documented significant species turnover along local environmental gradients in western Europe (e.g. Tattersfield, 1990; Magnin *et al.*, 1995; Hermida *et al.*, 2000; Ondina & Mato, 2001) and Pacific Island (e.g. Cowie *et al.*, 1995; Barker & Mayhill, 1999) faunas. Unfortunately, these (and all other published snail ordination) studies have been conducted only at limited ecological (< four sampled habitat types) and geographical (maximum separation of no more than 300 km) scales.

The following study addresses these concerns by using global nonmetric multi-dimensional scaling (NMDS) ordination and model-based cluster analysis to analyse land snail composition patterns within 26 habitat types across a 1400-km extent of central North America. These data will be used to address: (1) if land snail community composition predictably varies across this sub-continental region; and (2) what environmental and geographical factors underlie any such patterns. This study represents not only the first use of NMDS in the analysis of land snail communities, but also represents the first time North American faunas have been subjected to ordination.

METHODS

Study region

Land snail faunas were sampled across a 1400 × 800 km area centred on the western portion of the Great Lakes basin in eastern and central North America (Fig. 1). This area covers a wide range of bedrock, climate and vegetation types. Both Palaeozoic sedimentary and Precambrian igneous bedrock outcrops in the region. One of the more prominent sedimentary exposures is the Niagaran Escarpment, a band of Silurian limestones and dolomites extending from western New York state to north-eastern Iowa. Outcrops along the western Lake Superior shore typically represent late-Precambrian mafic igneous rocks associated with the Keewenawan mid-continental rift system (Anderson, 1983). Average

Table 1 Distribution of samples among surveyed habitat types. Habitat descriptions can be found in Nekola (1999)

Group	Habitat type	Sites sampled	Geographic range
Rock outcrop	Carbonate cliff	129	Illinois, Iowa, Minnesota, Michigan, Ontario, New York, Wisconsin
	Lakeshore carbonate ledge	23	Michigan, Ontario, Wisconsin
	Algific talus slope	27	Illinois, Iowa
	Igneous cliff	72	Michigan, Minnesota
	Sandstone/quartzite cliff	5	Wisconsin
	Shale cliff	3	New York
Upland forest	Oak–hickory forest	2	Wisconsin
	Maple–basswood forest	3	Wisconsin
	Hemlock–birch forest	1	Wisconsin
	Lakeshore forest	16	Michigan, Wisconsin
	Rocky woodland	26	Iowa, Michigan, Ontario, Wisconsin
Lowland forest	Floodplain forest	2	Wisconsin
	Black ash swamp	6	Wisconsin
	Tamarack swamp	33	Minnesota, Michigan, Ontario, Wisconsin
	White cedar swamp	16	Michigan, Ontario, Wisconsin
	Shrub-carr	2	Wisconsin
Upland grassland	Tallgrass prairie	1	Iowa
	Sand dune	1	Wisconsin
	Bedrock glade	13	Iowa
	Alvar	6	Michigan, Wisconsin
	Igneous shoreline	4	Michigan
	Successional old field	4	Wisconsin
Lowland grassland	Sedge meadow	5	Michigan, Wisconsin
	Fen	29	Iowa, Michigan, New York, Wisconsin
	Calcareous meadow	7	Michigan, Wisconsin
	Cobble beach	7	Michigan, Wisconsin

minimum winter temperatures range from −25 °C in northern Minnesota to −10 °C in western New York State. Average maximum summer temperatures range from 25 °C along the western Lake Superior shore to 30 °C in south-eastern Iowa. The average length of the 0 °C growing season varies from 100 to 110 days in northern Minnesota and Michigan to 180–190 days in southern Iowa, southern Ontario, and western New York state. In areas adjacent to or downwind from (east of) the Great Lakes (especially the Lower Peninsula of Michigan, southern Ontario, and western New York State), the climate tends to be buffered over that normally experienced in the continental interior, being warmer in the winter, cooler in the summer and having a longer growing season with more constant precipitation (Eichenlaub, 1979). Matrix vegetation varies from tallgrass prairie in the west to deciduous forest in the east to mixed boreal–hardwood forest in the north (Barbour & Billings, 1988).

Study sites

Four hundred and forty-three sites (Fig. 1) were surveyed across the range of habitats known to support diverse land snail assemblages (Nekola, 1999). The 26 habitats surveyed were broadly grouped into five major categories: rock outcrops, upland forests, lowland forests, upland grasslands and lowland grasslands (Table 1). While sites generally represent undisturbed examples of their respective habitats, an effort was also made to sample some (25 rock outcrop, 12 upland forest, nine lowland forest, four upland grassland and eight lowland grassland) that had been disturbed anthropogenically by grazing, logging, recreational/urban development or bedrock/soil removal. Examples of such sites include field-edge stone piles, abandoned agricultural fields, abandoned building foundations, old quarries, pastures, road verges and exploited forests.

Field methods

Documentation of terrestrial gastropods from each site was accomplished by hand collection of larger shells and litter sampling for smaller taxa from representative 100–1000 m^2 areas. Soil litter sampling was primarily used as it provides the most complete assessment of site faunas (Oggier *et al.*, 1998). As suggested by Emberton *et al.* (1996), collections were made at places of high micromollusc density, with a constant volume of soil litter (approximately 4 L) being gathered from each site. For woodland sites, sampling was concentrated: (1) along the base of rocks or trees; (2) on soil covered bedrock ledges; and/or (3) at other places found to have an abundance of shells. For grassland sites, samples consisted of: (1) small blocks (*c*. 125 cm^3) of turf; (2) loose soil and leaf litter accumulations under or adjacent to shrubs, cobbles, boulders and/or hummocks; and (3) other locations observed to have an abundance of shells.

The latitude–longitude location of each sample was determined using either USGS 7.5 minute topographic maps or a hand-held GPS. To minimize bias from use of polar-coordinates, these locations were converted subsequently to Cartesian UTM Zone 16 coordinates using ARCINFO.

The presence or absence of anthropogenic disturbance and soil surface architecture (duff vs. turf) was also recorded from each site. For purposes of this study 'duff' soils represent sites where the organic horizon was deep (> 4 cm) and subtended by a friable upper A horizon consisting largely of humus and mineral soil. 'Turf' soils represent sites where the organic horizon is thin (< 4 cm) and immediately subtended by an upper A horizon firmly bound together by living plant roots. While many habitats only supported a single soil architecture type (e.g. all carbonate cliffs were duff, and all bedrock glades were turf), some (such as white cedar swamps) could possess either turf or duff surface layers, depending upon individual site conditions. Thus, habitat type could not be used as a surrogate for soil surface architecture.

Laboratory procedures

Samples were dried slowly and completely in either a low-temperature soil oven (*c*. 80–95 °C) or in a greenhouse. Dried samples were then soaked in water for 3–24 h, and subjected to careful but vigorous water disaggregation through a standard sieve series (ASTME 3/8′ (9.5 mm), #10 (2.0 mm), #20 (0.85), and #40 (0.425 mm) mesh screens). These fractions were then dried and passed again through the same sieve series, and hand-picked against a neutral-brown background. All shells and shell fragments were removed.

All identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht Collection at the Field Museum of Natural History (FMNH). Identification of some additional specimens representing Holarctic taxa more common in western Europe were verified by Robert Cameron of the University of Sheffield, UK. All specimens have been catalogued and are housed in the author's reference collection at the University of Wisconsin — Green Bay. Nomenclature generally follows that of Hubricht (1985), with updates and corrections by Frest (1990, 1991) and Nekola (2002).

Statistical procedures

Ordination

Species lists were determined for each sample. Sites with four or fewer taxa were excluded from further analysis, as such samples can bias results and obscure compositional trends. The remaining sites were subjected to global nonmetric multidimensional scaling (NMDS) using DECODA (Minchin, 1990). NMDS was used as it makes no assumptions regarding the underlying nature of species distributions along compositional gradients. As such, NMDS is the most robust form of ordination for detection of ecological patterns (Minchin, 1987).

To ordinate sites, a matrix of dissimilarity coefficients was calculated between all pairwise combinations of sites using the Czekanowski (Bray–Curtis) index (Faith *et al*., 1987). All species (including the most rarely encountered) were considered. NMDS in one to four dimensions was then performed, with 200 maximum iterations, a stress ratio stopping value of 0.9999, and a small stress stopping value of 0.01. Output was scaled in half-change units, so that an interpoint distance of 1.0 will correspond, on average, to a 50% turnover in species composition.

Because a given NMDS run may locate a local (rather than the global) stress minimum, multiple NMDS runs must be conducted on a given set of data from different initial random starting points to assess the stability of an individual solution (Minchin, 1987). For this ordination, DECODA used a total of 20 random starting configurations. Solutions in each of the four dimensions were compared using a Procrustes transformation to identify those that were statistically identical. The number of unique solutions, and number of runs which fell into each, was then calculated across each of the four dimensions (Minchin, 1990). The modal solution of 20 runs was identified, and was considered a global optimum when it was achieved in at least 50% of starts.

Identification of compositional groups

The chosen optimal NMDS solution was then subjected to model-based cluster analysis (Banfield & Raftery, 1992) to identify the number of compositional groups most supported by the data. Clustering was performed on the selected ordination output, rather than raw data, as ordination results are more robust and less susceptible to sampling or other inadvertent errors (Equihua, 1990). A sum-of-squares model was chosen, as it assumes that clusters will be spherical in ordination space, making them maximally compact and similar in composition. The approximate weight of evidence for k clusters (AWE_k) was calculated via the S + MCLUST algorithm (Statistical Sciences, 1995) for $k = 1$ to $n - 1$ clusters (where n = the total number of ordinated sites). The larger the AWE_k, the more evidence exists for that number of clusters. After the optimum number of clusters was determined, kmeans iterative relocation (Hartigan, 1975) was used to assign each site to a cluster. Kmeans clustering was chosen as it operates under the same sum-of-squares criteria used for AWE_k calculation.

Ordination interpretation

The number of occurrences (and frequency) of each species within each kmeans cluster was calculated. Species frequencies between clusters were compared using a Spearman's rank correlation. The 10 most frequent taxa, taxa reaching modal frequency and species richness for each cluster were calculated.

The frequency of the five major habitat groups between the compositional clusters was analysed using a contingency table. As predicted values were sparse (< 5) in more than one-fifth of cells, log-linear modelling was used to estimate significance (Zar, 1984).

The maximum correlation vectors for the four recorded environmental variables (UTM E coordinate, UTM N coordinate, soil surface type, presence of anthropogenic disturbance) was calculated by DECODA. The significance of each was estimated through Monte-Carlo simulations using 1000 replications.

Discriminant analysis was used to help further describe the impact of soil surface type and anthropogenic disturbance on site position in ordination space. Three tests were conducted: (1) effect of soil surface architecture (duff vs. turf) and the effect of anthropogenic disturbance separately for (2) duff and (3) turf soils.

Lastly, the number of duff and turf sites containing and lacking each species was calculated. The significance of observed differences in these ratios between duff and turf sites was estimated using log-linear modelling. As this test was repeated for each species, a Bonferroni correction was used to adjust the significance threshold. This conservative adjustment was used so that only the most robust deviations would be used for data interpretation.

RESULTS

Site ordination

One hundred and eight terrestrial gastropod taxa were identified from the 443 inventoried sites (Appendix I). Twenty-two sites were species poor (four or fewer taxa) and removed from further analysis. These included eight igneous cliffs, three lakeshore forests, three tamarack wetlands and single shale cliff, oak–hickory forest, maple–basswood forest, floodplain forest, sand dune, old field, sedge meadow and cobble beach sites.

Table 2 NMDS summary statistics from an ordination of 421 sites with five or more taxa

Dimensions	Stress level	Runs achieving minimum stress	Unique solutions	Number of runs in modal solution
1	0.339103	20	11	5
2	0.197412	20	6	10
3	0.147405	18	16	3
4	0.116912	18	18	1

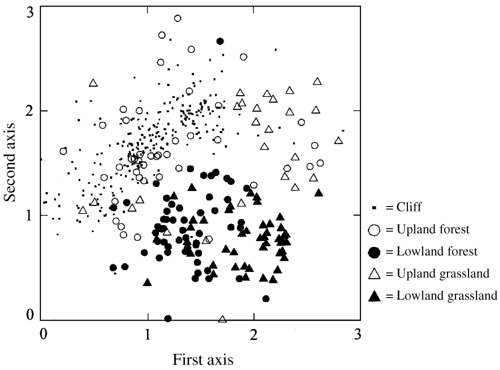

Fig. 2 NMDS ordination of 421 sites with land snail richness of 5 or more, showing distribution of the five main habitat groups. Units are scales in half-change units, such that a distance of 1 represents a 50% turnover in fauna composition.

Table 3 Approximate weight of evidence for k clusters (AWE_k) in land snail ordination based on a sum-of-squares model

No. of clusters	AWE_k	% Change from AWE_k to AWE_{k-1}
1	0	—
2	298.3	—
3	767.8	157.4
4	919.4	19.7
5	1097.8	19.4
6	1244.0	13.3
7	1335.2	7.3
8	1411.4	5.7
9	1456.7	3.2
10	1508.9	3.6
53	2131.5	—

NMDS of the remaining 421 sites demonstrated that the only stable solution occurred along two axes of variation, where one was achieved in 50% of starts. The minimum stress configuration of this solution was 0.197412. In other dimensions, the most stable solution(s) were achieved in five (one dimension), three (three dimensions) and one (four dimensions) runs (Table 2).

Identification and description of compositional clusters

Visual observation of the chosen NMDS ordination solution demonstrated apparent natural clustering in faunal composition, with at least one well-defined group existing in the lower-centre of the diagram (Fig. 2). AWE_k analysis demonstrated that the maximum score (2131.5) was achieved at the 53rd cluster. As this result provides too many groups to be useful for generalization of faunistic trends, AWE_k scores from k = 1–10 were calculated, along with the percentage increase in AWE_k from k to $k + 1$ clusters (Table 3). These data demonstrate that over 50% of maximum AWE_k was achieved by the 6th cluster. The percentage increase in AWE_k fell by almost 50% for cluster 7 (7.3%), and decreased steadily to the 3.4% range by cluster 10. Based on this, the optimal number of clusters was set at six (Fig. 3), even though it does not represent maximum AWE_k.

Contingency table analysis (Table 4) demonstrates that habitat representation significantly ($P < 0.00005$) varies between the six nonoverlapping kmeans clusters. Clusters A–C were equally ($P = 0.3778$) represented by rock outcrop and upland forest sites, while cluster D was dominated by lowland forests, cluster E by lowland grasslands and cluster F by upland grasslands. The 10 most frequent taxa also varied greatly,

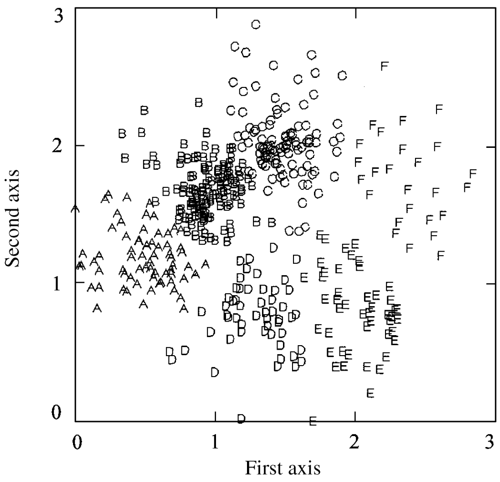

Fig. 3 NMDS ordination of 421 sites with land snail richness of five or more. Letters represent each of the six compositional clusters assigned via Kmeans Clustering.

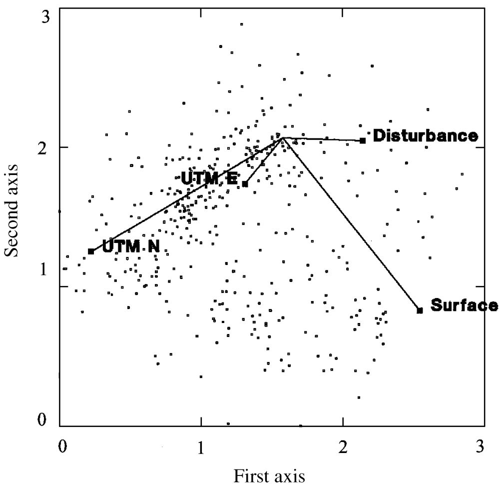

Fig. 4 Environmental biplot for NMDS ordination. The direction of each vector represents the angle of maximum correlation, while the length represents the strength of the correlation.

with approximately 50% turnover occurring between even the most similar groups (Table 5). Spearman's rank correlations of species occurrence frequencies indicated that clusters D and E were most similar (0.831), while clusters A and F were the most different (0.316). Six species possessed modal occurrence frequencies in cluster A, 25 in cluster B, 32 in cluster C, five in cluster D, 20 in cluster E and 20 in cluster F (Table 6). Forty-one total taxa were encountered in cluster A, 78 in cluster B, 87 in cluster C, 58 in cluster D, 60 in cluster E and 60 in cluster F (Appendix I).

Analysis of environmental co-variables

Monte Carlo testing of the maximum correlation vectors for the four recorded environmental variables (Fig. 4) demonstrated that all were highly significant ($P < 0.0005$), having maximum r-

Table 4 Contingency table analysis of main habitat groups vs. compositional clusters, with species richness within each cluster

Compositional cluster	Habitat group 1	2	3	4	5	Total sites	Species richness
A	57	6	2	4	0	69	41
B	100	20	2	1	0	123	78
C	86	9	4	3	0	102	87
D	2	2	37	2	11	54	58
E	0	1	10	2	34	47	60
F	5	5	0	15	1	26	60
Comparison	*Log-likelihood ratio statistic*					*d.f.*	*P*
Entire table	451.898					20	< 0.00005
Clusters A,B,C	8.593					8	0.3778
Clusters D,E,F	112.053					8	< 0.00005

Table 5 Ten most frequent taxa in each of the six compositional clusters

Rank order	Cluster A	Cluster B	Cluster C	Cluster D	Cluster E	Cluster F
1	*Discus catskillensis* (82.61%)	*Discus catskillensis* (93.50%)	*Punctum vitreum* (89.22%)	*Carychium exiguum* (88.89%)	*Gastrocopta tappaniana* (93.62%)	*Hawaiia minuscula* (57.69%)
2	*Nesovitrea binneyana* (82.61%)	*Punctum minutissimum* (91.06%)	*Gastrocopta contracta* (88.24%)	*Striatura milium* (83.33%)	*Carychium exiguum* (85.11%)	*Vallonia costata* (46.15%)
3	*Zonitoides arboreus* (82.61%)	*Zonitoides arboreus* (90.24%)	*Carychium exile* (88.24%)	*Nesovitrea electrina* (81.48%)	*Nesovitrea electrina* (85.11%)	*Cochlicopa lubrica* (46.15%)
4	*Vertigo cristata* (72.46%)	*Strobilops labyrinthica* (87.80%)	*Vertigo gouldi* (87.25%)	*Strobilops labyrinthica* (72.22%)	*Vertigo elatior* (74.47%)	*Helicodiscus parallelus* (46.15%)
5	*Striatura milium* (71.01%)	*Anguispira alternata* (84.55%)	*Anguispira alternata* (85.29%)	*Striatura exigua* (72.22%)	*Euconulus alderi* (70.21%)	*Gastrocopta contracta* (42.31%)
6	*Punctum minutissimum* (62.32%)	*Vertigo gouldi* (83.74%)	*Strobilops labyrinthica* (79.41%)	*Zonitoides arboreus* (68.52%)	*Hawaiia minuscula* (59.57%)	*Gastrocopta similis* (42.31%)
7	*Zoogenetes harpa* (53.62%)	*Columella simplex* (83.74%)	*Gastrocopta holzingeri* (78.43%)	*Vertigo elatior* (59.26%)	*Gastrocopta contracta* (57.45%)	*Punctum vitreum* (42.31%)
8	*Euconulus fulvus* (49.28%)	*Striatura milium* (73.98%)	*Hawaiia minuscula* (78.43%)	*Punctum minutissimum* (59.26%)	*Oxylama retusa* (55.32%)	*Gastrocopta holzingeri* (38.46%)
9	*Vertigo paradoxa* (49.28%)	*Helicodiscus shimeki* (66.67%)	*Gastrocopta pentodon* (74.51%)	*Gastrocopta tappaniana* (53.70%)	*Stenotrema leai* (55.32%)	*Vallonia pulchella* (38.46%)
10	*Striatura exigua* (46.38%)	*Euconulus fulvus* (65.85%)	*Zonitoides arboreus* (74.51%)	*Euconulus alderi* (48.15%)	*Deroceras* spp. (55.32%)	*Vertigo pygmaea* (38.46%)

Table 6 Taxa reaching modal frequencies in each compositional cluster

Cluster A	Cluster B	Cluster C	Cluster D	Cluster E	Cluster F
Nesovitrea binneyana	*Carychium nannodes*	*Allogona profunda*	*Carychium exiguum*	*Catinella avara*	*Catinella 'vermeta'*
Vertigo cristata	*Cochlicopa morseana*	*Anguispira alternata*	*Planogyra asteriscus*	*Catinella exile*	*Cepaea nemoralis*
Vertigo modesta modesta	*Columella simplex*	*Carychium exile*	*Striatura exigua*	*Cochlicopa lubricella*	*Cochlicopa lubrica*
Vertigo modesta parietalis	*Discus catskillensis*	*Catinella 'gelida'*	*Striatura milium*	*Discus cronkhitei*	*Gastrocopta armifera*
Vertigo paradoxa	*Discus patulus*	*Deroceras* spp.	*Vertigo nylanderi*	*Euconulus alderi*	*Gastrocopta procera*
Zoogenetes harpa	*Euconulus fulvus*	*Discus macclintockii*		*Gastrocopta tappaniana*	*Gastrocopta rogersensis*
	Euconulus polygyratus	*Gastrocopta contracta*		*Hawaiia* n.sp.	*Gastrocopta similis*
	Glyphyalinia rhoadsi	*Gastrocopta corticaria*		*Helicodiscus* n.sp.	*Glyphyalinia wheatleyi*
	Helicodiscus shimeki	*Gastrocopta holzingeri*		*Nesovitrea electrina*	*Helicodiscus inermis*
	Mesomphix cupreus	*Gastrocopta pentodon*		*Oxyloma peoriensis*	*Helicodiscus parallelus*
	Mesomphix inornatus	*Glyphyalinia indentata*		*Oxyloma retusa*	*Helicodiscus singleyanus*
	Oxychylus draparnaudi	*Guppya sterkii*		*Pomatiopsis lapidaria*	*Pupilla muscorum*
	Paravitrea multidentata	*Haplotrema concavum*		*Punctum* n.sp.	*Pupoides albilabris*
	Punctum minutissimum	*Hawaiia minuscula*		*Stenotrema leai*	*Succinea indiana*
	Striatura ferrea	*Hendersonia occulta*		*Strobilops affinis*	*Vallonia costata*
	Strobilops labyrinthica	*Mesodon clausus*		*Triodopsis multilineata*	*Vallonia excentrica*
	Triodopsis albolabris	*Mesodon pennsylvanicus*		*Vertigo elatior*	*Vallonia parvula*
	Triodopsis denotata	*Mesodon thyroidus*		*Vertigo milium*	*Vallonia pulchella*
	Triodopsis tridentata	*Oxychylus cellarius*		*Vertigo morsei*	*Vertigo pygmaea*
	Vallonia gracilicosta	*Punctum vitreum*		*Vertigo ovata*	*Zonitoides nitidus*
	Vertigo n.sp.	*Stenotrema barbatum*			
	Vertigo bollesiana	*Stenotrema fraternum*			
	Vertigo hubrichti	*Strobilops aenea*			
	Vitrina limpida	*Succinea ovalis*			
	Zonitoides arboreus	*Trichia striolata*			
		Triodopsis alleni			
		Triodopsis fosteri			
		Vallonia perspectiva			
		Vertigo gouldi			
		Vertigo meramecensis			
		Vertigo tridentata			
		Zonitoides limatulus			

Table 7 Two-dimensional correlation statistics for environmental variables in land snail ordination space

Variable	Maximum *r*	Angle to first axis	*P*
Entire ordination			
UTM E-W coordinate	0.2111	129.4	< 0.0005
UTM N-S coordinate	0.7909	148.9	< 0.0005
Soil surface type	0.7843	52.1	< 0.0005
Disturbance presence	0.2829	1.7	< 0.0005
Duff soil sites only			
UTM E-W coordinate	0.1020	100.4	0.190
UTM N-S coordinate	0.8409	134.7	< 0.0005
Disturbance presence			
Turf soil sites only	0.4812	31.9	< 0.0005
UTM E-W coordinate	0.5067	150.4	< 0.0005
UTM N-S coordinate	0.6690	162.0	< 0.0005
Disturbance presence	0.0671	1.3	0.820

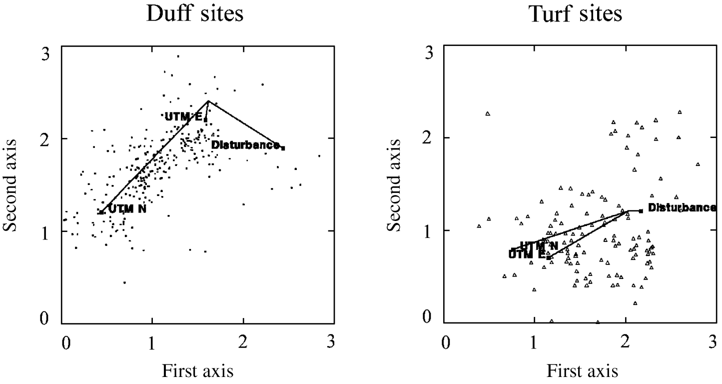

Fig. 5 Environmental biplots for duff and turf sites. The direction of each vector represents the angle of maximum correlation, while the length represents the strength of the correlation.

values ranging from 0.2111 to 0.7909 (Table 7). In duff sites, only UTM N coordinate and anthropogenic disturbance were found to correlate significantly ($P < 0.0005$) with the ordination diagram (Table 7). Northern sites tended to occur in the lower left of this group (maximum r = 0.8409), while disturbed sites tended to occur further to the right (maximum $r = 0.4812$; Fig. 5). In turf sites, only UTM N and E coordinates were found to correlate significantly ($P < 0.0005$) with the ordination diagram (Table 7). In this group, more northern (maximum r = 0.6690) and eastern (maximum r = 0.5067) sites tended to occur to the lower left (Fig. 5).

Discriminant analysis demonstrated that the location of duff and turf sites in ordination space differs significantly ($P < 0.0005$) (Table 8), with duff sites being essentially limited to the upper left half of the diagram, and turf sites being found largely in the lower right (Fig. 6). The classification summary for this analysis indicates that only 33 of the 421 sites (7.8%) were classified improperly when soil surface type was used as the sole predictor variable.

Discriminant analyses conducted separately on duff and turf sites demonstrated that disturbed duff sites were significantly ($P < 0.0005$) shifted to the right of undisturbed ones (Fig. 7). The

Table 8 Summary statistics for discriminant analysis of substrate and disturbance comparisons in land snail community ordination

	Comparison		
Factor	Duff vs. turf (all sites)	Disturbed vs. pristine (duff sites only)	Disturbed vs. pristine (turf sites only)
Canonical correlation	0.784	0.482	0.067
Eigenvalue	1.596	0.302	0.005
Likelihood ratio	0.385	0.768	0.996
Approximate *F*	322.74	43.915	0.278
Number d.f.	2	2	2
Density d.f.	417	291	123
P	< 0.0005	< 0.0005	0.758

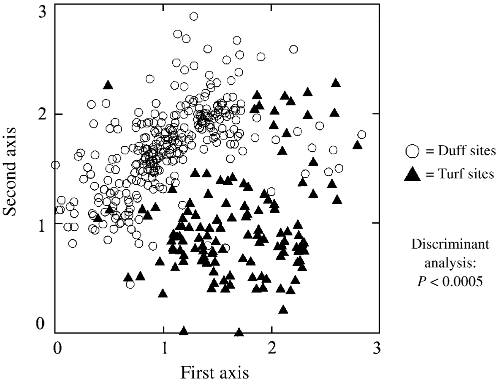

Fig. 6 Location of duff and turf sites within the ordination diagram.

classification summary for this analysis indicates that only 50 of the 295 duff sites (16.9%) were improperly classified when anthropogenic disturbance was used as the sole predictor variable. However, no significant differences ($P = 0.758$) were noted in the location of disturbed vs. undisturbed turf sites (Table 8).

Faunistic turnover between duff and turf soils

As differences in occurrence frequency between duff and turf sites were analysed for all 108 species, the significance threshold was lowered using a Bonferroni correction to $P = 0.000463$. Species with *P*-values ranging from 0.05 to 0.000463 were considered to possess statistically nonsignificant trends in their response to soil surface architecture. Species with *P*-values exceeding 0.05 were considered generalists.

Thirty-six species demonstrated no significant differences in their occurrence frequencies between duff and turf soils (Appendix I). Sixteen of these (*Cochlicopa lubricella*, *Deroceras* spp., *Discus cronkhitei*, *Gastrocopta armifera*, *Gastrocopta contracta*, *Haplotrema concavum*, *Hawaiia*

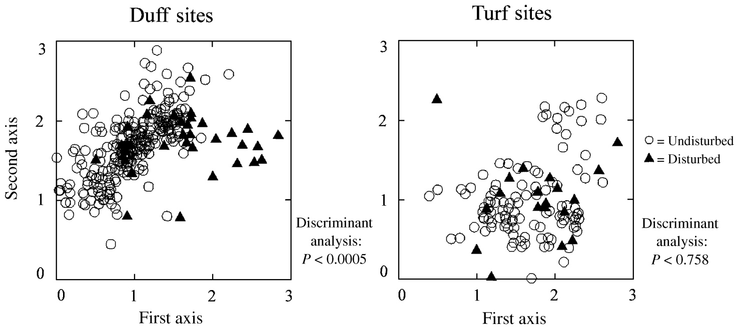

Fig. 7 Location of disturbed and undisturbed sites in the ordination diagram for duff and turf sites.

minuscula, *Helicodiscus parallelus*, *Helicodiscus singleyanus*, *Planogyra asteriscus*, *Striatura ferrea*, *Striatura milium*, *Triodopsis multilineata*, *Vallonia costata*, *Vertigo pygmaea*, *Vitrina limpida*) were found in 10 or more sites, and clearly represent generalists. However, the remaining 20 (*Carychium nannodes*, *Cepaea nemoralis*, *Discus patulus*, *Glyphyalinia wheatleyi*, *Helicodiscus inermis*, *Mesodon pennsylvanicus*, *Mesomphix cupreus*, *Mesomphix inornatus*, *Oxychylus cellarius*, *Oxychylus draparnaudi*, *Oxyloma peoriensis*, *Pomatiopsis lapidaria*, *Pupilla muscorum*, *Succinea indiana*, *Trichia striolata*, *Triodopsis denotata*, *Triodopsis fosteri*, *Vallonia excentrica*, *Vertigo modesta parietalis*, *Zonitoides limatulus*) are known from fewer locations, making Type 2 errors a significant concern. Additional data will be needed to adequately assess the response of these species to duff vs. turf soils.

Eighteen species (*Cochlicopa lubrica*, *Cochlicopa morseana*, *Discus macclintockii*, *Mesodon clausus clausus*, *Mesodon thyroidus*, *Punctum minutissimum*, *Punctum vitreum*, *Stenotrema barbatum*, *Strobilops aenea*, *Strobilops labyrinthica*, *Succinea ovalis*, *Triodopsis albolabris*, *Triodopsis alleni*, *Triodopsis tridentata*, *Vallonia perspectiva*, *Vertigo meramecensis*, *Vertigo modesta modesta*, *Vertigo tridentata*) nonsignificantly favoured duff sites. Another eight (*Gastrocopta procera*, *Gastrocopta rogersensis*, *Gastrocopta similis*, *Hawaiia* n.sp., *Helicodiscus* n.sp., *Striatura exigua*, *Vallonia pulchella*, *Zonitoides nitidus*) nonsignificantly favoured turf sites. While a number of these (e.g. *Discus macclintockii*, *Gastrocopta procera*, *Gastrocopta rogersensis*, *Vertigo meramecensis*) demonstrated very strong absolute preferences, their few total occurrences in combination with the conservative Bonferroni correction prevented them from exhibiting significant responses.

The remaining 46 species demonstrated clear and significant soil surface preferences. Twenty-eight species (*Allogona profunda*, *Anguispira alternata*, *Carychium exile*, *Catinella 'gelida'*, *Columella simplex*, *Discus catskillensis*, *Euconulus fulvus*, *Euconulus polygyratus*, *Gastrocopta corticaria*, *Gastrocopta holzingeri*, *Gastrocopta pentodon*, *Glyphyalinia indentata*, *Glyphyalinia rhoadsi*, *Guppya sterkii*, *Helicodiscus shimeki*, *Hendersonia occulta*, *Nesovitrea binneyana*, *Paravitrea multidentata*, *Stenotrema fraternum*, *Vallonia gracilicosta*, *Vertigo bollesiana*, *Vertigo cristata*, *Vertigo gouldi*, *Vertigo hubrichti*, *Vertigo* n.sp., *Vertigo paradoxa*, *Zonitoides arboreus*, *Zoogenetes harpa*) favoured duff soils, while another 18 (*Carychium exiguum*, *Catinella avara*, *Catinella exile*, *Catinella 'vermeta'*, *Euconulus alderi*, *Gastrocopta tappaniana*, *Nesovitrea electrina*, *Oxyloma retusa*, *Punctum* n.sp., *Pupoides albilabris*, *Stenotrema leai leai*, *Strobilops affinis*, *Vallonia parvula*, *Vertigo elatior*, *Vertigo milium*, *Vertigo morsei*, *Vertigo nylanderi*, *Vertigo ovata*) favoured turf soils.

DISCUSSION

These data demonstrate clearly that at large environmental and spatial scales most land snail species possess pronounced ecological preferences. They thus represent a paradox, being generalists at small scales, yet responding to specific environmental factors at larger ones. At large scales, species tend to congregate into six major compositional clusters related to habitat type, soil surface architecture, geography, moisture levels and presence of anthropogenic disturbance.

Habitat type

The six compositional clusters significantly differ in their habitat representations. Clusters A–D generally consist of forested sites while clusters E–F generally consist of grasslands. These results are in agreement with previous studies from other regions, including north-western Spain (Ondina & Mato, 2001), southern France (Magnin *et al.*, 1995), western Switzerland (Baur *et al.*, 1996), Croatia (Stamol, 1991, 1993), Hungary (Bába, 1989) and north-eastern Nevada (Ports, 1996). The contrast between open-ground and forest faunas is not limited to terrestrial gastropods. Other soil invertebrate groups that demonstrate this pattern include fungus-eating microarthropods (Branquart *et al.*, 1995), carabid beetles (McCracken, 1994), terrestrial amphipods (Taylor *et al.*, 1995) and collembola (Greenslade, 1997). In an ordination of global earthworm communities, Lavelle *et al.* (1995) demonstrated that open-ground and forest assemblages were distinct from the warm-tropics to the arctic. The distinction between forest and grassland faunas thus appears to be a general driving factor in soil biota community composition.

Soil surface architecture

The greater similarity of most lowland forest faunas to lowland grasslands, as opposed to upland forests and rock outcrops (Fig. 2), suggests additional factors underlie observed land snail composition patterns. The potential importance of soil surface architecture is implied as many lowland forest sites (e.g. tamarack, white cedar and most black ash swamp forests), and all lowland grasslands, possess turf soils. Only 8% of sites were improperly classified when soil surface type was used as the sole predictor variable (Table 7). Even this rate may be exaggerated, as most misclassifications were limited to two specific instances. First, even though having turf soils, igneous shoreline habitats had faunas almost identical to surrounding rock outcrop sites. Snails in this habitat, however, were largely restricted to friable accumulations of organic matter under stunted white cedar trees. Secondly, almost all duff sites with faunas similar to upland grasslands had experienced severe levels of anthropogenic disturbance.

Striking differences exist between the species of duff and turf sites: 43% of taxa significantly favoured one soil surface type over the other (even with use of a conservative Bonferroni-corrected significance threshold), while only 15% of frequent taxa (10 + occurrences) showed no preference. Inspection of these data indicate that for eight groups of closely related taxa within the same genus (24 total), one or more significantly favour duff soils, while the other(s) significantly favour turf (Table 9). In another four groups (10 additional taxa), one or more taxa significantly favour one of these soil types, while the other(s) exhibit a nonsignificant preference (Table 9). These 12 groups represent a wide variety of phylogenetic stocks (representing nine families: Carychiidae, Helicarionidae, Polygyridae, Punctidae, Pupillidae, Strobilopsidae, Succineidae, Valloniidae, Zonitidae), shell shapes (five wider than tall, five taller than wide and two equally tall as wide), and maximum shell dimensions (0.8 mm–12 mm). The presence of so many pairs of closely related duff- and turf-specialist taxa across such a wide range of phylogenies, shell shapes and dimensions suggests that very strong selective pressures between these soil surface types have extended over evolutionary time scales.

Table 9 Closely related intergeneric species pairs that demonstrate significant differences and/or nonsignificant trends in their soil surface preferences. A significance level of ** represents those species which possess $P < 0.000463$; * represent those species where $0.000463 < P < 0.05$

Duff-specialist	Sign. level	Turf-specialist	Sign. level	Family	Shell shape	Shell size (mm)
Carychium exile	**	*Carychium exiguum*	**	Carychiidae	Tall	1.5–2
Catinella 'gelida'	**	*Catinella avara*, *C. exile*, *C. 'vermeta'*	**	Succineidae	Tall	4–6
Euconulus fulvus	**	*Euconulus alderi*	**	Helicarionidae	Equal	3–4
Gastrocopta pentodon	**	*Gastrocopta tappaniana*	**	Pupillidae	Tall	2
Nesovitrea binneyana	**	*Nesovitrea electrina*	**	Zonitidae	Wide	4–7
Punctum minutissimum, *P. vitreum*	*	*Punctum* n.sp.	**	Punctidae	Wide	0.8–1.5
Stenotrema fraternum	**	*Stenotrema leai*	**	Polygyridae	Wide	8–12
Strobilops labyrinthica	*	*Strobilops affinis*	**	Strobilopsidae	Equal	2–3
Vallonia perspectiva	*	*Vallonia parvula*	**	Valloniidae	Wide	2
Vertigo gouldi 'group' (*V. bollesiana*, *V. cristata*, *V. gouldi*)	**	*Vertigo ovata 'group'* (*V. elatior*, *V. morsei*, *V. ovata*)	**	Pupillidae	Tall	1.5–3
Vertigo hubrichti, *V. paradoxa*, *V.* n.sp.	**	*Vertigo nylanderi*	**	Pupillidae	Tall	1.5–2
Zonitoides arboreus	**	*Zonitoides nitidus*	*	Zonitidae	Wide	4–6

It is not possible via the current analyses to definitively identify what such factors might be. They must be limited to the detritusphere (Coleman & Crossley, 1996), as almost 90% of snails live within 5 cm of the soil surface (Hawkins *et al*., 1998). One possible mechanism is increased competition with living plant roots in turf soils for inorganic nutrients (Lavelle *et al*., 1995). Another may be the greater organic litter thickness in duff soils, as the abundance (Berry, 1973), diversity (Cain, 1983; Locasciulli & Boag, 1987) and composition (Cameron & Morgan-Huws, 1975; Baur *et al*., 1996; Barker & Mayhill, 1999) of land snail communities often correlates positively with litter depth. The architecture of organic litter (Burch, 1956; Cameron, 1986; Young & Evans, 1991; Alvarez & Willig, 1993), and the underlying soil (Cameron, 1982; Hermida *et al*., 2000) may also have strong impacts on land snail community structure.

Similarly, the composition and abundance of other soil taxa communities can be influenced by organic litter depth and architecture, including amphipods (Taylor *et al*., 1995), microarthropods (Borcard & Matthey, 1995; Branquart *et al*., 1995; Kay *et al*., 1999; Whitford & Sobhy, 1999), collembola (Kovac & Miklisova, 1997) and ground beetles (McCracken, 1994). Thus, like habitat type, upper soil layer architecture appears to be another vital factor driving soil biota composition.

Geography

The geographical location of sites also influences community composition, particularly in duff soils (Fig. 5). Each of the three duff clusters have an unique geographical affiliation, with cluster A being largely restricted to the most northern sites, cluster B to sites in the northern half of the Lake Michigan–Huron basin, and cluster C to sites in Iowa, Illinois, and southern Wisconsin.

While a significant correlation with both latitude and longitude was also observed in turf sites, this result is almost certainly an artefact of the limitation of upland grassland sites to the south-west of the study region. Fens and lowland forests, found throughout, exhibited little geographical trends inside of the ordination diagram. Geographical location was presumably less important for these sites due to the overriding importance of habitat type and soil moisture.

Soil moisture and temperature

Soil moisture and sunlight levels also appear to influence land snail community composition in turf sites, with the driest and sunniest habitats (upland grasslands) being most different in composition from wet, shaded lowland forests. However, temperature and relative humidity, not sunlight, are probably the important driving factors (Suominen, 1999), as in both duff and turf sites the coolest and wettest habitats (northern cliff, upland forest and lowland forest) were most different in composition from the hottest and driest sites (southern cliff, upland forest and upland grassland).

Disturbance and conservation

Anthropogenic disturbance influences snail composition differentially between duff and turf sites. While turf faunas were not impacted, the most disturbed duff sites had faunas more characteristic of upland grasslands. Typical species found on such disturbed sites include *Cochlicopa lubrica*, *Pupilla muscorum*, *Vallonia costata*, *Vallonia excentrica*, *Vallonia pulchella* and *Vertigo pygmaea*. These faunistic differences may be related to differential changes in soil surface architecture with disturbance. Because undisturbed turf soils usually have thinner and less structurally complex organic litter layers, they may be less susceptible to soil compaction (and changes in composition) as compared to duff sites.

As anthropogenic soil compaction negatively impacts soil invertebrates more severely than plants in the same communities (Duffey, 1975), conservation of duff-specialist land snails will likely require protection of the soil litter layer architecture, perhaps by limiting forestry and recreation activities in duff soil sites of conservation importance. While turf sites appear to be more tolerant of human disturbance, this should not indicate that their land snail communities are immune to human activity. For instance, heavy grazing can negatively impact grassland snails (Cameron & Morgan-Huws, 1975), while the use of fire-management can lead to significant reductions in both species richness and abundance (Nekola, 2002b).

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI165/DDI165sm.htm

Appendix 1

Table S1 Species occurrences and frequencies within the six main ordination clusters, and within sites with duff or turf organic horizons.

REFERENCES

Alvarez, J. & Willig, M.R. (1993) Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* **25**, 100–110.

Anderson, W.I. (1983) *Geology of Iowa*, p. 268. Iowa State University Press, Ames, Iowa.

Bába, K. (1989) Zoogeographical conditions of snails living on grass-associations of two Hungarian lowland regions. *Tiscia* **24**, 59–67.

Banfield, J.D. & Raftery, A.E. (1992) Model-based Gaussian and non-Gaussian clustering. *Biometrics* **49**, 803–822.

Barbour, M.G. & Billings, W.D. (1988) *North American terrestrial vegetation*, p. 434. Cambridge University Press, New York.

Barker, G.M. & Mayhill, P.C. (1999) Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru Ecological District, northeastern New Zealand. *Journal of Biogeography* **26**, 215–238.

Baur, B., Joshi, J., Schmid, B., Hänggi, A., Borcard, D., Stary, J., Pedroli-Christen, A., Thommen, G.H., Luka, H., Rusterholz, H.P., Oggier, P., Ledergerber, S. & Erhardt, A. (1996) Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. *Revue Suisse de Zooligie* **103**, 801–833.

Berry, F.G. (1973) Patterns of snail distribution at Ham Street Woods National Nature Reserve, East Kent. *Journal of Conchology* **28**, 23–35.

Borcard, D. & Matthey, W. (1995) Effect of a controlled trampling of *Sphagnum* mosses on their Oribatid mite assemblages (Acari, Oribatei). *Pedobiologia* **39**, 219–230.

Boycott, A.E. (1934) The habitats of land mollusca in Britain. *Journal of Ecology* **22**, 1–38.

Branquart, E., Kime, R.D., Dufrêne, M., Tavernier, J. & Wauthy, G. (1995) Macroarthropod-habitat relationships in oak forests in South Belgium. 1. Environments and communities. *Pedobiologia* **39**, 243–263.

Burch, J.B. (1956) Distribution of land snails in plant associations in eastern Virginia. *Nautilus* **70**, 60–64.

Burch, J.B. & Pearce, T.A. (1990) Terrestrial Gastropoda. *Soil Biology Guide* (ed. by D.L. Dindal), pp. 201–309. John Wiley & Sons, New York.

Cain, A.J. (1983) Ecology and ecogenetics of terrestrial molluscan populations. *The Mollusca*, Vol. 6. Ecology (ed. by W.D. Russell-Hunter), pp. 597–647. Academic Press, New York.

Cameron, R.A.D. (1982) Life histories, density, and biomass in a woodland snail community. *Journal of Molluscan Studies* **48**, 159–166.

Cameron, R.A.D. (1986) Environment and diversities of forest snail faunas from coastal British Columbia. *Malacologia* **27**, 341–355.

Cameron, R.A.D. (2002) Some species/area relationships in the British land mollusc fauna and their implications. *Journal of Conchology* **37**, 337–348.

Cameron, R.A.D. & Morgan-Huws, D.I. (1975) Snail faunas in the early stages of a chalk grassland succession. *Biological Journal of the Linnean Society* **7**, 215–229.

Coleman, D.C. & Crossley, D.A. Jr (1996) *Fundamentals of soil ecology*. Academic Press, New York.

Cowie, R.H. & Jones, J.S. (1987) Ecological interactions between *Cepaea nemoralis* and *Cepaea hortensis*:

competition, invasion, but no niche displacement. *Functional Ecology* **1**, 91–97.

Cowie, R.H., Nishida, G.M., Basset, Y. & Gon, S.M. III (1995) Patterns of terrestrial gastropod distribution in a montane habitat on the island of Hawaii. *Malacologia* **36**, 155–169.

Duffey, E. (1975) The effects of human trampling on the fauna of grassland litter. *Biological Conservation* **7**, 255–274.

Eichenlaub, V.L. (1979) *Weather and climate of the Great Lakes region*. University of Notre Dame Press, Notre Dame, Indiana.

Emberton, K.C., Pearce, T.A. & Randalana, R. (1996) Quantitatively sampling land-snail species richness in Madagascan rainforests. *Malacologia* **38**, 203–212.

Equihua, M. (1990) Fuzzy clustering of ecological data. *Journal of Ecology* **78**, 519–534.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57–68.

Frest, T.J. (1990) Final report, field survey of Iowa spring fens. Contract no. 65–2454. Iowa Department of Natural Resources, Des Moines.

Frest, T.J. (1991) *Summary status reports on eight species of candidate land snails from the Driftless Area (Paleozoic Plateau), Upper Midwest*. Final Report, contract no. 301–01366, USFWS Region 3. Ft. Snelling, Minnesota.

Greenslade, P. (1997) Are Collembola useful as indicators of the conservation value of native grasslands? *Pedobiologia* **41**, 215–220.

Hartigan, J.A. (1975) *Clustering Algorithms*. John Wiley Press, New York.

Hawkins, J.W., Lankester, M.W. & Nelson, R.R.A. (1998) Sampling terrestrial gastropods using cardboard sheets. *Malacologia* **39**, 1–9.

Hermida, J., Ondina, M.P. & Rodriguez, T. (2000) The relative importance of edaphic factors on the distribution of some terrestrial gastropod species: autecological and synecological approaches. *Acta Zoologica Academiae Scientiarum Hungaricae* **46**, 265–274.

Hubricht, L. (1985) The distributions of the native land mollusks of the eastern United States. *Fieldiana N.S.* **24**, 1–191.

Kay, F.R., Sobhy, H.M. & Whitford, W.G. (1999) Soil microarthopods as indicators of exposure to environmental stress in Chihuahuan Desert rangelands. *Biology and Fertility of Soils* **28**, 121–128.

Kerney, M.P. & Cameron, R.A.D. (1979) *Field guide to the land snails of the British Isles and northwestern Europe*, p. 288. Collins Press, London.

Kovac, L. & Miklisova, D. (1997) Collembolan communities (Hexapoda, Collembola) in arable soils of East Slovakia. *Pedobiologia* **41**, 62–68.

Lavelle, P., Lattaud, C., Trigo, D. & Barois, I. (1995) Mutualism and biodiversity in soils. *Plant and Soil* **170**, 23–33.

Locasciulli, O. & Boag, D.A. (1987) Microdistribution of terrestrial snails (Stylommatophora) in forest litter. *Canadian Field Naturalist* **101**, 76–81.

Magnin, F., Tatoni, T., Roche, P. & Baudry, J. (1995) Gastropod communities, vegetation dynamics and landscape changes along an old-field succession in Provence, France. *Landscape and Urban Planning* **31**, 249–257.

Mason, C.F. (1970) Snail populations, beech litter production, and the role of snails in litter decomposition. *Oecologia* **5**, 215–239.

McCracken, D.I. (1994) A fuzzy classification of moorland ground beetle (Coleoptera: Carabidae) and plant communities. *Pedobiologia* **38**, 12–27.

Minchin, P.R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**, 89–108.

Minchin, P.R. (1990) *DECODA Software*. Australian National University, Canberra.

Nekola, J.C. (1999) Terrestrial gastropod richness of carbonate cliff and associated habitats in the Great Lakes region of North America. *Malacologia* **41**, 231–252.

Nekola, J.C. (In press) Terrestrial gastropod fauna of northeastern Wisconsin and the southern Upper Peninsula of Michigan. *American Malacological Bulletin*, in press.

Nekola, J.C. (2002) Effects of fire management on the richness and abundance of central North American grassland land snail faunas. *Animal Biodiversity and Conservation* **25**: 53–66.

Nekola, J.C. & Smith, T.A. (1999) Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. *Malacologia* **41**, 253–269.

Oggier, P., Zschokke, S. & Baur, B. (1998) A comparison of three methods for assessing the gastropod community in dry grasslands. *Pedobiologia* **42**, 348–357.

Ondina, P. & Mato, S. (2001) Influence of vegetation type on the constitution of terrestrial gastropod communities in northwest Spain. *Veliger* **44**, 8–19.

Pearce, T.A. (1997) Interference and resource competition in two land snails: adults inhibit conspecific juvenile growth in field and laboratory. *Journal of Molluscan Studies* **63**, 389–399.

Ports, M.A. (1996) Habitat affinities and distributions of land gastropods from the Ruby Mountains and East Humboldt Range of northeastern Nevada. *Veliger* **39**, 335–341.

Schmid, G. (1966) Die mollusken des Spitzbergs. *Der Spitzberg bei Tübingen, Natur und Landschaftsschutzgebiete, Baden-Würtemburg* **3**, 596–701.

Smallridge, M.A. & Kirby, G.C. (1988) Competitive interactions between the terrestrial gastropods *Thebia pisana* (Müller) and *Cernuella virgata* (DaCosta) from South Australia. *Journal of Molluscan Studies* **54**, 251–258.

Stamol, V. (1991) Coenological study of snails (Mollusca: Gastropoda) in forest phytocoenoses of Medvednica mountain (NW Croatia, Yugoslavia). *Vegetatio* **95**, 33–54.

Stamol, V. (1993) The influence of ecological characteristics of phytocoenoses on the percentage proportions of zoogeographical elements in the malacocoenoses of land snails (Mollusca: Gastropoda terrestrial). *Vegetatio* **109**, 71–80.

Statistical Sciences (1995) *S-PLUS Guide to Statistical and Mathematical Analysis*, Version 3.3. Seattle, Washington.

Suominen, O. (1999) Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia. *Ecography* **22**, 651–658.

Tattersfield, P. (1990) Terrestrial mollusc faunas from some South Pennine woodlands. *Journal of Conchology* **33**, 355–374.

Taylor, R.J., Walsh, A.M. & Brereton, R.N. (1995) Local distributions of terrestrial amphipods within highland wet forests in central Tasmania. *Pedobiologia* **39**, 78–85.

Theler, J.L. (1997) The modern terrestrial gastropod (land snail) fauna of western Wisconsin's hill prairies. *Nautilus* **110**, 111–121.

Van Es, J. & Boag, D.A. (1981) Terrestrial molluscs of central Alberta. *Canadian Field-Naturalist* **95**, 76–79.

Wäreborn, I. (1970) Environmental factors influencing the distribution of land molluscs in an oligotrophic area in southern Sweden. *Oikos* **21**, 285–291.

Whitford, W.G. & Sobhy, H.M. (1999) Effects of repeated drought on soil microarthropod communities in the northern Chihuahuan Desert. *Biology and Fertility of Soils* **28**, 117–120.

Young, M.S. & Evans, J.G. (1991) Modern land mollusc communities from Flat Holm, South Glamorgan. *Journal of Conchology* **34**, 63–70.

Zar, J.H. (1984) *Biostatistical Analysis*. Prentice Hall, Inc., Englewood Cliffs, New Jersey.

Trimethylamine induces migration of waterfleas

It has long been known that the waterflea *Daphnia hyalina* exhibits diel vertical migration in the water column, but the chemical that triggers this behaviour has not been identified. We find that trimethylamine (TMA), which is a major component of the odour produced by decaying fish, induces *Daphnia* to migrate to greater depths during the day, presumably to avoid predation by fish[1,2]. We observed a gradual increase in average depth of *Daphnia* with increasing TMA concentration. Changes in light intensity are known to trigger migration[3], and chemicals produced by their predators must also be present[4]. Because migration has demographic and physiological costs, this chemical cue ensures that zooplankton migration occurs only when fish are present.

It has been shown that, whatever the migration trigger substance may be, it is produced only by fish in the presence of bacteria. This led to the hypothesis that trimethylamine-*N*-oxide (TMAO), which is important for cell volume regulation[5] and protein stabilization[6] in marine and freshwater fish, could be a precursor of the kairomone. Surplus TMAO is deposited in fish scales[7], and bacteria of the skin mucus layer are known to reduce TMAO to TMA[8].

We tested the hypothesis that TMA induces vertical migration in *Daphnia* by using a range of different concentrations, from 0 to 500 μM TMA, in autoclaved lake water[9] (Fig. 1). Five individuals of a single *Daphnia hyalina* clone were put into each of four Perspex tubes (1 m long and 1.5 cm in diameter) per treatment. The tubes were then placed in a water bath with a temperature gradient from top to bottom of 20 to 10 °C. We used a spectrophotometric assay procedure[10] to establish the TMA concentration in 10 litres of the medium that had previously contained four fish (ides, *Leuciscus idus*, 10 cm long), and recorded the resulting vertical migration behaviour of daphnids exposed to this medium. TMA concentration in this 'fish' water was between 10 and 25 μM.

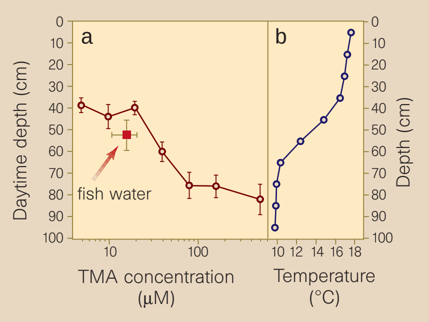

Figure 1 Behavioural responses of *Daphnia hyalina* to trimethylamine. **a**, Average day depth (± standard error) of five daphnids (four replicates per treatment) on three consecutive days of different TMA concentrations. The day:night cycle was 16:8 hours. The reaction of the daphnids is plotted against the concentration of TMA in fish water. Bacterial decay of TMA was prevented by the addition of ampicillin. Migration depth increased in all tubes from day 1 to day 3. **b**, Temperature profile of the tubes. As TMA concentration increases, daphnids migrate to greater depths and colder water during the day.

We found that even low concentrations of TMA induce *Daphnia* to migrate to deeper waters during the day in our test system. At night, they migrate back to the surface when exposed to small amounts of TMA, and stay near the bottom when TMA levels are high (more than 100 μM). When the lowest TMA concentration that induces vertical migration is compared with the activity in the fish water, it is clear that the reaction of *Daphnia* to fish water is stronger than just to TMA alone. This indicates that, although TMA is an active component of the 'fish factor', it is likely to be part of a cocktail of substances that deter *Daphnia*. The other substances probably help to reduce the chemical threshold that induces migration. It is not clear whether the TMA concentrations used in this study represent realistic values for aquatic systems, as we could find no published details of TMA concentrations in aquatic systems.

It has been shown[9] that the fish kairomone is broken down by bacteria. We therefore compared the average day depth of daphnids exposed to 75 μM TMA in autoclaved water, and with the antibiotic ampicillin added and the TMA dissolved in non-autoclaved lake water. The migration activity of the *Daphnia* in non-sterile water slowly decreased over time (Fig. 2). After 72 hours, the average day depth of the animals in non-sterile conditions was no longer significantly different from the average day depth of animals in sterile control medium.

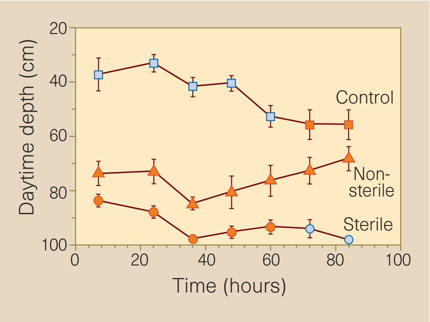

Figure 2 Average day depth (± s.e.) of five daphnids. There were eight replicates per treatment. Symbols with different colours indicate significant differences between the treatments (Tukey post hoc comparison after analysis of variance, with treatment as a factor and time as a repeated measurement factor). Sterile and non-sterile treatments are not significantly different from each other, but were significantly different from the control for the first 60 hours; after 72 hours, daphnids kept under sterile conditions are significantly deeper than the control animals and those kept under non-sterile conditions.

To investigate whether simply adding any substance to the water induces vertical migration, we added the same amount of TMAO and triethylamine to sterile water (both at 75 μM). As with the control *Daphnia*, there was no significant increase in day depth. We therefore conclude that the reaction to TMA is a specific one, and not simply a response to a change in conductivity or ionic strength of the medium.

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1. Stich, H. B. & Lampert, W. *Nature* **293,** 396–398 (1981).
2. Gliwicz, M. Z. *Nature* **320,** 746–748 (1986).
3. Ringelberg, J. *J. Mar. Biol. Assoc. UK* **75,** 15–25 (1995).
4. Larsson, P. & Dodson, S. *Arch. Hydrobiol.* **129,** 129–155 (1993).
5. Lange, R. & Fugelli, K. *Comp. Biochem. Physiol.* **25,** 283–292 (1965).
6. Yancey, P. H. & Somero, G. N. *Biochem. J.* **183,** 317–323 (1979).
7. Hill, R. W. *Comparative Physiology of Animals* (Harper & Row, New York, 1976).
8. Gram, L., Wedell Neergaard, C. & Huss, H. H. *Int. J. Food Microbiol.* **10,** 303–316 (1990).
9. Loose, C. J., von Elert, E. & Dawidowicz, P. *Arch. Hydrobiol.* **126,** 329–337 (1993).
10. Kakác, B. & Vejdelek, Z. J. *Handbuch der Photometrischen Analyse Organischer Verbindungen* (Chemie, Weinheim, 1974).

Ancient stunted trees on cliffs

An undisturbed ancient woodland, dominated by tiny, slow-growing and widely spaced trees, grows on vertical cliffs of the Niagara escarpment in southern Canada[1]. To investigate whether this woodland is unusual or is part of a previously undetected global pattern, we sampled ages and radial growth rates for trees on cliffs in the United States and in western Europe. We find that vertical cliffs often support populations of widely spaced trees that are exceptionally old, deformed and slow growing. Some of the most ancient and least-disturbed wooded habitat types on Earth are found on cliffs, even at sites close to heavy agricultural and industrial development.

We selected 21 cliffs for sampling in 15 eastern states of the United States, and 25 cliffs in eastern and southern Germany, eastern and southern France, central and northern England and Wales. All areas have been heavily developed for industry and agriculture over a long time. The cliffs visited were at least 500 metres long and between 20 and 1,500 metres high. We extracted increment cores for analysis from near the base of 224 mature trees. Some individual living trees grew as thin stem-strips on large amounts of dead wood. We

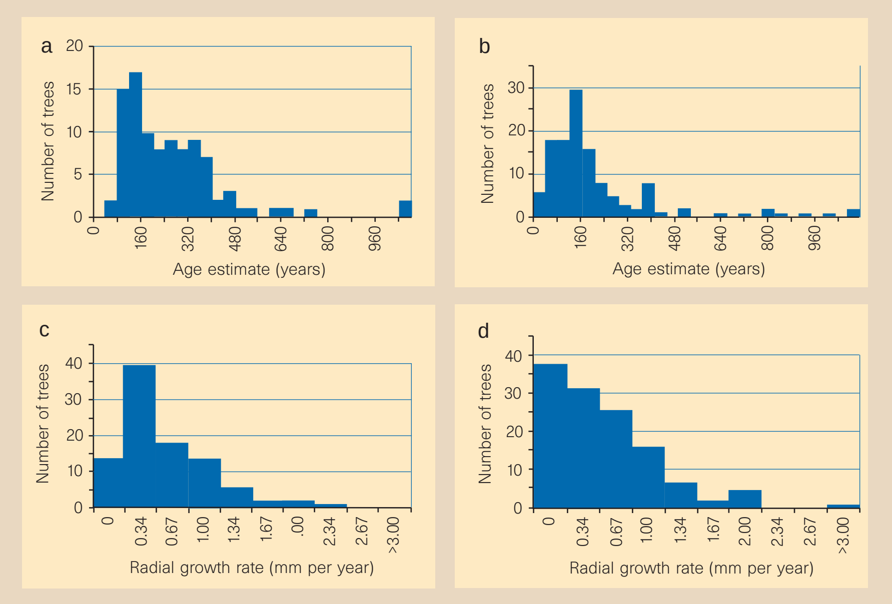

Figure 1 Age estimates and growth rates of trees on cliffs. Frequency distributions of estimated tree ages (**a**, **b**) and radial growth rates (**c**, **d**) for mature trees growing on cliffs in the United States (**a**, **c**, *n*=97) and Europe (**b**, **d**, *n*=127).

sometimes took cross-sections from the dead parts of these trees to allow for more accurate dating of core samples extracted from the living portions.

We recorded the diameter of each tree and the location of the pith for more accurate age estimations when core samples did not include the pith[2]. We then used the distance from the cambium to the youngest ring to calculate radial growth rate, expressed as millimetres of new wood per year. All sample cores or sections were mounted and sanded[3]. Results were plotted as frequency distributions for both age estimate and growth rate, and US and European results were compared using non-parametric tests[4,5]. For age estimates, we expected to find evidence of a negative exponential frequency distribution if the mature trees on the cliffs were part of a self-maintaining natural woodland[6]. For growth rate, we expected to find a tight clustering of very low values if the mature trees were highly constrained in their productivity[7].

Most of the US trees sampled are between 160 and 400 years old, with two trees being more than 1,000 years old and very few less than 100 years old. The trees were mainly *Thuja occidentalis* in the northern states and *Juniperus virginiana* in the rest. Despite our non-random sampling, the portion of the curve above 80 years of age has the shape of a negative exponential (Fig. 1a). European trees also have a negative exponential age distribution when the youngest age category is excluded (Fig. 1b), and some *J. phoenicea* and *Taxus baccata* trees in France and the United Kingdom, respectively, were more than 1,000 years old. We found unevenly aged living tree populations on all cliffs, and observed coarse woody debris in a variety of decay states. The findings indicate that the populations on both continents have remained undisturbed for long periods, and have had continuous, rather than pulsed, recruitment over the past millennium.

Radial growth rates for trees in the United States (Fig. 1c) and Europe (Fig. 1d) were mostly less than 1 millimetre per year, similar to the rate for trees growing on the Niagara escarpment[1]. They must be some of the slowest-growing woody plants on Earth. All the trees were grossly deformed as well as stunted. A 1.5-metre-tall, 1,140-year-old *J. phoenicea* tree, for example, from the Verdon Gorge, France, had a radius of nearly 8 cm and an annual radial growth rate slightly more than 0.06 mm. Its axial morphology was typical of cliff trees in exhibiting partial cambial mortality and an inverted morphology. All core samples from cliff-face trees showed radial growth rates that were the same in the sapling and the mature stages of development.

The ages of the trees may indicate the ages and growth rates of the entire plant communities on the cliffs. Cliffs across the world may support ancient, slow-growing, open woodland communities that have escaped major human disturbance, even when they are situated close to agricultural and industrial activity, which has destroyed or altered most other natural habitats[8–10].

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1. Larson, D. W. & Kelly, P. E. *Can. J. Bot.* **69,** 1628–1636 (1991).
2. Kelly, P. E. & Larson, D. W. *J. Ecol.* **85,** 467–478 (1997).
3. Kelly, P. E., Cook, E. R. & Larson, D. W. *Can. J. Forest. Res.* 24, 1049–1057 (1994).
4. Zar, J. H. *Biostatistical Analysis* (Prentice-Hall, Englewood Cliffs, NJ, 1974).
5. Conover, W. J. *Practical Non-parametric Statistics* 2nd edn (Wiley, New York, 1971).
6. Hett, J. M. & Loucks, O. L. *J. Ecol.* **64,** 1029–1044 (1976).
7. Kelly, P. E., Cook, E. R. & Larson, D. W. *Int. J. Plant Sci.* **153,** 117–127 (1992).
8. Vitousek, P. M. *Ecology* **75,** 1861–1876 (1994).
9. Spencer, J. W. & Kirby, K. J. *Biol. Conserv.* **62,** 77–93 (1992).
10. Peterken, G. F. *Natural Woodland* (Cambridge Univ. Press. 1996).

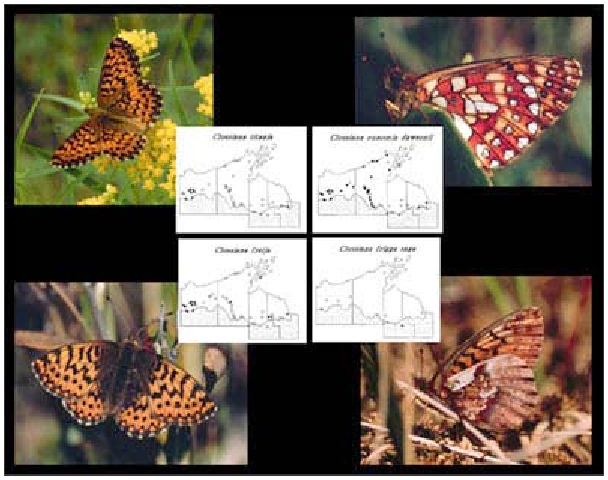
Molecular basis of triclosan activity

Triclosan (5-chloro-2-(2,4-dichlorophenoxy) phenol) has been used for more than 30 years as a general antibacterial and antifungal agent, and is found in formulations as diverse as toothpastes, cosmetics, antiseptic soaps, carpets, plastic kitchenware and toys. It has recently been suggested that triclosan blocks lipid biosynthesis by specifically inhibiting the enzyme enoyl–acyl carrier protein reductase (ENR)[1]. We have carried out a structural analysis and inhibition experiments on a complex of ENR from the bacterium *Escherichia coli* with triclosan and NAD^+. We find that triclosan acts as a site-directed, very potent inhibitor of the enzyme by mimicking its natural substrate.

ENR catalyses the final, regulatory step in the fatty-acid synthase cycle: the reduction of a carbon–carbon double bond in an enoyl moiety that is covalently linked to an acyl carrier protein. ENR has been identified as a target for the diazaborines[2], a family of antibacterial agents, and many triclosan-resistant strains of *E. coli* have been found to be resistant to diazaborines[1].

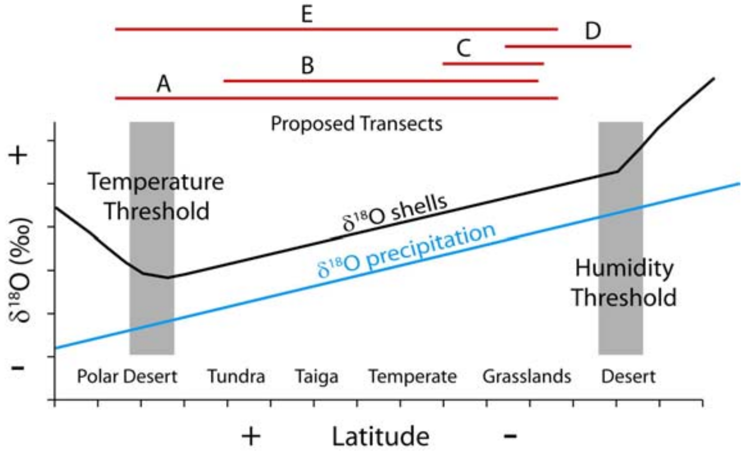
The structure of the *E.coli* ENR complexed with NAD^+ and triclosan (triclosan was provided by Ciba Speciality Chemicals and Coalite Chemicals) was determined to 2.2 Å resolution. The electron density map of the complex is of high quality (Fig. 1a) and reveals the mode of binding of the triclosan adjacent to the nicotinamide ring of the nucleotide cofactor in the enzyme's active site. The phenol ring of triclosan forms a face-to-face interaction with the

Section III: Spatio-Temporal Ecology



Ecological patterns are not solely based upon the local, contemporaneous environment. Due to the lags inherent in complex systems, these patterns are also often impacted by drivers separated by distance in either space or time. As a result, simply knowing local conditions is often not enough to accurately predict what patterns will develop. Understanding how ecological systems change over space and time, and how spatial and temporal contingencies effect current patterns has been a long-standing focus of my research efforts. These investigations help determine the nature of spatial and temporal heterogeneities in ecological systems, and the extent to which these systems are in equilibrium with the local environment.

Additionally, there is no better way to determine the potential impacts of global environmental change than to empirically study how past changes have impacted ecological systems. Land snails are excellent for this purpose as they are found across all of Earth's terrestrial biomes and represent one of the most diverse groups of multicellular life. Their shells also represent one of the most common fossils in the temperate terrestrial geological record. As a result, this group has the potential to be as important in generating paleoclimate proxies for terrestrial systems as foraminifera are in the deep sea. Along with Jeffery Pigati of the US Geological Survey and Jason Rech of Miami University, our team first documented through a series of highly cited papers that many land snail phylogenetic groups have shells that are in equilibrium with environmental ^{14}C and thus can be used to accurately date terrestrial sediments that lack traditional organic carbon sources (e.g., wood, peat). We have now turned our efforts to O-isotopes. Our current NSF grant (running through 2018) will document climatic, environmental and biological controls on the oxygen isotopic composition of land snail shells. We anticipate that this work will lead to a subsequent proposal which, if funded, will establish through field surveys across North America the fidelity of shell O-isotopes ratios in the documentation of modern and prior



Theoretical relation between δ^{18}O of land snail shell carbonate and latitude. The red horizontal lines marked A-E denote our five proposed transects to calibrate land snail $\delta^{18}O_{shell}$ systematics regional climatic conditions. This work has the potential to revolutionize terrestrial paleoclimatic proxies given that the same shells can theoretically provide not only useful chronometric but also environmental data.

Additionally, along with Michal Horsák and Jan Divíšek I am exploring macroevolutionary process in Holarctic land snails using modern macroecology of these species in combination with their current molecular phylogenetics. These data are being applied to Late Glacial Maximum climate models to identify reasons for allopatric replacement within the boreal land snail fauna between three general regions: Europe, Beringia, and North America. Preliminary results suggest that geographic isolation of these regions during LGM times (climatic between Europe and Beringia; ice sheet between Beringia and North America) may well explain modern observed turnover patterns.

Representative Publications
[number of citations as of October 27, 2017]

Chytrý, M., M. Horsák, V. Syrovátka, J. Danihelka, N. Ermakov, D.A. German, M. Hájek, O. Hájek, P. Hájková, V. Horsáková, M. Kočí, S. Kubešová, P. Lustyk, **J.C. Nekola**, Z. Preislerová, P. Resl & M. Valachovi. 2017. Refugial ecosystems in central Asia as indicators of biodiversity change during the Pleistocene–Holocene transition. *Ecological Indicators*. 76:357-367. **[4]**

Bajc, A.F., P.F. Karrow, C.H. Yansa, B.B. Curry, **J.C. Nekola**, K. Seymour & G.L. Mackie. 2015. Geology and paleoecology of a Middle Wisconsin fossil occurrence in Zorra Township, southwestern Ontario, Canada. *Canadian Journal of Earth Sciences*. 52:386–404. **[4]**

Horsák, M., M. Chytrý, P. Hájková, M. Hájek, J. Danihelka, V. Horsáková, N. Ermakov, D.A. German, M. Kočí, P. Lustyk, **J.C. Nekola**, Z. Preislerová & M. Valachovič. 2015. European glacial relict snails and plants: environmental context of their modern refugial occurrence in southern Siberia. *Boreas*. 44:638-657. **[14]**

Pigati, J.S., J.P. McGeehin, D.R. Muhs, D.C. Grimley & **J.C. Nekola**. 2015. Radiocarbon dating loess deposits in the Mississippi Valley using terrestrial gastropod shells (Polygyridae, Helicinidae, Discidae). *Aeolian Research*. 16:25-33. **[5]**

Rakovan, M.T., J.A. Rech, J.S. Pigati, **J.C. Nekola** & G.C. Wiles. 2013. An evaluation of *Mesodon* and other large terrestrial gastropod shells for dating late Holocene and historic alluvium in the midwestern USA. *Geomorphology*. 193:47-56. **[11]**

Horsák, M., M. Hájek, D. Spitale, P. Hájková, D. Dítě & **J.C. Nekola**. 2012. The age of island-like habitats impacts habitat specialist species richness. *Ecology*. 93:1106-1114. **[46]**

Rech, J.A., **J.C. Nekola** & J.S. Pigati. 2012. Radiocarbon ages of terrestrial gastropods extend duration of ice-free conditions at the Two Creeks forest bed, Wisconsin, USA. *Quaternary Research*. 77:289-292. **[11]**

Pigati, J.S., D.M. Miller, S.A. Mahan, J.A. Bright, **J.C. Nekola** & J.B. Paces. 2011. Chronology, sedimentology, and microfauna of ground-water discharge deposits in the central Mojave Desert, Valley Wells, California. *Geological Society of America Bulletin*. 123:2224-2239. **[24]**

Rech, J.A., J.S. Pigati, S.B. Lehmann, C.N. McGimpsey, D.A. Grimley & **J.C. Nekola**. 2011. Assessing open-system behavior of 14-C in terrestrial gastropod shells. *Radiocarbon.* 53:325-335. **[17]**

Pigati, J.S., J.A. Rech & **J.C. Nekola**. 2010. Radiocarbon dating of small terrestrial gastropod shells in North America. *Quaternary Geochronology*. 5:519-532. **[94]**

Nekola, J.C. & C.E. Kraft. 2002. Spatial constraint of peatland butterfly occurrences within a heterogeneous landscape. *Oecologia.* 130:62-71. **[21]**

Kraft, C.E., P.J. Sullivan, A.Y. Karatayev, L.E. Burlakova, **J.C. Nekola**, L.E. Johnson & D.K. Padilla. 2002. Landscape patterns of an aquatic invader: assessing dispersal extent from spatial distributions. *Ecological Applications.* 12:749-759. **[68]**

Nekola, J.C. 1999. Paleorefugia and neorefugia: the influence of colonization history on community pattern and process. *Ecology.* 80: 2459-2473. **[121]**

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Research Paper

Radiocarbon dating of small terrestrial gastropod shells in North America

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ABSTRACT

Fossil shells of small terrestrial gastropods are commonly preserved in wetland, alluvial, loess, and glacial deposits, as well as in sediments at many archeological sites. These shells are composed largely of aragonite ($CaCO_3$) and potentially could be used for radiocarbon dating, but they must meet two criteria before their ^{14}C ages can be considered to be reliable: (1) when gastropods are alive, the ^{14}C activity of their shells must be in equilibrium with the ^{14}C activity of the atmosphere, and (2) after burial, their shells must behave as closed systems with respect to carbon. To evaluate the first criterion, we conducted a comprehensive examination of the ^{14}C content of the most common small terrestrial gastropods in North America, including 247 AMS measurements of modern shell material (3749 individual shells) from 46 different species. The modern gastropods that we analyzed were all collected from habitats on carbonate terrain and, therefore, the data presented here represent worst-case scenarios. In sum, ~78% of the shell aliquots that we analyzed did not contain dead carbon from limestone or other carbonate rocks even though it was readily available at all sites, 12% of the aliquots contained between 5 and 10% dead carbon, and a few (3% of the total) contained more than 10%. These results are significantly lower than the 20–30% dead carbon that has been reported previously for larger taxa living in carbonate terrain. For the second criterion, we report a case study from the American Midwest in which we analyzed fossil shells of small terrestrial gastropods (7 taxa; 18 AMS measurements; 173 individual shells) recovered from late-Pleistocene sediments. The fossil shells yielded ^{14}C ages that were statistically indistinguishable from ^{14}C ages of well-preserved plant macrofossils from the same stratum. Although just one site, these results suggest that small terrestrial gastropod shells may behave as closed systems with respect to carbon over geologic timescales. More work on this subject is needed, but if our case study site is representative of other sites, then fossil shells of some small terrestrial gastropods, including at least five common genera, *Catinella*, *Columella*, *Discus*, *Gastrocopta*, and *Succinea*, should yield reliable ^{14}C ages, regardless of the local geologic substrate.

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1. Introduction

Gastropods are one of the most successful animal groups on Earth, with at least 70,000 extant species occupying terrestrial, marine, and freshwater habitats. Globally, terrestrial gastropods encompass at least 35,000 species (Barker, 2001), span 4–5 orders of magnitude in shell volume, and represent a variety of trophic levels, including polyphagous detritivores, herbivores, omnivores, and carnivores (Kerney and Cameron, 1979; Burch and Pearce, 1990). They are so exceptionally diverse in their appearance, ecology, and physiology that determining their phylogenetic relationships from conchological and/or anatomical characteristics remains difficult and controversial (e.g., Ponder and Lindberg, 1997 and references therein). It is clear, however, that the preference for terrestrial habitats of North American gastropods developed independently in three of six basal clades (Neritomorpha, Caenogastropoda, and Heterobranchia), with the informal group Pulmonata representing more than 99% of the continental fauna. Of the Pulmonata, the most common size class[1] in both modern and fossil assemblages are individuals with adult shells that are <10 mm in maximum dimension (Nekola, 2005) (Fig. 1).

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[1] Size classes of gastropods are categorized by the maximum shell dimension (length or diameter) as follows: large (>20 mm), medium (10–20 mm), small (5–10 mm), minute (2–5 mm), and micro (<2 mm). Although the size of the gastropods targeted in this study range from small to micro, for simplicity, we refer to them collectively as “small”.

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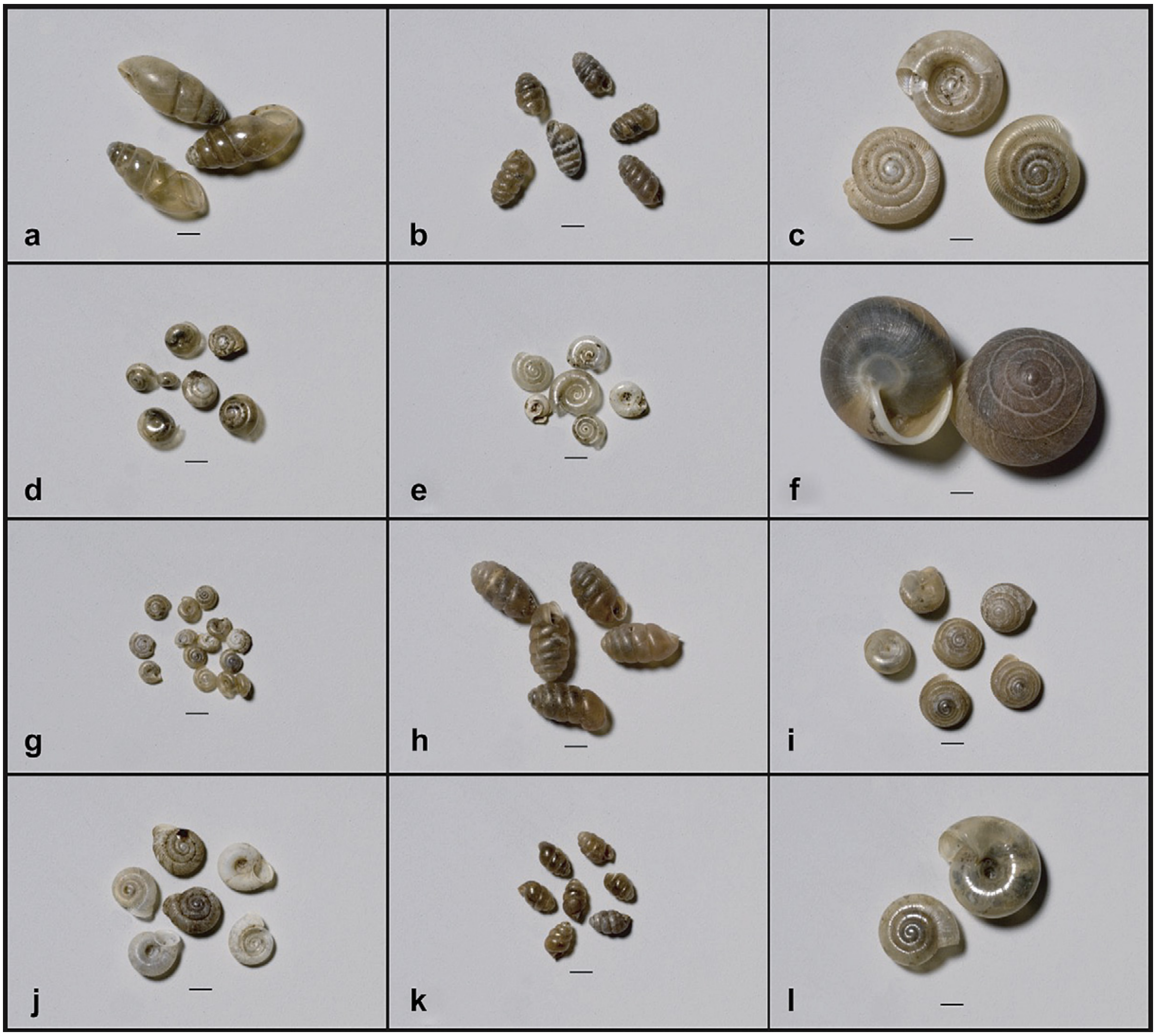

Fig. 1. Photographs of select small terrestrial gastropods included in this study (1 mm bar in each panel for scale). (a) *Cochlicopa lubricella*, (b) *Columella columella alticola*, (c) *Discus macclintockii*, (d) *Euconulus fulvus*, (e) *Hawaiia miniscula*, (f) *Hendersonia occulta*, (g) *Punctum minutissimum*, (h) *Pupilla muscorum*, (i) *Strobilops labyrinthica*, (j) *Vallonia gracilicosta*, (k) *Vertigo elatior*, and (l) *Zonitoides arboreus*.

Today, small terrestrial gastropods occupy and thrive in incredibly diverse habitats, from marshes, wet meadows, and grasslands to upland forests and tundra. Species are known from all continents, save Antarctica, and occupy almost all climate regimes except hyperarid deserts and the high Arctic. Their distribution in the fossil record is equally diverse. Gastropod shells are commonly preserved in wetland, alluvial, loess, and glacial deposits, as well as within sediments at archeological sites worldwide (e.g., Evans, 1972). But even though their distribution is widespread and their aragonitic shells contain ~12% by weight carbon, terrestrial gastropods are often avoided for ^{14}C dating because many taxa incorporate ^{14}C-deficient (or "dead") carbon from limestone and other carbonate rocks when building their shells. This phenomenon, referred to as the "Limestone Problem" by Goodfriend and Stipp (1983), can cause ^{14}C ages of gastropod shells to be as much as ~3000 yrs too old.

Despite the Limestone Problem, geochronologists have continued to investigate the possibility of using terrestrial gastropod shells for ^{14}C dating because of their widespread occurrence and potential for dating Quaternary sediments. Most ^{14}C studies of gastropod shells have found that gastropods consistently incorporate dead carbon from limestone in their shells when it is available (Frye and Willman, 1960; Leighton, 1960; Rubin et al., 1963; Tamers, 1970; Evin et al., 1980; Goodfriend and Hood, 1983; Goodfriend and Stipp, 1983; Goslar and Pazdur, 1985; Yates, 1986; Goodfriend, 1987; Zhou et al., 1999; Quarta et al., 2007; Romaniello et al., 2008). These studies, however, were generally limited to a few individual gastropods collected from a small number of sites, and were biased toward large taxa and warm climates. Brennan and Quade (1997) analyzed a number of small terrestrial gastropod taxa and found that small shells generally yielded reliable ^{14}C ages for late-Pleistocene paleowetland deposits in the American Southwest. Pigati et al. (2004) followed by measuring the ^{14}C activities of a suite of small gastropods living in alluvium dominated by Paleozoic carbonate rocks in Arizona and Nevada and found that while some of the small gastropods did incorporate dead carbon from limestone when building their shells, others did not.

Based in part on these initial positive results, small terrestrial gastropod shells have been used recently to date Quaternary wetland and lacustrine deposits in the Americas (e.g., Pedone and Rivera, 2003; Placzek et al., 2006; Pigati et al., 2009). However, it is unclear if the results obtained from modern gastropods collected from a limited number of sites in the American Southwest can be extrapolated to all geologic, ecologic, and climatic environments. Moreover, it is not known if results for one taxonomic level (family, genus, or species) can be extrapolated to other members of the same level living elsewhere, or even between individuals living within the same population.

Here we report the results of a comprehensive analysis of the Limestone Problem for small terrestrial gastropods from 163 localities in North America (Fig. 2). All samples that we analyzed were collected from habitats on carbonate terrain and, therefore, the data reported here represent worst-case scenarios. In addition, we measured the ^{14}C activities of a number of fossil shells recovered from well-dated sediments at a late-Pleistocene site in the American Midwest as a case study to determine if the shells remain closed systems with respect to carbon over geologic timescales. Positive results for both tests for a particular taxon would allow us to consider ^{14}C ages derived from fossil shells of that taxon to be reliable, regardless of the local geologic substrate.

2. Shell carbonate and ^{14}C dating

All materials (organic and inorganic) that yield reliable ^{14}C ages have two common characteristics. First, the initial ^{14}C activity of the material – a plant, for example – was in equilibrium with atmospheric ^{14}C at the time that it was alive. In other words, the ^{14}C activity of a plant that lived T yrs ago was the same as the ^{14}C activity of the atmosphere T yrs ago (after accounting for isotopic fractionation). Second, after death, the material behaved as a closed system; carbon was neither added to nor removed from the sample material. If both of these criteria are met, then the measured ^{14}C activity is a function of only two parameters: the initial ^{14}C activity of the atmosphere and the amount of time elapsed since the death of the organism.

The measured ^{14}C activity and the ^{14}C age of the material are related by the familiar decay equation

$$A = A_o e^{-\lambda t} \qquad (1)$$

where A and A_o are the measured and initial ^{14}C activities of the material, respectively, λ is the decay constant, and t is the time elapsed since the death of the organism. Conventional radiocarbon ages assume that the atmospheric ^{14}C activity is invariant through time (i.e., $A_o = 1$). Radiocarbon ages can be converted to calendar year ages to account for temporal variations in the ^{14}C activity of the atmosphere (Reimer et al., 2009).

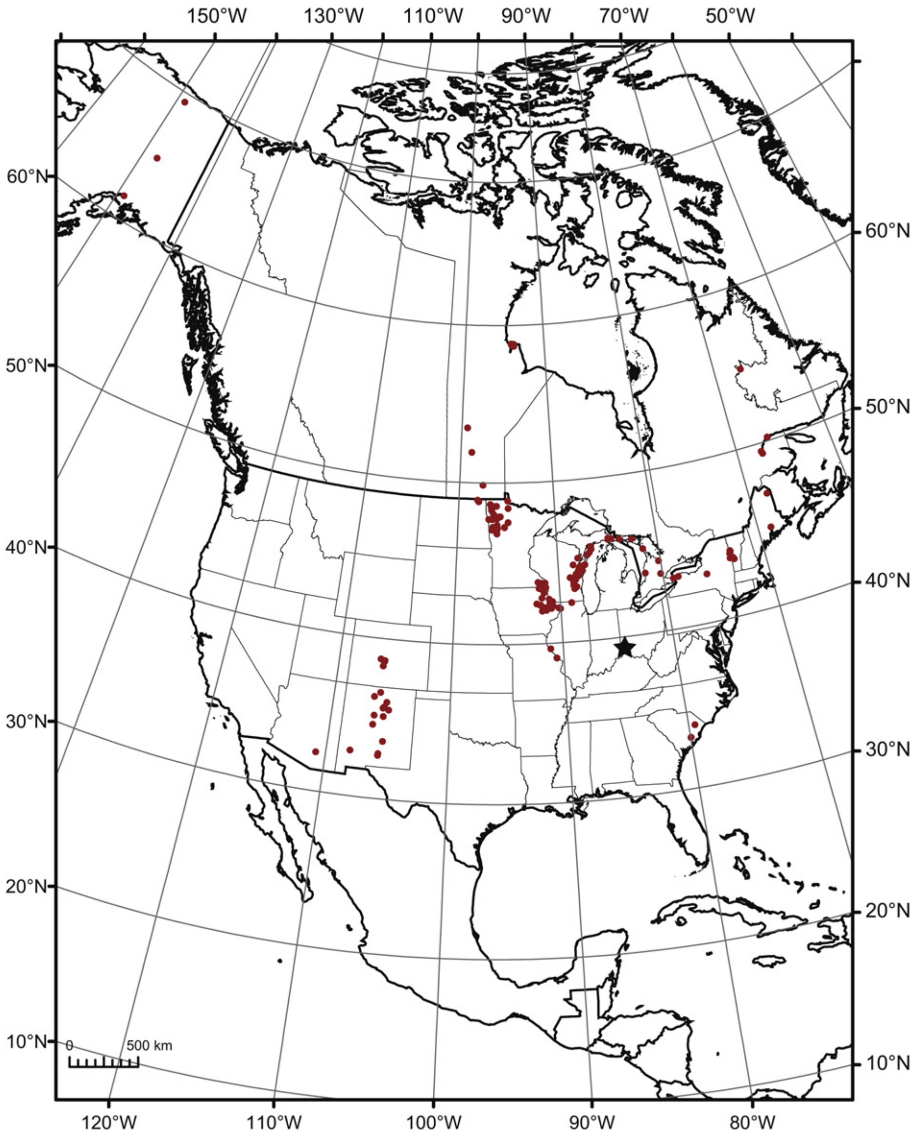

Fig. 2. Locations of modern localities (red dots) and the fossil locality at the Oxford East outcrops in southwestern Ohio (star). Modern localities and collection information are listed in Tables S1 and S2, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

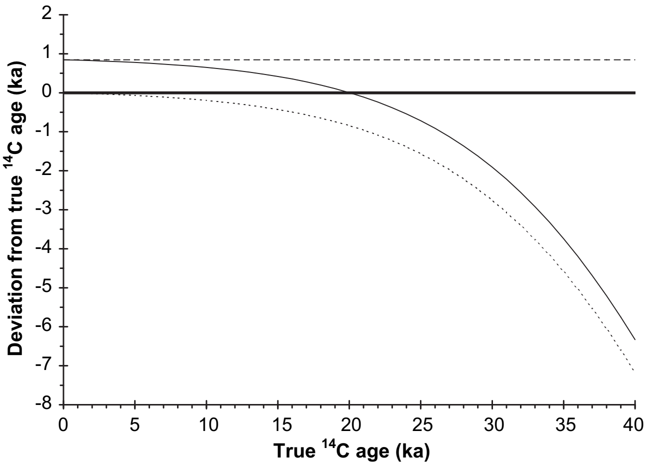

Fig. 3. Modeled deviation from the true ^{14}C age for four scenarios: (1) closed-system behavior and no dead carbon (thick solid line), (2) closed-system behavior and 10% dead carbon (dashed line), (3) open-system behavior equivalent to 1% modern carbon contamination and 10% dead carbon (thin solid line), and (4) open-system behavior equivalent to 1% modern carbon contamination and no dead carbon (dotted line).

2.1. Sources of shell carbon

In order to evaluate the validity of a ^{14}C age of a given sample, the ^{14}C contents of the original sources of the carbon and their contribution to the total carbon content must be known. Carbon in gastropod shell carbonate originates from as many as four different sources: atmospheric CO_2, food, water, and carbonate rocks.

Gastropods incorporate atmospheric CO_2 in their shell carbonate via respiration. Respired CO_2 is introduced to the bicarbonate pool in the gastropod's hemolymph and passed along to the extrapallial fluid, from which the shell carbonate is ultimately precipitated (Wilbur, 1972). Estimates of the contribution of atmospheric CO_2 to gastropod shell carbonate vary between negligible (Stott, 2002), 16–48% (Romaniello et al., 2008), and 30–60% (Goodfriend and Hood, 1983).

Carbon from food sources (e.g., living plants, fungi, organic detritus) is incorporated into the extrapallial fluid through two mechanisms: direct digestion and breakdown of urea. When gastropods consume and digest food, carbon is introduced to the hemolymph and passed along to the extrapallial fluid in the same manner as atmospheric CO_2. There it mixes with atmospheric carbon before becoming incorporated in the shell carbonate (Wilbur, 1972). Carbon derived from urea takes a more indirect pathway. Urea that is not expelled by the gastropod breaks down into CO_2 and NH_3 via a urease reaction (Stott, 2002). The resulting CO_2 is then reintroduced directly to the extrapallial fluid and ultimately incorporated into the shell carbonate. Estimates of the amount of carbon derived from plants, either directly or indirectly through urea, vary between 25 and 40% (Goodfriend and Hood, 1983), 36–73% (Romaniello et al., 2008), and ~100% (Stott, 2002).

Terrestrial gastropods ingest water from multiple sources, including dew, soil moisture, standing water, and precipitation, all of which contain some amount of dissolved inorganic carbon (DIC). Water is taken up through the foot of the gastropod by contact rehydration (Balakrishnan and Yapp, 2004) and introduced to the hemolymph before being passed on to the extrapallial fluid. Pigati et al. (2004) found that aqueous carbon sources account for ~10% of the shell carbon for one species of *Catinella*, but it is not known if this value is constant across the entire Succineidae family. To our knowledge, data for other terrestrial taxa do not exist.

Finally, some terrestrial gastropods are able to scrape carbonate rocks (limestone, dolomite, soil carbonate), and ingest the powder or granules which then dissolve in their stomach acid to produce CO_2. As before, the dead carbon from the rocks is introduced to the hemolymph, passed on to the extrapallial fluid, and ultimately incorporated in the shell carbonate. Dead carbon from limestone can account for up to ~30% of the total carbon in shells of large terrestrial gastropods. (Goodfriend and Stipp, 1983).

2.2. Effects of carbon sources on ^{14}C ages of shell carbonate

In most environments, the ^{14}C activities of live plants are in equilibrium with atmospheric carbon. Gastropods that obtain their shell carbon from live plants and the air, therefore, should yield reliable ^{14}C ages, assuming they behave as closed systems after burial (Fig. 3). Gastropods that consume organic detritus (i.e., decaying plant litter) typically do not pose a significant problem for ^{14}C dating because the time between plant death, its incorporation into decomposition products, and consumption by gastropods is usually quite short, on the order of a few yrs.

The ^{14}C activity of water that is available for consumption by terrestrial gastropods (e.g., dew, standing water, precipitation) is at or near equilibrium with atmospheric ^{14}C and, therefore, water is unlikely to introduce a significant error to ^{14}C ages of terrestrial gastropod shells. Exceptions include gastropods living directly adjacent to springs that discharge waters from deeply-circulating carbonate aquifers, lakes or rivers with significant hard water effects, or in active volcanic areas where ^{14}C-deficient CO_2 in surface waters may be abundant (e.g., Riggs, 1984; Grosjean, 1994). ^{14}C ages of gastropods living in such areas should be evaluated carefully.

The incorporation of ^{14}C from limestone and other carbonate rocks can present a significant problem for ^{14}C dating of terrestrial gastropod shells. The ^{14}C activity of atmospheric carbon, plants, and water consumed by gastropods is essentially the same, ~100% modern carbon (pMC). In contrast, because most carbonate rocks are of pre-Quaternary age, their ^{14}C activity is typically 0 pMC. Thus, for ^{14}C dating, the magnitude of the potential error introduced by carbonate rocks is a direct function of the amount of carbon from rocks that is incorporated in the gastropod shell (Fig. 3). Unfortunately, a simple correction that accounts for the incorporation of ^{14}C-deficient carbon in gastropod shells is not possible because we cannot know *a priori* how much of the shell carbon was derived from carbonate rocks versus other sources. Thus, to be confident in ^{14}C ages derived from terrestrial gastropod shells, it is imperative that we identify and avoid taxa that incorporate dead carbon from rocks altogether.

2.3. Open-system behavior

Even if some terrestrial gastropods consistently manage to avoid the Limestone Problem regardless of the local geologic substrate or environmental conditions, there is another hurdle that must be overcome before we can confidently use their shells for ^{14}C dating. That is, gastropod shells must remain closed systems with respect to carbon after burial. For reliable ^{14}C dating, the pool of carbon atoms measured during the ^{14}C dating process must consist solely of carbon atoms that originally resided in the shell. Thus, following burial, shells must resist the addition or exchange of ^{14}C atoms with the local environment. Shells that exhibit open-system behavior typically yield ^{14}C ages that are too young, and the magnitude of the error depends upon the degree of such behavior (Fig. 3).

Previous work has suggested that ^{14}C ages from small terrestrial gastropod shells recovered from fossil deposits in arid environments may be reliable back to at least ~30,000 ^{14}C yrs B.P., but a small degree of open-system behavior appears to compromise ^{14}C dates obtained from shells older than this (Pigati et al., 2009). In

Fig. 4. Photographs of the three genera of the Succineidae family: *Catinella* (left panels), *Oxyloma* (middle panels), and *Succinea* (right panels); all are ~10 mm in length. The simple shells of the three genera contain few diagnostic characteristics and, therefore, species-level identification is based on soft-body reproductive organ morphology, which is rarely preserved in the fossil record.

this study, we analyzed fossil shells from the American Midwest because of their abundance in Quaternary deposits in the region, the presence of multiple calcareous substrates (Paleozoic limestone, calcareous till, and loess), and the humid climate (annual precipitation in southwestern Ohio is ~100 cm yr^{-1}). If fossil shells exhibit even a small degree of open-system behavior in arid environments, it may be exacerbated and, therefore, more easily detected in humid environments where interaction between shells and DIC in ground water is more prevalent.

3. Methods

3.1. Live gastropods

Previous ecological sampling by one of us (JCN) has resulted in an extensive collection of modern terrestrial gastropods from North America, constituting ~250 taxa and over 470,000 individuals from more than 1000 modern environments. Gastropods were collected at each site from a representative 100–1000 m^2 area by hand collection of larger taxa and litter sampling of smaller taxa, which provides the most complete assessment of site faunas (Oggier et al., 1998; Cameron and Pokryszko, 2005). Collections were made at places of high mollusc density, such as loosely compacted leaf litter lying on top of highly compacted damp soil or humus (Emberton et al., 1996). Litter was removed by hand and sieved by shaking, tapping, or other agitation in the field using a shallow sieve (ASTME #10; 2.0 mm mesh) nested inside a second sieve (ASTME #30; 0.6 mm mesh). The process was continued for 15–60 min during which time 50–500 mg of material was collected and retained.

Gastropods and detritus were dried at room temperature in the laboratory and then hand-picked against a neutral background. All shells, shell fragments, and slug plates were removed and identifiable material was assigned to species using JCN's reference collection. Nomenclature generally follows that of Hubricht (1985) with updates and corrections by Nekola (2004).

We selected 247 aliquots of shell material (3749 individual shells) from 163 sites across the United States and southern Canada for ^{14}C analysis. Nearly all of the specimens that we chose for analysis were collected live, but at a few sites, only recently-dead gastropods were available, which were identified by a translucent appearance or the retention of color in the shells. Shells of small gastropods that are dead for more than a year or so become increasingly white and opaque with time (J. Nekola, unpublished data), and were excluded from our study.

In the fossil record, species-level identification of fossil shells is possible for most small terrestrial gastropods and, therefore, the results of our investigation of modern gastropods can be applied directly to the fossil record. An exception is the Succineidae family, which is composed of three genera (*Catinella*, *Oxyloma*, and *Succinea*) that are difficult to differentiate in modern faunas, let alone the geologic record (Fig. 4). Their simple shells exhibit few diagnostic characteristics and, therefore, species-level identification is based on soft-body reproductive organ morphology, which is rarely preserved in the fossil record. This presents a significant problem for geochronologists; that is, can we be confident in ^{14}C ages derived from shells from any taxon within the Succineidae family, or do we need to target a specific genus or species? To address this issue, we measured the ^{14}C activity of 100 aliquots of gastropod shell material (802 individual shells) for twelve species of the Succineidae family to determine the level of identification (i.e., family, genus, or species) required to apply our results to the fossil record.

We prepared aliquots of modern shell material for ^{14}C analysis at the University of Arizona Desert Laboratory (JSP) and Miami University (JAR). We selected multiple shells at random for X-ray diffraction (XRD) analysis using a Siemens Model D-500 diffractometer to verify that only shell aragonite remained prior to preparation for ^{14}C analysis. There was no evidence of primary or secondary calcite in any of the shells that we analyzed. When possible, shells were broken, the adhering soft parts were removed using forceps, and the shells were treated with 6% NaOCl for 18–24 h at room temperature to remove all remnants of organic matter. Shells were not powdered during pretreatment to minimize the potential for adsorption of atmospheric ^{14}C (Samos, 1949). We selectively dissolved some of the shells by briefly introducing dilute HCl to remove secondary carbonate (dust) from primary shell material. Shells were washed repeatedly in ASTM Type 1, 18.2 MΩ (hereafter "ultrapure") water, sonicated for a few seconds to remove adhered solution, washed again with ultrapure water, and dried in a vacuum oven overnight at ~70 °C.

Shell aragonite was converted to CO_2 using 100% H_3PO_4 under vacuum at either 50 or 75 °C until the reaction was visibly complete (~1 h). Water, SO_x, NO_x, and halide species were removed using passive Cu and Ag traps held at ~600 °C and the resulting CO_2 was split into two aliquots. One aliquot was converted to graphite by catalytic reduction of CO (modified after Slota et al., 1987) and submitted to the Arizona-NSF Accelerator Mass Spectrometry (AMS) facility for ^{14}C analysis. The second aliquot was submitted for δ^{13}C analysis in order to correct the measured ^{14}C activity of the shell carbonate for isotopic fractionation.

^{14}C data for modern gastropods are presented as Δ^{14}C values in per mil (Stuiver and Polach, 1977; Reimer et al., 2004) and analytical uncertainties are reported at the 2σ (95%) confidence level. δ^{13}C values are given in the usual delta (δ) notation as the per mil deviation from the VPDB standard. Analytical uncertainties for δ^{13}C measurements are less than 0.1‰ based on repeated measurements of standards.

We also measured the ^{14}C content of several gastropod bodies for comparison to their corresponding shells. The bodies were treated with 10% HCl for 15–30 min to remove any remnants of the carbonate shell, rinsed repeatedly, and dried in a vacuum oven at

~70 °C. The dried bodies were placed in 6 mm quartz tubes along with ~100 mg of cupric oxide (CuO) and a small piece (1 mm × 5 mm) of silver foil, all of which were pre-combusted at 900 °C for 4–6 h. The tube was evacuated, sealed with a glass-blower's torch, and combusted offline at 900 °C. The resulting CO_2 gas was isolated and converted to graphite as above.

3.2. *Modeling of ^{14}C values of gastropod diets*

To quantify the amount of carbon in a gastropod shell that was derived from limestone or other carbonate rocks, it is necessary to compare the measured $\Delta^{14}C$ values of shells with $\Delta^{14}C$ values of the gastropod diet. $\Delta^{14}C$ values of live plants consumed by gastropods are identical to $\Delta^{14}C$ values of the atmosphere (Fig. 5a), which were calculated using ^{14}C data averaged over the Northern Hemisphere (Hua, 2004). We assigned a 5‰ uncertainty to the atmospheric values to account for short-term, regional variations (Hsueh et al., 2007) and small changes in atmospheric ^{14}C values that occur at a given site during the short (usually annual) lifespan of the small gastropods (Manning et al., 1990; Meijer et al., 1995).

Plant detritus from previous years' primary production has a higher ^{14}C activity than live plants because of the ^{14}C "bomb-spike" (Hua, 2004). Simply comparing the $\Delta^{14}C$ values of shells with the $\Delta^{14}C$ of the atmosphere or live plants during the year that the gastropod was alive, therefore, would ignore the potential impact of detritus in the gastropod diet. We estimated the amount of detritus from a given year that was available for consumption using a wide range of carbon turnover rates (0.2–0.002 yr^{-1}; Fig. 5b), which are applicable to O horizons and the upper few centimeters of A horizons in which small terrestrial gastropods typically live (Guadinski et al., 2000; Torn et al., 2005; Brovkin et al., 2008). We intentionally chose a wide range of carbon turnover rates, which are equivalent to mean residence times for carbon of 5–500 yrs, to encompass the potentially wide range of detritus ages at the 163 localities included in our study. We then used Monte Carlo simulation to generate 10,000 values for the $\Delta^{14}C$ of the gastropod diets for each of the past 13 yrs (the time span of our collections), which allowed two factors to vary randomly: the carbon turnover rate (0.2–0.002 yr^{-1}) and the age of the detritus fraction included in the diet (range of 0–1000 yrs). We also ran simulations in which we let the age of the detritus vary up to 10,000 yrs, but the results did not change significantly.

We took the average and standard deviation of the 10,000 generated values as the gastropod diet $\Delta^{14}C$ value for each year of collection between 1996 and 2008 (Fig. 5c). All uncertainties are reported at the 2σ (95%) confidence level. As expected, the modeled $\Delta^{14}C$ value of the gastropod diet for a given year is slightly higher than the atmospheric $\Delta^{14}C$ value for the same year. Uncertainties associated with the modeled values are relatively large, on the order of ~35%, because of the large range of detritus $\Delta^{14}C$ values that could be present at a given site.

Shells with $\Delta^{14}C$ values that are lower than the modeled $\Delta^{14}C$ value of the gastropod diet during the year in which the gastropod was alive indicate the presence of dead carbon from limestone or other carbonate rocks. When applicable, the difference between the $\Delta^{14}C$ values was converted into ^{14}C yrs to estimate the "limestone effect", which represents the potential error introduced by the incorporation of dead carbon in the shells. The magnitude of the limestone effect should be considered a maximum value because the calculation assumes that all of the dead carbon came from carbonate rocks, rather than older (but not infinitely-aged) organic matter. Because of the uncertainties associated with modeling the $\Delta^{14}C$ of the gastropod diet, we are unable to discern limestone effects smaller than ~300 ^{14}C yrs.

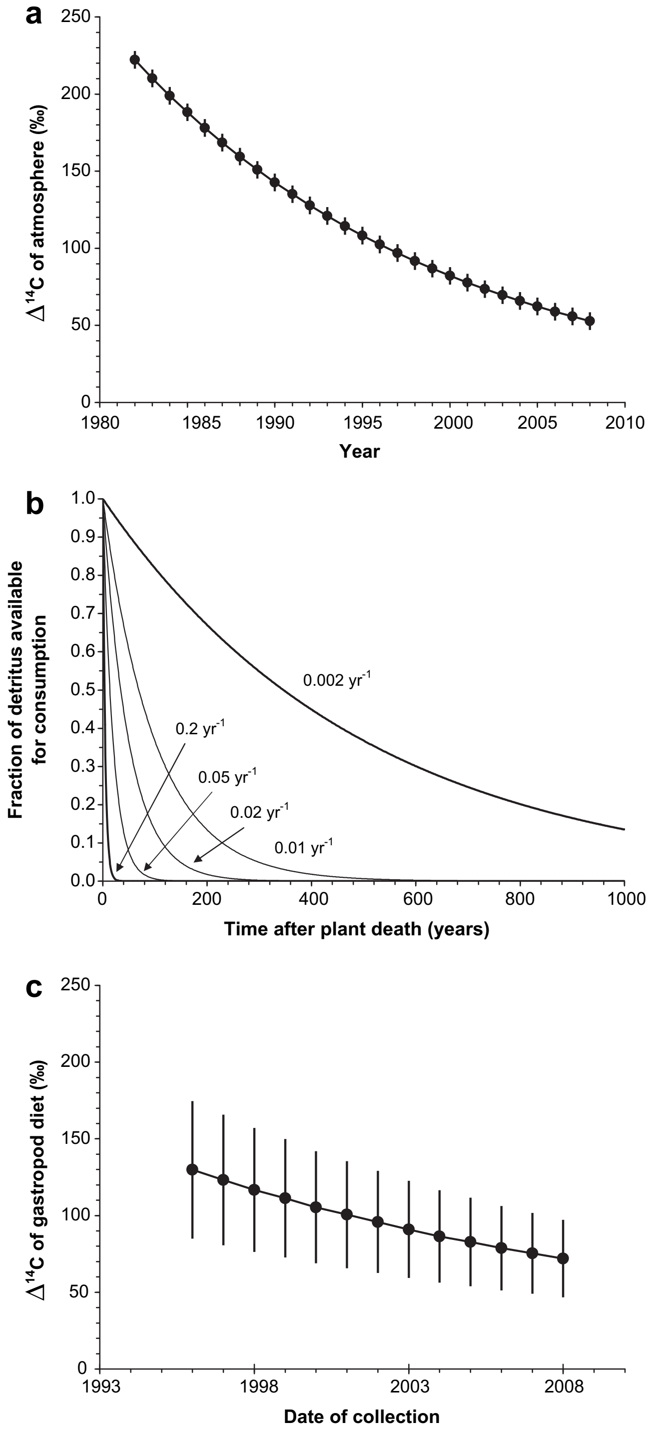

Fig. 5. Modeling results for (a) the ^{14}C activity of the gastropod diet using measured atmospheric values for the northern hemisphere (after Hua, 2004), (b) carbon turnover rates (CTRs) ranging from 0.2 to 0.002 yr^{-1}, and (c) Monte Carlo simulation to generate estimates of the $\Delta^{14}C$ values of gastropod diets for each of the past 13 yrs.

3.3. *Fossil gastropods*

Fossil gastropod shells were collected from glacial deposits at the Oxford East glacial outcrops in southwestern Ohio as a case study to determine if the shells remain closed systems with respect to carbon over geologic timescales. These outcrops contain a series of glacial diamictons from the Miami Lobe of the Laurentide Ice

Sheet that are separated by thin (3–5 cm) units of calcareous organic-rich silt that contain gastropods, plant macrofossils, and rooted tree stumps. AMS ^{14}C dating of plant macrofossils and *in situ* tree stumps has shown that the age of this unit is between ~20,100 and 21,400 ^{14}C yrs B.P. (Eckberg et al., 1993; Lowell, 1995). Gastropod taxa identified previously from this unit include *Columella columella*, *Discus cronkhitei*, *Euconulus fulvus*, *Hendersonia occulta*, *Pupilla muscorum*, *Vertigo elatior*, and multiple Succineidae taxa (Dell, 1991).

Gastropod-bearing sediment was collected and placed in deionized water with a deflocculant for several days to soften the sediment enough to pass through a 0.5 mm sieve. A few samples were placed in an ultrasonic bath for ~1 h to further disaggregate the sediment. Fossil shells were hand-picked from the retained fraction, placed in a beaker of ultrapure water, subjected to an ultrasonic bath for a few seconds, and then repeatedly dunked in a second beaker of ultrapure water to remove sediment that adhered to the shell surface or was lodged within the shell itself. The recovered shells were broken and examined under a dissecting microscope to ensure that the interior whorls were free of secondary carbonate and detritus. Fossil shells that were free of detritus were then processed for ^{14}C in the same manner as the modern specimens, including random selection of shells for XRD analysis. None of the fossil shells that we analyzed contained measurable quantities of either primary or secondary calcite.

Organic samples, which included bark, charcoal, plant fragments, and wood, were subjected to a standard acid–base–acid (ABA) chemical pretreatment with 1N HCl (1 h at 60 °C), 1N NaOH (18–24 h at 60 °C), and 1N HCl again (2–4 h at 60 °C) before combustion at 900 °C in the presence of cupric oxide and silver foil. The resulting CO_2 was purified and converted to graphite in the same manner as above.

Conventional radiocarbon ages are reported in ^{14}C yrs and, after calibration, in calendar yrs. For calibration, we used the IntCal09.14C dataset (CALIB 6.0.0, Stuiver and Reimer, 1993; Reimer et al., 2009).

4. Results

4.1. Modern shells

A few aliquots (11 of 247, or 4.5% of the total) yielded Δ^{14}C values that were higher than the modeled dietary Δ^{14}C values of the corresponding year of collection, which indicates these individuals consumed unusually high amounts of bomb-spike carbon (Table S1, Fig. 6). Data from these shells were excluded from further analysis. For the remaining 236 aliquots of gastropod shells from the 46 different species that we analyzed, ~78% did not contain any dead carbon from limestone or other carbonate rocks even though it was readily available at all sites, ~12% contained between 5 and 10% dead carbon, and a few (3% of the total) contained more than 10% (Table S1, Fig. 6). Δ^{14}C values for all taxa ranged from −97.5 to 158.4‰, and limestone effects averaged only ~180 ^{14}C yrs.

Dead carbon was not detected in the shells of at least 23 different species, including (number of shells in parentheses) *Catinella avara* (99), *Catinella gelida* (66), *Catinella vermeta* (39), *Cochlicopa lubricella* (17), *Cochlicopa morseana* (16), *Columella columella* (94), *Discus catskillensis* (40), *Discus cronkhitei* (47), *Discus macclintockii* (5), *Euconulus alderi* (71), *Euconulus polygyratus* (57), *Gastrocopta pentodon* (131), *Nesovitrea binneyana* (46), *Punctum minutissimum* (542), *Pupilla hebes* (7), *Strobilops affinis* (36), *Succinea bakeri* (27), *Succinea grosvernori* (1), *Succinea* n. sp. 'Minnesota A' (1), *Succinea ovalis* (50), *Succinea strigata* (14), *Vertigo hubrichti* (144), and *Vertigo modesta* (73).

Δ^{14}C values were most negative (i.e., contained the most dead carbon) for shells from the *Pupilla* and *Vallonia* genera. Maximum limestone effects for these genera ranged from 780 ± 310 ^{14}C yrs for *P. muscorum* to 1590 ± 280 ^{14}C yrs for *P. sonorana*, and from 1010 ± 380 ^{14}C yrs for *Vallonia perspectiva* to 1500 ± 270 ^{14}C yrs for *V. cyclophorella*, respectively (Table 1). The only other species that exhibited a limestone effect that was greater than 1000 ^{14}C yrs was *H. occulta* (1210 ± 250 ^{14}C yrs).

These results can be applied directly to the fossil record if it is possible to identify the taxa to the species-level based on shell morphology. For the Succineidae family, the data must be evaluated at the family or genus level to be applicable. Taking the Succineidae family as a whole, 85% of the shell aliquots that we analyzed did not contain measurable amounts of dead carbon; the remaining aliquots contained an average of 5.2% dead carbon. Within the family, Δ^{14}C values for the genus *Catinella* ranged from 63.7 to 147.0‰, *Oxyloma* values ranged from −0.8 to 135.0‰, and *Succinea* values ranged from 16.1 to 147.8‰. Members of the *Catinella* genus incorporate little, if any, dead carbon from limestone or other carbonate rocks in their shells; 32 of 33 aliquots (97%) of *Catinella* shells did not contain measurable amounts of dead carbon. The remaining sample (DL-170) contained only a very small amount of dead carbon, equivalent to a limestone effect of 320 ± 310 ^{14}C yrs. Similarly, 36 of 39 aliquots (92%) of *Succinea* shells did not contain dead carbon. The remaining three aliquots were all *Succinea indiana*; limestone effects for these shells ranged from 430 ± 370 to 610 ± 380 ^{14}C yrs. For *Oxyloma*, 15 of 24 aliquots (63%) did not contain measurable amounts of dead carbon. Limestone effects for the remaining samples ranged between 250 ± 210 and 670 ± 240 ^{14}C yrs.

4.2. Modern gastropod bodies

We also measured the ^{14}C activity of the bodies of eight gastropods to determine the magnitude of the offset between the body carbon and shell carbonate (Table 2). Ideally, we would have preferred to measure the ^{14}C content of the extrapallial fluid to compare with the shell carbonate to determine if carbon isotopes are fractionated when the shells are formed, but this was not feasible because the gastropod bodies were simply too small. Regardless, the measured Δ^{14}C values of gastropod body carbon ranged from 42 to 101‰, similar to the Δ^{14}C values of shell carbonate from the same sites, which ranged from 43 to 133‰. However, we did not observe a clear relation between the ^{14}C activity of gastropod body carbon and shell carbonate. Δ^{14}C values of bodies of *Oxyloma retusa* collected from Maquokata River Mounds, Iowa were indistinguishable from the Δ^{14}C values of their corresponding shells ($\Delta^{14}C_{body} = 42 \pm 6$‰, $\Delta^{14}C_{shell} = 43 \pm 10$‰), as were values for *S. ovalis* from Dave Pepin Homestead, Minnesota ($\Delta^{14}C_{body} = 101 \pm 8$‰, $\Delta^{14}C_{shell} = 110 \pm 8$‰). In contrast, Δ^{14}C values for bodies of *S. ovalis* were significantly lower than their shells from Brewer Boat Ramp, Maine ($\Delta^{14}C_{body} = 55 \pm 6$‰, $\Delta^{14}C_{shell} = 82 \pm 5$‰) and Zippel Bay State Park, Minnesota ($\Delta^{14}C_{body} = 84 \pm 6$‰, $\Delta^{14}C_{shell} = 133 \pm 12$‰). The reason(s) for this difference is unclear.

4.3. Fossil shells

Well-preserved fossil organic material (bark, plant macrofossils, and wood) recovered from sediments at the Oxford East outcrops yielded calibrated ages that ranged from 24.60 ± 0.40 to 25.28 ± 0.55 ka, with an average of 24.93 ± 0.30 ka ($n = 5$; Table 3, Fig. 7). Gastropod shells recovered from the same stratigraphic unit yielded ages that ranged from 23.92 ± 0.66 to 25.81 ± 0.94 ka, and averaged 24.73 ± 0.44 ka ($n = 18$). Average ages of six of the seven fossil taxa were indistinguishable from the average age of the organic matter: *Discus shimeki* (24.80 ± 0.17 ka; $n = 3$), *P. muscorum* (24.34 ± 0.32 ka; $n = 3$), *Vallonia gracilicosta* (24.20 ± 0.40 ka; $n = 2$), *Vertigo hannai* (24.90 ± 0.77 ka; $n = 1$), *V. modesta*

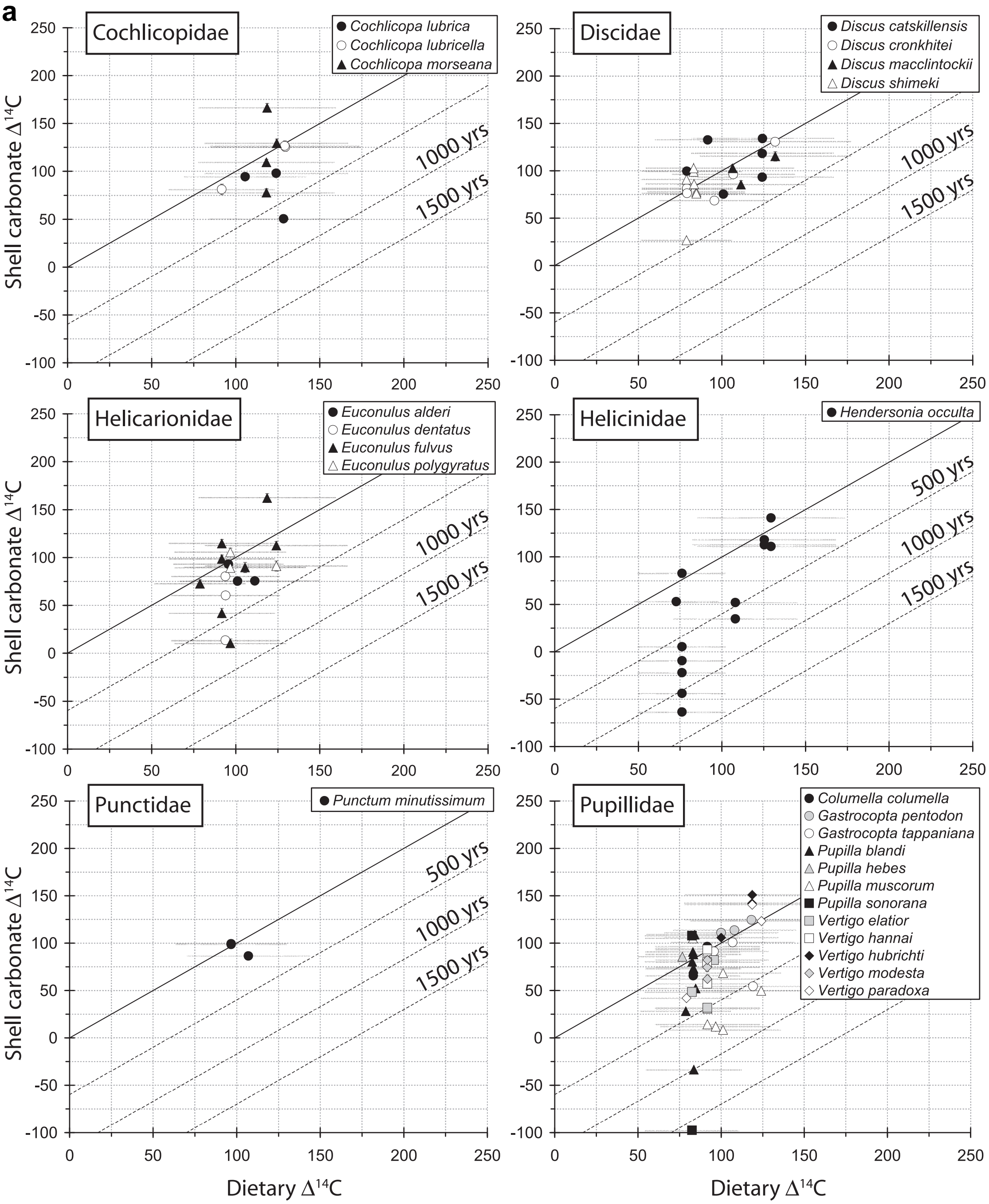

Fig. 6. Shell carbonate Δ^{14}C values compared to modeled dietary Δ^{14}C values for modern gastropods. Data points that fall on the solid black line in each panel represent gastropods that obtained their carbon from live plants and the atmosphere. Data points that fall below the solid line indicate that dead carbon from limestone or other carbonate rocks was incorporated during shell construction. The magnitude of this phenomenon, called the "limestone effect", depends upon the amount of shell carbon that was derived from rocks as shown by the dashed lines.

(24.86 ± 0.32 ka; $n = 3$), and Succineidae (25.29 ± 0.54 ka; $n = 3$). The average age of *H. occulta* (24.34 ± 0.15 ka; $n = 3$) was slightly younger than the organic ages.

5. Discussion

5.1. Small terrestrial gastropods and the limestone problem

Approximately 78% of the modern shells that we analyzed did not contain any dead carbon from limestone or other carbonate rocks even though it was readily available at all sites, ~12% of the aliquots contained between 5 and 10% dead carbon, and a few (3% of the total) contained more than 10%. Even at the high end, the amount of dead carbon in the small shells is significantly less than the 20–30% dead carbon that has been previously reported for larger taxa (e.g., Goodfriend and Stipp, 1983).

If we extrapolate our results to the fossil record and assume that the shells behave as closed systems with respect to carbon over geologic timescales, then small terrestrial gastropod shells should provide accurate ^{14}C ages ~78% of the time and ages that are

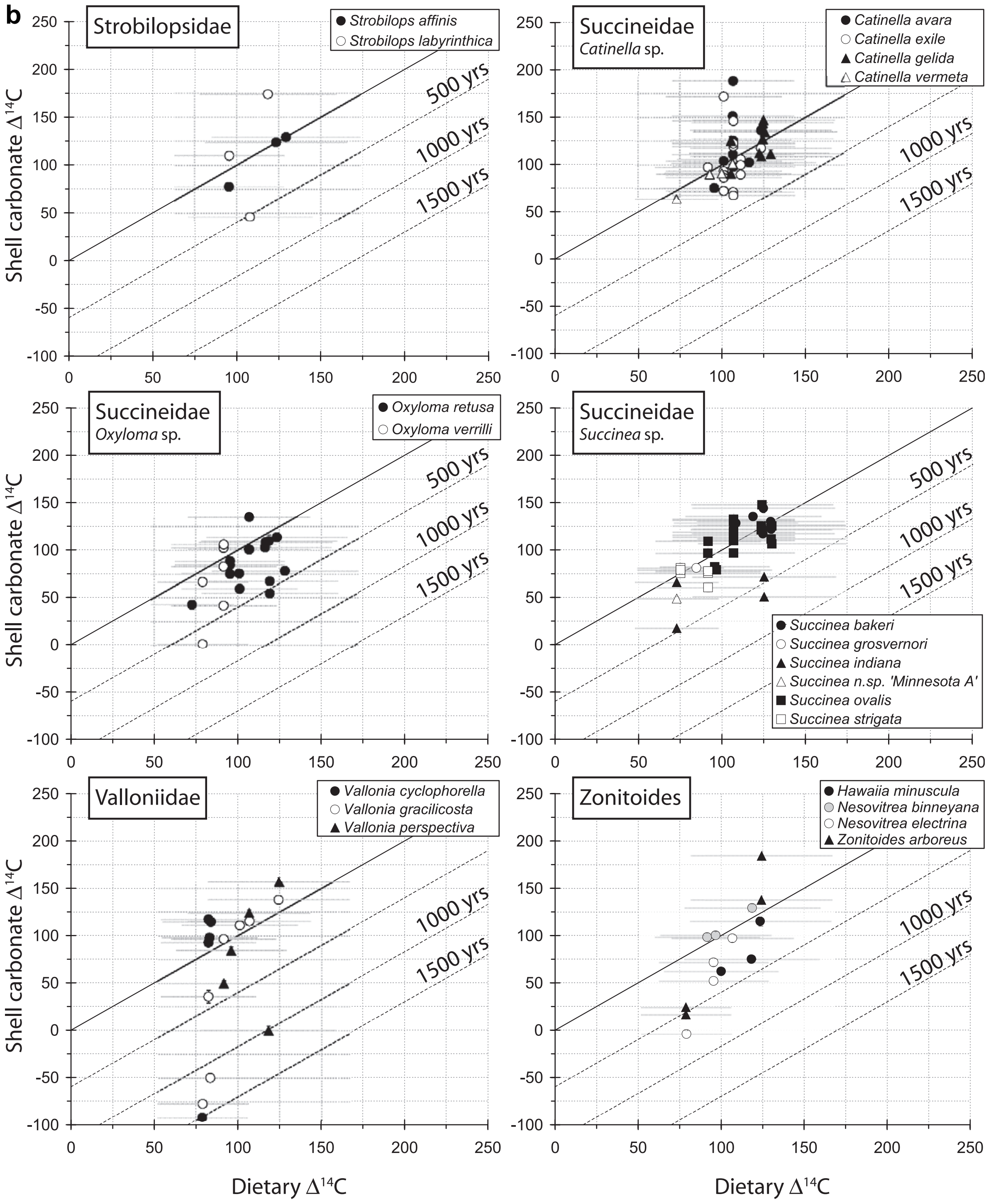

Fig. 6. (*continued*).

within ~1000 ^{14}C yrs of the true age ~97% of the time. Shells from at least 23 different species did not contain dead carbon, and therefore should yield reliable ^{14}C ages if the modern shell data can be applied directly to the fossil record.

For the Succineidae family as a whole, 85% of the shell aliquots that we analyzed did not contain measurable amounts of dead carbon; the remaining aliquots contained an average of 5.2% dead carbon, equivalent to a limestone effect of 425 ^{14}C yrs. At the genus level, shells of the genus *Catinella* should yield reliable ^{14}C ages ~97% of the time, again assuming closed-system behavior, and ages that are within ~300 ^{14}C yrs of the true age every time. Similarly, *Succinea* shells should yield reliable ^{14}C ages ~92% of the time and ages that are within ~600 ^{14}C yrs of the true age every time. Results for the genus *Oxyloma* suggest that some caution should be used when evaluating ^{14}C ages derived from these shells. AMS results for the *Oxyloma* shells show that nearly 1 in 3 aliquots contained at least some dead carbon. Although the amount was relatively minor, <7% of the total, dead carbon was present in *Oxyloma* shells more frequently than in either *Catinella* or *Succinea* shells.

Table 1
Summary of ^{14}C results for modern gastropod shells.

					Limestone effect[a] (^{14}C yrs)	
Family	Genus	Species	Aliquots	Shells	Negligible[b]	Maximum[c]
Cochlicopidae	*Cochlicopa*	*Cochlicopa lubrica*	3	17	53%	650 ± 390
		Cochlicopa lubricella	3	17	100%	–
		Cochlicopa morseana	4	16	100%	–
Discidae	*Discus*	*Discus catskillensis*	6	40	100%	–
		Discus cronkhitei	6	47	100%	–
		Discus macclintockii	3	5	100%	–
		Discus shimeki	7	33	97%	430 ± 240
Helicarionidae	*Euconulus*	*Euconulus alderi*	3	71	100%	–
		Euconulus dentatus	3	34	68%	670 ± 290
		Euconulus fulvus	8	107	57%	730 ± 300
		Euconulus polygyratus	3	57	100%	–
Helicinidae	*Hendersonia*	*Hendersonia occulta*	13	13	46%	1210 ± 250
Punctidae	*Punctum*	*Punctum minutissimum*	3	542	100%	–
Pupillidae	*Columella*	*Columella columella*	3	94	100%	–
	Gastrocopta	*Gastrocopta pentodon*	3	131	100%	–
		Gastrocopta tappaniana	3	105	92%	540 ± 360
	Pupilla	*Pupilla blandi*	9	90	67%	1000 ± 270
		Pupilla hebes	1	7	100%	–
		Pupilla muscorum	8	80	38%	780 ± 310
		Pupilla sonorana	2	29	66%	1590 ± 280
	Vertigo	*Vertigo elatior*	3	113	38%	500 ± 280
		Vertigo hannai	3	123	65%	280 ± 270
		Vertigo hubrichti	3	144	100%	–
		Vertigo modesta	3	73	100%	–
		Vertigo paradoxa	3	124	74%	380 ± 240
Strobilopsidae	*Strobilops*	*Strobilops affinis*	3	36	100%	–
		Strobilops labyrinthica	3	43	65%	520 ± 320
Succineidae	*Catinella*	*Catinella avara*	9	99	100%	–
		Catinella exile	15	316	97%	320 ± 310
		Catinella gelida	9	66	100%	–
		Catinella vermeta	4	39	100%	–
	Oxyloma	*Oxyloma retusa*	17	136	65%	540 ± 360
		Oxyloma verrilli	7	47	57%	670 ± 240
	Succinea	*Succinea bakeri*	8	27	100%	–
		Succinea grosvernori	1	1	100%	–
		Succinea indiana	4	6	17%	610 ± 380
		Succinea n.sp. 'Minnesota A'	1	1	100%	–
		Succinea ovalis	19	50	100%	–
		Succinea strigata	6	14	100%	–
Valloniidae	*Vallonia*	*Vallonia cyclophorella*	6	129	95%	1500 ± 270
		Vallonia gracilicosta	7	155	60%	1370 ± 270
		Vallonia perspectiva	5	221	68%	1010 ± 380
Zonitidae	*Hawaiia*	*Hawaiia minuscula*	3	152	29%	340 ± 270
	Nesovitrea	*Nesovitrea binneyana*	3	46	100%	–
		Nesovitrea electrina	4	33	73%	710 ± 240
	Zonitoides	*Zonitoides arboreus*	4	20	85%	530 ± 240

[a] Defined as the theoretical difference between the measured and true ^{14}C ages for gastropods that incorporate the same amount of dead carbon in their shells as the aliquots measured here. These values are based on the difference between the modeled diet and shell carbonate Δ^{14}C values and converted into ^{14}C yrs.

[b] Percent of shells measured by AMS that did not contain dead carbon from limestone or other carbonate rocks (i.e., the Δ^{14}C values for the shells were statistically indistinguishable from the modeled diet Δ^{14}C value).

[c] Maximum limestone effect for a given taxon (given in ^{14}C yrs). Uncertainties are given at the 2σ (95%) confidence level.

5.2. *Ca-limiting hypothesis*

Large gastropod shells (>20 mm in maximum dimension) routinely contain 20–30% dead carbon when living in habitats on carbonate terrain (e.g., Evin et al., 1980; Goodfriend and Stipp, 1983), whereas the small shells measured in this study rarely contained more than ~10%. We speculate that calcium may hold the clues to determining the reasons for the difference. Gastropod shell carbonate (aragonite) is composed of three elements – calcium, carbon, and oxygen. The latter two elements are readily available in the environments in which gastropods live and, therefore, cannot be considered as possible limiting factors for shell construction. In most settings, however, calcium is present in plants and water in low concentrations (typically parts per million). If small terrestrial gastropods can acquire enough calcium from their "normal" diet (plants, detritus, and water), then they may not have to consume carbonate rocks to supplement their calcium intake when building their shells. Larger taxa may find it more difficult to obtain enough calcium from these sources without turning to carbonate rocks when they are available.

Our results support this hypothesis, but only on a gross scale. There is clearly a significant difference in the amount of dead carbon incorporated in the shells of large taxa previously studied and the small taxa studied here. However, shell size alone is not the only factor to consider when evaluating the results within the small body size class. For example, in the present study, we did not observe a significant correlation between shell size and measured Δ^{14}C values ($R^2 = 0.015$). The largest taxon that we included in our analysis, *H. occulta*, averaged 15.6 mg per shell and contained approximately the same amount of dead carbon as *P. muscorum* and *Vallonia* shells, which averaged only 1.4 and 0.7 mg per shell, respectively. Similarly, we did not find a clear correlation between shell size and measured Δ^{14}C values even within a single family. For Succineidae, *Catinella* shells were generally the smallest, averaging 1.1 mg per shell and contained the least amount of dead carbon, and

Table 2

^{14}C results for modern gastropod bodies and corresponding shells.

Lab #	AA #	Taxon	Site[a]	Lat (°N)	Long (°W)	Mass (mg)	δ^{13}C (vpdb)	F^{14}C[b]	Shell Δ^{14}C	Atmos Δ^{14}C	Diet Δ^{14}C	Limestone Effect[c] (^{14}C yrs)
Bodies												
MU-109	80177	*Succinea ovalis*	1	44.819	68.723	4.22	−24.9	1.0547 ± 0.0064	55 ± 6	70 ± 5	96 ± 33	330 ± 280
MU-114	80181	*Succinea ovalis*	2	48.410	94.819	8.64	−24.8	1.0996 ± 0.0082	101 ± 8	80 ± 5	107 ± 36	50 ± 300
MU-108	80176	*Succinea ovalis*	3	48.906	96.027	3.79	−25.1	1.0946 ± 0.0062	96 ± 6	80 ± 5	107 ± 36	90 ± 300
MU-111	80178	*Succinea ovalis*	4	47.874	96.422	11.05	−26.0	1.0877 ± 0.0062	89 ± 6	80 ± 5	107 ± 36	150 ± 300
MU-117	80183	*Oxyloma retusa*	5	42.559	90.713	9.04	−26.1	1.0419 ± 0.0064	42 ± 6	52 ± 5	73 ± 25	250 ± 210
MU-115	80182	*Succinea ovalis*	6	50.264	66.411	12.88	−25.0	1.0485 ± 0.0072	49 ± 7	57 ± 5	79 ± 27	250 ± 230
MU-112	80179	*Succinea strigata*	7	64.858	147.862	4.01	−24.2	1.0740 ± 0.0060	74 ± 6	54 ± 5	75 ± 26	0 ± 210
MU-113	80180	*Succinea ovalis*	8	48.866	94.843	6.88	−23.5	1.0833 ± 0.0060	84 ± 6	80 ± 5	107 ± 36	180 ± 300
Shells												
MU-162	80928	*Succinea ovalis*	1	44.819	68.723	8.80	−10.0	1.0817 ± 0.0048	82 ± 5	70 ± 5	96 ± 33	110 ± 270
MU-128	80194	*Succinea ovalis*	2	48.410	94.819	11.72	−9.8	1.1090 ± 0.0084	110 ± 8	80 ± 5	107 ± 36	0 ± 300
MU-179	80942	*Oxyloma retusa*	5	42.559	90.713	13.08	−11.0	1.0425 ± 0.0100	43 ± 10	52 ± 5	73 ± 25	250 ± 220
MU-141	80910	*Succinea ovalis*	8	48.866	94.843	8.91	−9.6	1.1316 ± 0.0116	133 ± 12	80 ± 5	107 ± 36	0 ± 300

Uncertainties are given at the 2σ (95%) confidence level.

[a] Key to sites: 1 = Brewer Boat Ramp, Maine; 2 = Dave Pepin Homestead, Minnesota; 3 = Duxby, Minnesota; 4 = Huot Forest WMA, Minnesota; 5 = Maquokata River Mounds, Iowa; 6 = September Islands, Quebec; 7 = University of Alaska – Fairbanks; 8 = Zippel Bay State Park, Minnesota.

[b] F^{14} C values are derived from the measured ^{14}C activity, corrected for fractionation, and account for decay that occurred between the time of collection and the AMS measurement.

[c] Defined in Table 1.

Oxyloma shells averaged 2.1 mg per shell and contained the most dead carbon. *Succinea* shells were the largest, averaging 5.8 mg per shell, but were between *Catinella* and *Oxyloma* in terms of the amount of dead carbon in their shells (Table S1).

The results presented here suggest that the Limestone Problem for small terrestrial gastropods is often negligible and always much less than the 20–30% dead carbon for larger taxa. However, there are additional factors that apparently influence the dietary intake of carbonate rocks of small terrestrial gastropods living side by side, which may include opportunistic behavior, variations in microhabitats, and the dietary needs or wants of individual gastropods.

Table 3

^{14}C results for the Oxford East outcrops.

Lab #	AA #	Taxon	N[a]	Mass (mg)	δ^{13}C (vpdb)	F^{14}C	^{14}C age (ka)	Calendar age (ka)[b]	P[c]
Organics									
MU-212	82584	bark	–	4.47	−24.6	0.0731 ± 0.0026	21.02 ± 0.28	25.15 ± 0.34	1.00
MU-213	82585	bark	–	3.28	−25.1	0.0767 ± 0.0025	20.62 ± 0.27	24.64 ± 0.37	1.00
MU-214	82586	twig	–	3.80	−24.9	0.0721 ± 0.0028	21.13 ± 0.32	25.28 ± 0.55	1.00
MU-211	82583	wood	–	3.82	−22.6	0.0743 ± 0.0042	20.88 ± 0.45	24.97 ± 0.63	1.00
MU-210	82582	wood chip	–	4.29	−23.6	0.0772 ± 0.0025	20.58 ± 0.26	24.60 ± 0.40	1.00
		Average						**24.93** ± **0.30**	
Gastropod shells									
MU-194	82567	*Discus shimeki*	2	9.20	−6.4	0.0758 ± 0.0052	20.72 ± 0.55	24.73 ± 0.75	1.00
MU-195	82568	*Discus shimeki*	2	10.94	−6.9	0.0762 ± 0.0052	20.68 ± 0.54	24.67 ± 0.74	1.00
MU-196	82569	*Discus shimeki*	2	14.99	−6.4	0.0745 ± 0.0053	20.87 ± 0.57	25.00 ± 0.79	1.00
		Average						**24.80** ± **0.17**	
MU-188	82561	*Hendersonia occulta*	1	12.41	−6.4	0.0805 ± 0.0051	20.24 ± 0.51	24.18 ± 0.67	1.00
MU-189	82562	*Hendersonia occulta*	1	10.29	−6.1	0.0787 ± 0.0055	20.42 ± 0.56	24.37 ± 0.68	1.00
MU-190	82563	*Hendersonia occulta*	1	18.42	−7.1	0.0777 ± 0.0055	20.52 ± 0.57	24.47 ± 0.70	1.00
		Average						**24.34** ± **0.15**	
MU-199	82572	*Pupilla muscorum*	8	10.86	−6.5	0.0760 ± 0.0052	20.71 ± 0.55	24.71 ± 0.74	1.00
MU-200	82573	*Pupilla muscorum*	9	11.88	−6.4	0.0805 ± 0.0052	20.24 ± 0.52	24.18 ± 0.68	1.00
MU-201	82574	*Pupilla muscorum*	10	14.13	−6.4	0.0809 ± 0.0051	20.20 ± 0.51	24.13 ± 0.67	1.00
		Average						**24.34** ± **0.32**	
MU-191	82564	Succineidae	8	10.58	−5.3	0.0712 ± 0.0052	21.23 ± 0.59	25.33 ± 0.80	1.00
MU-192	82565	Succineidae	4	9.32	−5.5	0.0689 ± 0.0056	21.49 ± 0.65	25.81 ± 0.94	1.00
MU-193	82566	Succineidae	15	9.53	−5.8	0.0759 ± 0.0055	20.71 ± 0.58	24.73 ± 0.78	1.00
		Average						**25.29** ± **0.54**	
MU-202	82575	*Vallonia gracilicosta*	15	10.72	−6.0	0.0776 ± 0.0058	20.53 ± 0.60	24.49 ± 0.76	1.00
MU-203	82576	*Vallonia gracilicosta*	15	11.08	−6.2	0.0824 ± 0.0058	20.05 ± 0.56	23.92 ± 0.66	0.98
		Average						**24.20** ± **0.40**	
MU-205	82577	*Vertigo hannai*	30	10.46	−6.5	0.0750 ± 0.0052	20.81 ± 0.55	24.90 ± 0.77	1.00
MU-206	82578	*Vertigo modesta*	15	11.47	−6.7	0.0751 ± 0.0052	20.80 ± 0.55	24.88 ± 0.77	1.00
MU-207	82579	*Vertigo modesta*	15	14.14	−7.0	0.0771 ± 0.0053	20.59 ± 0.55	24.54 ± 0.71	1.00
MU-208	82580	*Vertigo modesta*	20	15.28	−6.7	0.0729 ± 0.0053	21.04 ± 0.58	25.18 ± 0.77	1.00
		Average						**24.86** ± **0.32**	

Uncertainties for the raw and calibrated ^{14}C ages are given at the 2σ (95%) confidence level.

[a] Number of shells per aliquot.

[b] Calibrated ages were calculated using CALIB v. 6.0.0, IntCal09.14C dataset; limit 50.0 calendar ka B P. Calibrated ages are reported as the midpoint of the calibrated range. Uncertainties are reported as the difference between the midpoint and either the upper or lower limit of the calibrated age range, whichever is greater. Multiple ages are reported when the probability of a calibrated age range exceeds 0.05.

[c] P = probability of the calibrated age falling within the reported range as calculated by CALIB.

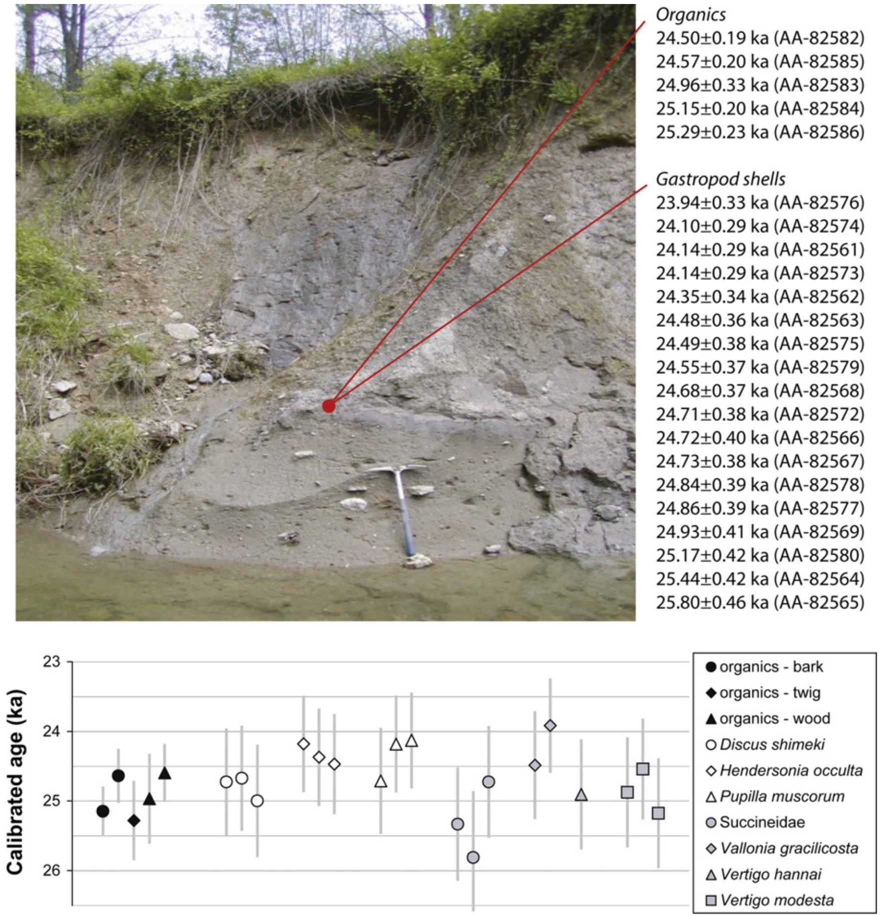

Fig. 7. Photograph of the section at the Oxford East outcrops and the calibrated ages obtained from the organic material and fossil gastropod shells.

5.3. *Small terrestrial gastropods and open-system behavior*

The present study includes only a single fossil locality, the Oxford East outcrops of southwestern Ohio, which we present here as a case study. Average ages of organic materials and fossil gastropod shells from the Oxford East outcrops were statistically indistinguishable; 24.93 ± 0.30 ka for the organics and 24.73 ± 0.44 ka for the shells. Six of the seven taxa that we analyzed (*D. shimeki*, *P. muscorum*, Succineidae, *V. gracilicosta*, *V. hannai*, and *V. modesta*) yielded average ^{14}C ages that are indistinguishable from the organic ages; the seventh (*H. occulta*) yielded ages that were slightly younger than the organic ages. The range of ages of the shell material, 1.8 ka, is significantly larger than the range of ages of the organics, 0.8 ka. If the dispersion of shell ages was related to open-system behavior, then we would expect the ages to be systematically younger than the organic matter ages, which they are not. It may be that the small number of organic samples fails to adequately capture the full range of time represented by the sampled stratum. More work needs to be done on this subject, including additional comparisons of shell and organic ages from other sites, but the results from the Oxford East outcrops suggest that small terrestrial gastropod shells may behave as closed systems with respect to carbon in the American Midwest for at least the past ~25 ka.

6. Summary and conclusions

Fossil shells of small terrestrial gastropods are commonly preserved in Quaternary sediment across North America, including loess, wetland, glacial, and alluvial deposits, as well as in sediments at many archeological sites. Their aragonitic shells contain ~12% by weight carbon, and therefore contain sufficient carbon for ^{14}C dating. However, terrestrial gastropod shells in carbonate terrains are often avoided for ^{14}C dating because large taxa are known to incorporate dead carbon from limestone or other carbonate rocks when building their shells, which can cause their ^{14}C ages to be up to 3000 yrs too old. Previous studies suggested that small terrestrial gastropod shells may yield reliable ^{14}C ages in arid environments, but a systematic and comprehensive analysis was needed before ages derived from their shells could be considered reliable outside of the Desert Southwest.

To this end, we measured the ^{14}C activity of 247 aliquots of modern shell material (3749 individual shells) from 163 localities across North America. Approximately 78% of the aliquots did not contain measurable amounts of dead carbon even though limestone or other carbonate rocks were readily available at all sites, ~12 of the aliquots contained between 5 and 10% dead carbon, and the remaining few (3% of the total) contained more than 10%. The average Limestone Effect for these samples was only ~180 ^{14}C yrs, which is significantly less than the 2000–3000 ^{14}C yrs that previous researchers found for larger taxa. Assuming that the small gastropod shells behave as closed systems with respect to carbon after burial, they should yield reliable ^{14}C ages ~78% of the time, and ages that are within ~1000 yrs of the true age ~97% of the time, regardless of the taxon analyzed, local bedrock type, climate, or environmental conditions. If fossil shells can be identified to the species level, then at least 23 different species should yield reliable ^{14}C ages if the modern shell data can be applied directly to the fossil record.

The terrestrial gastropod family Succineidae is one of the most common gastropod taxa in North America. Unlike the other gastropods studied here, our ^{14}C data for Succineidae must be evaluated at the genus or even family level because species-level identification is based on soft-part morphology, which is rarely preserved in the fossil record. Based on the data from modern shells, the Succineidae family as a whole should yield reliable ^{14}C ages ~85% of the time, and ages that are within ~700 ^{14}C yrs every time. At the genus level, *Catinella* should yield reliable ^{14}C ages ~97% of the time, again assuming closed-system behavior, and ages that are within ~300 ^{14}C yrs of the true age every time. Similarly, *Succinea* shells should yield reliable ^{14}C ages ~92% of the time and ages that are within ~600 ^{14}C yrs of the true age every time. Caution should be used when evaluating shells of the genus *Oxyloma*, however, as nearly 1 in 3 aliquots contained dead carbon, equivalent to a limestone effect of up to ~700 ^{14}C yrs.

Fossil shells of small terrestrial gastropods recovered from well-dated, late-Pleistocene sediments in the Midwest yielded ages that were statistically indistinguishable from ages obtained from well-preserved plant macrofossils (wood, bark, plant remains). Although just one site, these results suggest that small terrestrial gastropod shells may behave as closed systems with respect to carbon over geologic timescales. More work on this subject is needed, but if our case study site is representative of other sites, then fossil shells of some small terrestrial gastropods, including at least five common genera, *Catinella*, *Columella*, *Discus*, *Gastrocopta*, and *Succinea*, should yield reliable ^{14}C ages, regardless of the local geologic substrate. Fossil shells of these and other small terrestrial gastropods are common in a wide range of Quaternary deposits in North America and, therefore, our results may have broad chronologic applications to Quaternary geology and New World archeology.

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Appendix. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.quageo.2010.01.001.

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References

Balakrishnan, M., Yapp, C.J., 2004. Flux balance models for the oxygen and carbon isotope compositions of land snail shells. Geochimica et Cosmochimica Acta 68, 2007–2024.

Barker, G.M., 2001. Gastropods on land: phylogeny, diversity, and adaptive morphology. In: Barker, G.M. (Ed.), Biology of Terrestrial Molluscs. CABI Publishing, Oxon, U.K, pp. 1–146.

Brennan, R., Quade, J., 1997. Reliable Late-Pleistocene stratigraphic ages and shorter groundwater travel times from ^{14}C in fossil snails from the southern Great Basin. Quaternary Research 47, 329–336.

Brovkin, V., Cherkinsky, A., Goryachkin, S., 2008. Estimating soil carbon turnover using radiocarbon data: a case study for European Russia. Ecological Modelling 216, 178–187.

Burch, J.B., Pearce, T.A., 1990. Terrestrial Gastropoda. Soil Biology Guide. John Wiley & Sons, New York.

Cameron, R.A.D., Pokryszko, B.M., 2005. Estimating the species richness and composition of land mollusc communities. Journal of Conchology 38, 529–547.

Dell, A.M., 1991. Reconstruction of late Pleistocene paleoecology in southwestern Ohio from nonmarine gastropod assemblages. Unpublished M.S., University of Cincinnati, 97 p.

Eckberg, M.P., Lowell, T.V., Stuckenrath, R., 1993. Late Wisconsin glacial advance and retreat patterns in southwestern Ohio, USA. Boreas 22, 189–204.

Emberton, K.C., Pearce, T.A., Randalana, R., 1996. Quantitatively sampling land-snail species richness in Madagascan rainforests. Malacologia 38, 203–212.

Evans, J.G., 1972. Land Snails in Archaeology. Seminar Press, New York, NY.

Evin, J., Marechal, J., Pachiaudi, C., 1980. Conditions involved in dating terrestrial shells. Radiocarbon 22, 545–555.

Frye, J.C., Willman, H.B., 1960. Classification of the Wisconsinan stage in the Lake Michigan glacial lobe. Illinois Geological Survey Circular 285, 1–16.

Goodfriend, G.A., 1987. Radiocarbon age anomalies in shell carbonate of land snails from semi-arid areas. Radiocarbon 29, 159–167.

Goodfriend, G.A., Hood, D.G., 1983. Carbon isotope analysis of land snail shells: implications for carbon sources and radiocarbon dating. Radiocarbon 25, 810–830.

Goodfriend, G.A., Stipp, J.J., 1983. Limestone and the problem of radiocarbon dating of land-snail shell carbonate. Geology 11, 575–577.

Goslar, T., Pazdur, M.F., 1985. Contamination studies on mollusk shell samples. Radiocarbon 27, 33–42.

Grosjean, M., 1994. Paleohydrology of the Laguna Lejía (North Chilean Altiplano) and climatic implications for late-glacial times. Palaeogeography, Palaeoclimatology, Palaeoecology 109, 89–100.

Guadinski, J.B., Trumbore, S.E., Davidson, E.E., Zheng, S., 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates, and partitioning of fluxes. Biogeochemistry 51, 33–69.

Hsueh, D.Y., Karkauer, N.Y., Randerson, J.T., Xu, X., Trumbore, S.E., Southon, J.R., 2007. Regional patterns of radiocarbon and fossil fuel-derived CO_2 in surface air across North America. Geophysical Research Letters 34, L02816. doi:10.1029/2006GL027032.

Hua, Q., 2004. Review of tropospheric bomb ^{14}C data for carbon cycle modeling and age calibration purposes. Radiocarbon 46, 1273–1298.

Hubricht, L., 1985. The distributions of the native land mollusks of the eastern United States. Fieldiana: Zoology 24, 1–191.

Kerney, M., Cameron, R.A.D., 1979. Field Guide to the Land Snails of Britain and Northwestern Europe. Collins Press, London.

Leighton, M.M., 1960. The classification of the Wisconsin Glacial stage of north central United States. Journal of Geology 68, 529–552.

Lowell, T.V., 1995. The Application of Radiocarbon Age Estimates to the Dating of Glacial Sequences: an Example from the Miami Sublobe, Ohio, USA. Quaternary Science Reviews 4, 85–99.

Manning, M.R., Lowe, D.C., Melhuish, W.H., Sparks, R.J., Wallace, G., Brenninkmeijer, C.A.M., McGill, R.C., 1990. The use of radiocarbon measurements in atmospheric studies. Radiocarbon 32, 37–58.

Meijer, H.A.J., van der Plicht, J., Gislefoss, J.S., Nydal, R., 1995. Comparing long term atmospheric ^{14}C and ^{3}H records near Groningen, the Netherlands with Fruholmen, Norway and Izaña, Canary Islands ^{14}C stations. Radiocarbon 37, 39–50.

Nekola, J.C., 2004. Terrestrial gastropod fauna of northeastern Wisconsin and the southern Upper Peninsula of Michigan. American Malacological Bulletin 18, 21–44.

Nekola, J.C., 2005. Geographic variation in richness and shell size of eastern North American land snail communities. Records of the Western Australian Museum Supplement 68, 39–51.

Oggier, P., Zschokke, S., Baur, B., 1998. A comparison of three methods for assessing the gastropod community in dry grasslands. Pedobiologia 42, 348–357.

Pedone, V., Rivera, K., 2003. Groundwater-discharge deposits in Fenner Wash, eastern Mojave Desert. Geological Society of America Abstracts with Programs 35, 257.

Pigati, J.S., Bright, J.E., Shanahan, T.M., Mahan, S.A., 2009. Late Pleistocene Paleohydrology Near the Boundary of the Sonoran and Chihuahuan Deserts, Southeastern Arizona, USA. Quaternary Science Reviews 28, 286–300.

Pigati, J.S., Quade, J., Shanahan, T.M., Haynes Jr., C.V., 2004. Radiocarbon dating of minute gastropods and new constraints on the timing of spring-discharge deposits in southern Arizona, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 204, 33–45.

Placzek, C., Quade, J., Patchett, P.J., 2006. Geochronology and stratigraphy of late Pleistocene lake cycles on the southern Bolivian Altiplano: implications for causes of tropical climate change. Geological Society of America Bulletin 118, 515–532.

Ponder, W.F., Lindberg, D.R., 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zoological Journal of the Linnean Society 119, 83–265.

Quarta, G., Romaniello, L., D'Elia, M., Mastronuzzi, G., Calcagnile, L., 2007. Radiocarbon age anomalies in pre- and post-bomb land snails from the coastal Mediterranean basin. Radiocarbon 49, 817–826.

Reimer, P., Baillie, M., Bard, E., Bayliss, A., Beck, J., Blackwell, P., Ramsey, C.B., Buck, C., Burr, G., Edwards, R., Friedrich, M., Grootes, P., Guilderson, T., Hajdas, I., Heaton, T., Hogg, A., Hughen, K., Kaiser, K., Kromer, B., McCormac, F., Manning, S., Reimer, R., Richards, D., Southon, J., Talamo, S., Turney, C., van der Plicht, J., Weyhenmeyer, C., 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal B.P. Radiocarbon 51, 1111–1150.

Reimer, P.J., Brown, T.A., Reimer, R.W., 2004. Discussion: reporting and calibration of post-bomb ^{14}C data. Radiocarbon 46, 1299–1304.

Riggs, A.C., 1984. Major carbon-14 deficiency in modern snail shells from southern Nevada springs. Science 224, 58–61.

Romaniello, L., Quarta, G., Mastronuzzi, G., D'Elia, M., Calcagnile, L., 2008. ^{14}C age anomalies in modern land snails shell carbonate from Southern Italy. Quaternary Geochronology 3, 68–75.

Rubin, M., Likins, R.C., Berry, E.G., 1963. On the validity of radiocarbon dates from snail shells. Journal of Geology 71, 84–89.

Samos, G., 1949. Some observations on exchange of CO_2 between $BaCO_3$ and CO_2 gas. Science 110, 663–665.

Slota, P.J., Jull, A.J.T., Linick, T.W., Toolin, L.J., 1987. Preparation of small samples for ^{14}C accelerator targets by catalytic reduction of CO. Radiocarbon 29, 303–306.

Stott, L.D., 2002. The influence of diet on the δ^{13}C of shell carbon in the pulmonate snail *Helix aspersa*. Earth and Planetary Science Letters 195, 249–259.

Stuiver, M., Polach, H.A., 1977. Reporting of ^{14}C data. Radiocarbon 19, 355–363.

Stuiver, M., Reimer, P.J., 1993. Extended ^{14}C database and revised CALIB radiocarbon calibration program. Radiocarbon 35, 215–230.

Tamers, M.A., 1970. Validity of radiocarbon dates on terrestrial snail shells. American Antiquity 35, 94–100.

Torn, M.S., Vitousek, P.M., Trumbore, S.E., 2005. The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling. Ecosystems 8, 352–372.

Wilbur, K.M., 1972. Shell formation in mollusks. In: Florkin, M., Scheer, B.T. (Eds.), Chemical Zoology, Mollusca, vol. 7. Academic Press, New York, pp. 103–145.

Yates, T., 1986. Studies of non-marine mollusks for the selection of shell samples for radiocarbon dating. Radiocarbon 28, 457–463.

Zhou, W., Head, W.J., Wang, F., Donahue, D.J., Jull, A.J.T., 1999. The reliability of AMS radiocarbon dating of shells from China. Radiocarbon 41, 17–24.

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Spatial constraint of peatland butterfly occurrences within a heterogeneous landscape

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Abstract The occurrence of ten butterfly taxa (*Clossiana eunomia dawsonii, Clossiana freija, Clossiana frigga, Clossiana titania, Coenonympha inornata, Erebia discoidalis, Incisalia augustinus, Lycaena dorcas, Lycaena epixanthe, Oeneis jutta*) was analyzed within three acid peatland habitat types from the Lake Superior drainage basin of northwestern Wisconsin. Both first- (nearest-neighbor spatial analysis) and second-order (Ripley's K) spatial point process statistics were used to identify the extents over which each distribution pattern significantly deviated from random expectations. Versions of these tests were used that identified significant spatial pattern uncorrelated to habitat location and habitat preference. These analyses documented non-random occurrence patterns in seven species. Deviations from random were largely confined to two extents: <50 km and 70–100+ km. The majority of non-random patterns at <50 km extents were examples of aggregation, while the majority of non-random patterns noted at the 70–100+ km scale were examples of segregation. These results demonstrate that even for winged animals inside a limited landscape, spatially constrained processes can be important determinants of distribution. It is likely that metapopulation dynamics and dispersal limitation help explain why aggregation is dominant at small scales. The mechanisms underlying the predominance of segregation at large scales are less clear, but may be related to migration history and/or weak environmental gradients.

Keywords Butterflies · Metapopulation · Nearest-neighbor spatial analysis · Ripley's K · Spatial pattern

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Introduction

Species occurrence patterns have often been described as a simple reflection of species niche requirements and underlying environmental conditions (MacArthur 1972; Tilman 1988). This idea requires the assumption that dispersal never limits distribution at regional scales, giving all species access to all potential habitats (Krebs 1985). Saur (1988) equated this concept with Beijerinck's Law, which states that “everything is everywhere but the environment selects”. In such situations, species occurrences should not have significant spatial pattern beyond that exhibited by the physical environment.

However, the spatial relationship of populations, independent of the physical environment, may also influence occurrence patterns. Supply-side ecology (Roughgarden et al. 1987) and the mass effect (Shmida and Ellner 1984) demonstrate how proximity to potential source populations can positively influence occurrence frequency. Additionally, analyses of distance decay (Nekola and White 1999) and competitive co-equivalency (Shmida and Ellner 1984) demonstrate how habitat isolation can negatively influence population frequency. For these reasons, patch size and isolation can correlate as significantly to patch occupancy as does the physical environment (Moilanen and Hanski 1998). When such spatial factors are at work, non-random spatial occurrence patterns should be evident independent of the physical environment. Identification of such patterns is an important first step in the recognition of situations where spatially constrained processes are (or have been) important (Diggle 1983).

How frequently do populations deviate from random occurrence patterns, independent of their environment? One way of assessing this question is to compare distributions across a well-defined taxonomic group within a particular habitat in a given landscape. This allows for at least partial control of the environmental, geographic, temporal, and phylogenetic templates upon which distributions have developed.

Butterflies of northern Wisconsin acid peatlands represent such a system. Recent and historical investigations have documented ten species [*Clossiana eunomia dawsonii* (Nymphalidae), *Clossiana freija* (Nymphalidae), *Clossiana frigga* (Nymphalidae), *Clossiana titania* (Nymphalidae), *Coenonympha inornata* (Satyridae), *Erebia discoidalis* (Satyridae), *Incisalia augustinus* (Lycaenidae), *Lycaena dorcas* (Lycaenidae), *Lycaena epixanthe* (Lycaenidae), *Oeneis jutta* (Satyridae)], which live out their entire life cycles in these habitats (Masters 1971a, b, 1972; Ferge and Kuehn 1976; Kuehn 1983; Swengel 1995; Nekola 1998). Within the Lake Superior drainage basin of northwestern Wisconsin, three types of acid peatland habitats exist: muskeg, kettlehole, and coastal. Muskeg sites are dominated by open black spruce-cottongrass-wiregrass savanna, are relatively dry (except in the proximity of moats or lakes), and usually have an elevation similar to the surrounding uplands. Kettlehole peatlands are generally wetter, commonly contain floating sphagnum-leatherleaf mats, and are typically found fringing lakes or in kettlehole depressions. Coastal wetlands are limited to estuaries along the Lake Superior coast. Considerable similarity exists within the physical environment, habitat size, and flora of each peatland type, leading to the presence of very similar habitats throughout the region. However, subtle environmental and vegetation differences exist between peatland types, producing slightly different butterfly faunas within each (Nekola 1998).

The following paper analyzes the occurrence patterns of these butterflies within these habitats in order to identify the frequency of non-random distributions that are uncorrelated with environment, and the spatial extents at which the majority of any such non-random patterns occur. These results identify potentially important spatial processes, and can be used to guide conservation strategy.

Materials and methods

Site selection

Identification of all high quality peatlands within or adjacent to the Lake Superior drainage basin (Fig. 1) was accomplished by a fly-over of the study area on 20 May 1996 in a small aircraft. Approximately 5 h of flight time were required to survey the entire region at an altitude of 3,000–5,000 m in north-south transects running approximately 10 km apart. Other high-quality sites were identified through review of the Biological Conservation Database and discussions with the staff of the Wisconsin Department of Natural Resources Bureau of Endangered Resources. While an attempt was made to inventory all high-quality sites, some (like the Kakagon Sloughs) were not visited due to difficulty in political and/or physical access. As few such sites existed, and as they were spread across the study region, we assume that their absence from this analysis has not biased results.

Field sampling

The latitude-longitude location of each surveyed site was determined through digitization of USGS 7.5 min topographic quads using the ATLAS DRAW software package. The centroids for these sites were then converted to Zone 15 UTM coordinates using PC-ARCINFO.

The peatland habitat type represented by each site (muskeg, kettlehole, or coastal) was also recorded. Muskeg peatlands (37 to-

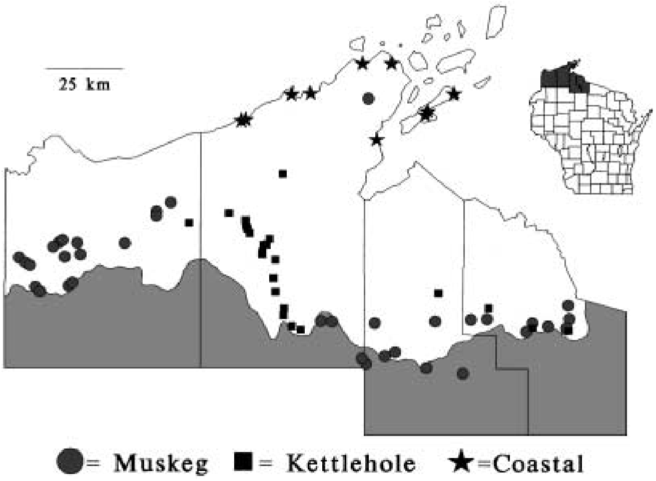

Fig. 1 Distribution of surveyed peatland habitats in northwestern Wisconsin. The *shaded area* in the south of the region represents areas outside of the Lake Superior drainage basin

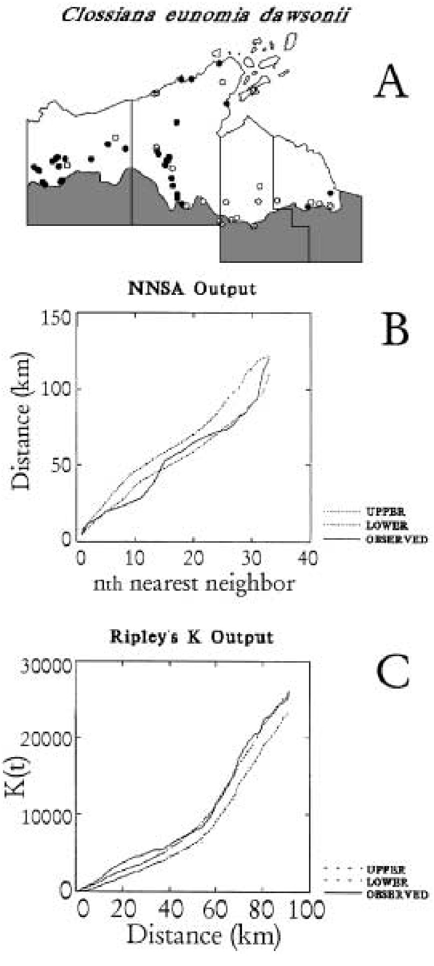

Fig. 2 **A** Occurrence pattern of *Clossiana eunomia dawsoni* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

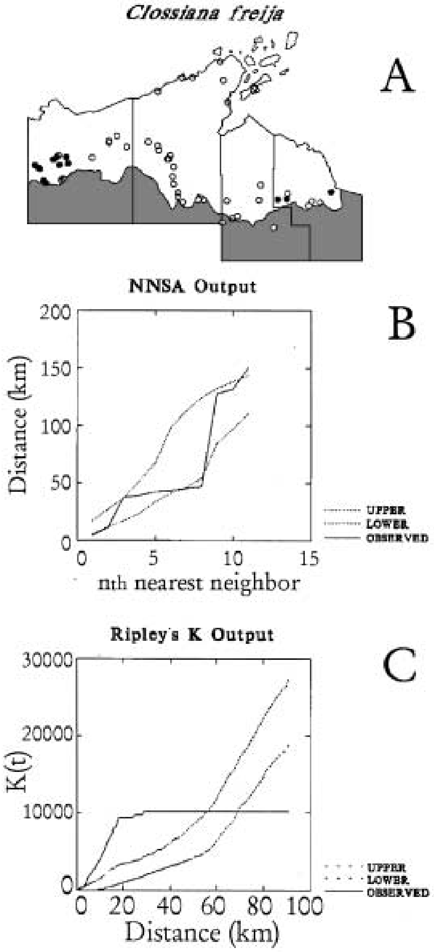

Fig. 3 **A** Occurrence pattern of *Clossiana freija* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

tal inventoried sites) were concentrated along the southern divide basin boundary in the western and eastern sides of the study area and were absent from the pitted outwash plain in the central region. Kettlehole peatlands (23 sites) were generally concentrated in the central outwash plain that lacked muskeg sites, although a few were also scattered throughout the eastern half. Coastal peatlands (10 sites) were limited to the Lake Superior shore in the Bayfield Peninsula and the Apostle Islands (Fig. 1).

Each site was visited 4–7 times during the 1996 flight season. Surveys were only conducted during sunny, dry weather when temperatures were 18°C or higher. Surveys were made at weekly intervals early in the flight season when a number of closely spaced adult emergences occur. Later in the season, when species emergence periods were more temporally separated and individual populations were in flight for longer periods of time, the survey interval increased to 3 weeks. Each site visit lasted for 15–90 min, depending upon site size, and all encountered peatland butterfly taxa were recorded. Voucher specimens are housed in the first author's collection at the University of Wisconsin-Green Bay. Nomenclature follows that of Miller and Brown (1981).

Cumulative presence-absence species lists for all peatland taxa from each site were compiled from site visit lists combined with any additional collections archived at the Milwaukee Public Museum and element occurrence records maintained by the Wisconsin Bureau of Endangered Resources.

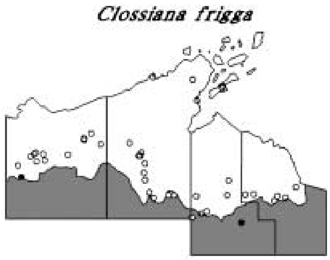

Fig. 4 Occurrence pattern of *Clossiana frigga* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time

As weather and logistical constraints prevented visitation of all sites during a given flight time, only sites inventoried during the flight duration for a given species were used for statistical analysis. Flight times for a given species were determined by noting the earliest and latest dates of adult encounters in the study region during 1996.

Statistical analyses

Two general approaches exist to analyze spatial point patterns: first-order statistics consider the mean distances between points, while second-order statistics consider the variance in these distances. One of the most commonly used first-order statistics is nearest-neighbor analysis (Diggle 1983; Manly 1991), while one of the most commonly used second-order statistics is Ripley's K analysis (Ripley 1977; Haase 1995). As little has been written to suggest whether first- or second-order statistics are more effective at identifying non-random patterns, both were used.

Both methods, as commonly employed, generate random null models from the assumption that occurrence is possible anywhere within the study region (e.g. Diggle 1983; Manly 1991). This is not appropriate for acid peatland butterflies, which cannot reside outside of peatland habitats. If peatlands are non-randomly distributed (as is the case in northwestern Wisconsin), it will be impossible to determine from such null models whether a non-random occurrence pattern for a given species is due to habitat distribution or other spatially constrained processes. Additionally, the physical environment may lead to significant non-random pattern when differences exist between habitats (as is also the case for peatland butterflies in our study). To more clearly test for non-random distributions uncorrelated to such environmental pattern, the first- and second-order statistics used in this study constrained random null models to actual peatland locations and to the actual occurrence frequencies of each species within each peatland type.

Nearest-neighbor spatial analysis (NNSA; Davis et al. 2000) was chosen as the first-order statistic. This method is related to the nearest-neighbor method described by Manly (1991), in which the average distance between 1st, 2nd, 3rd to *n*–1 nearest neighbors (where *n* equals the total number of occurrences of that species in the landscape) is calculated and compared to expected values generated from random distributions. Unlike Manly's test, the NNSA method generates random expectations based upon the subsampling of a larger finite set of points within a landscape. This permits factoring out spatial pattern caused solely by habitat distribution. This method also constrains random subsamples to be drawn at the same frequencies for which taxa were observed in that given habitat type. This allows any spatial pattern caused by habitat differences to be factored out (Davis et al. 2000).

NNSA null expectations were based on 5,000 Monte Carlo simulations. Two-tailed 95% confidence intervals were generated from this process, and plotted versus observed nearest-neighbor distances (Figs. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11). From these, the total

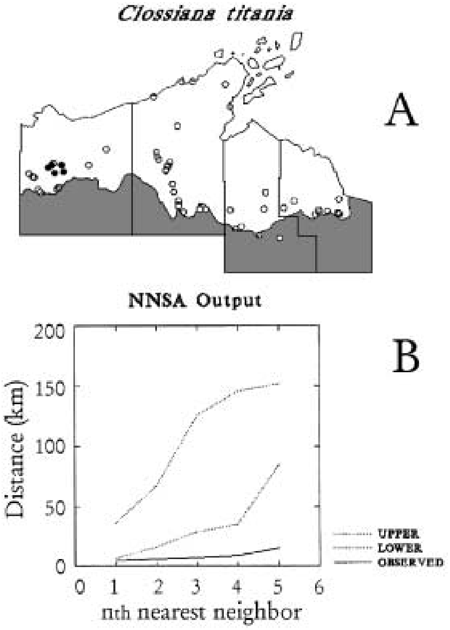

Fig. 5 **A** Occurrence pattern of *Clossiana titania* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations

range of distances were determined over which observed distributions deviated from random.

Ripley's K (Ripley 1977) was chosen as the second-order statistic. This test evaluates the expected number of points within a distance t of an arbitrary point in the area being evaluated (Haase 1995). If occurrences are randomly distributed, the expected value of $K(t)=\pi t^2$.

The unbiased estimate of $K(t)$ for an observed spatial point pattern is:

$$\hat{K}(t) = n^{-2}A\sum_{i\neq j}\sum_{i\neq j} w_{ij}^{-1} I_t(u_{ij}) \,,$$

where n is the number of points in the landscape area A; u_{ij} is the distance between events i and j; $I_t(u)$, the counter variable, equals 1 if $u<=t$ and 0 if $u>t$; w_{ij} is the proportion of the circumference of a circle centered at the event i with radius u_{ij} lying within A; and the summation is over all pairs of a given species occurrence (Ripley 1977).

Random expectations for $K(t)$ were based upon a random subsample of n peatlands in the landscape, with n representing the number of species occurrences, as is outlined in Kraft et al. (in press). Randomly chosen sites were selected according to the actual proportion of sites colonized by each species within each peatland type. In this way, spatial pattern due to habitat distribution and preference were factored out.

S-Plus was used for estimating Ripley's K (Venables and Ripley 1997). Null expectations were based on 5,000 Monte Carlo simulations. Two-tailed 95% confidence intervals were generated and plotted against observed values (Figs. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11). From these, the total range of distances was determined over which observed deviated from random.

Because our null expectations are based upon randomly selected subsets of given peatland sites, the expectation that $K(t)$ will approximate πt^2 is not valid. Thus, the boundary issues considered by Haase (1995) do not apply to our analysis, as occurrences are constrained to actual peatland locations. Any such boundary-based biases should be accounted for by our use of Monte Carlo simulations to estimate the 95% confidence interval for $K(t)$.

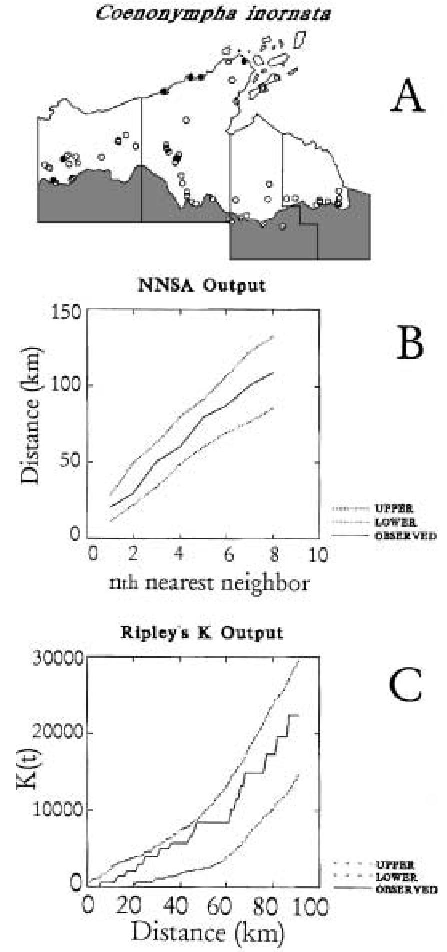

Fig. 6 **A** Occurrence pattern of *Coenonympha inornata* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

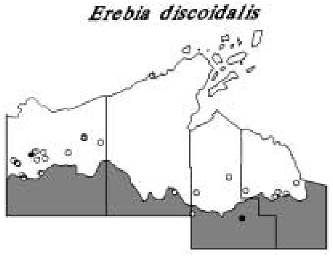

Fig. 7 Occurrence pattern of *Erebia discoidalis* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time

Results were summarized across all species via histograms documenting the total number of significant aggregations and segregations at each analyzed distance for both methods (ca. 0–150 km for NNSA, 0–91 km for Ripley's K).

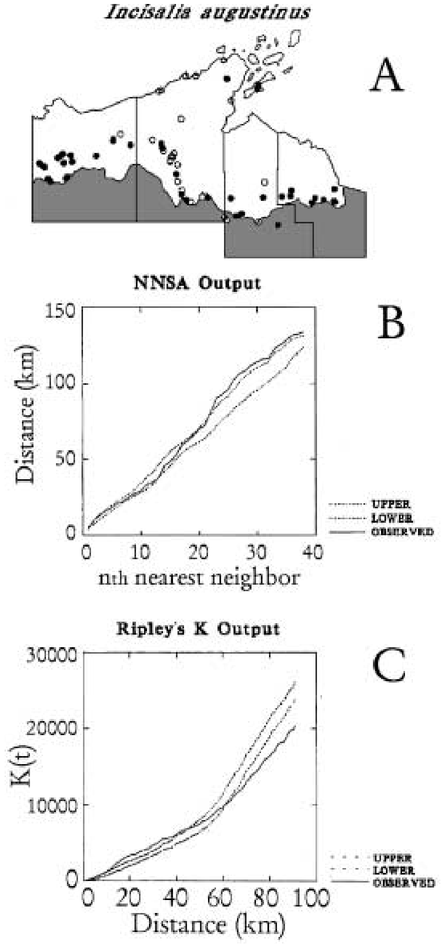

Fig. 8 **A** Occurrence pattern of *Incisalia augustinus* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

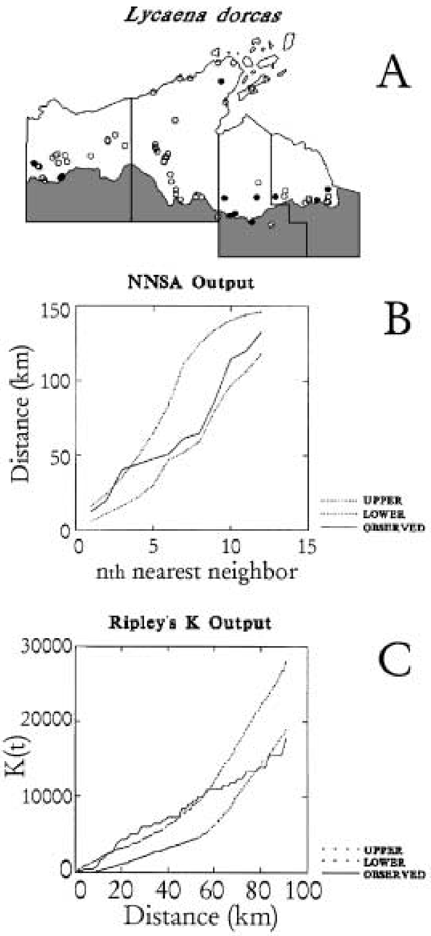

Fig. 9 **A** Occurrence pattern of *Lycaena dorcas* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

Results

Two taxa (*Clossiana frigga* and *Erebia discoidalis*) were only twice encountered. Their populations were limited to muskeg sites in the west and east. Although their distributions have been mapped for sake of completeness (Figs. 4, 7), their few occurrences precluded further statistical analysis.

Significant deviations from random were noted in the occurrences of seven of the remaining eight taxa. The only species which did not significantly deviate from random in either test was *Coenonympha inornata*, which was located at nine scattered sites (4 muskeg, 1 kettlehole, 4 coastal; Fig. 7).

Clossiana eunomia dawsonii was located at 34 sites (14 muskeg, 14 kettlehole, 4 coastal), with the majority being located in the western half of the study region (Fig. 2). NNSA identified significant aggregation in these occurrences from the 6th–14th (min. $P<0.0005$; 21–44 km), 25rd–27th (min. $P=0.008$; 73–77 km), and 29th ($P=0.021$; 85 km) nearest neighbors. Ripley's K identified significant clustering (min. $P<0.0005$) in these occurrences from 1–48 km and 67–87 km extents.

Clossiana freija was located at 12 muskeg sites, with populations being restricted to the far west and east (Fig. 3). NNSA identified significant aggregation over the 1st–2nd (min. $P=0.012$; 5–11 km) and 8th ($P=0.017$; 47 km) nearest neighbors. Significant segregation was noted at the 11th ($P=0.001$; 150 km) nearest neighbor. Ripley's K identified significant aggregation from 4–55 km (min. $P<0.0005$), and significant segregation from 69–91 km (min. $P<0.0005$).

Clossiana titania was located at 6 muskeg sites in the far west (Fig. 5). NNSA identified significant aggre-

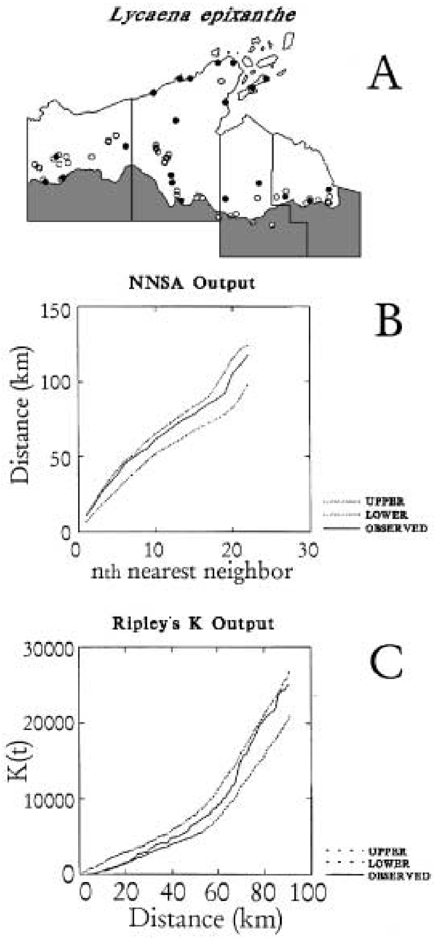

Fig. 10 **A** Occurrence pattern of *Lycaena epixanthe* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed* lines show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

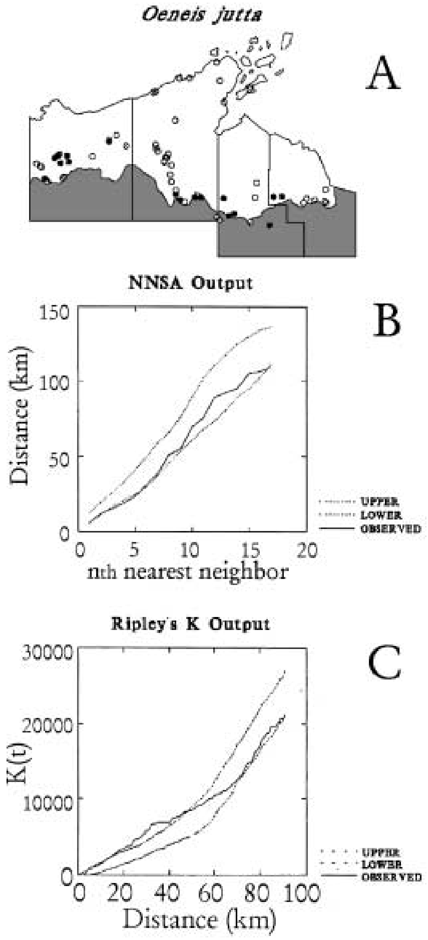

Fig. 11 **A** Occurrence pattern of *Oeneis jutta* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

gation (minimum $p<0.0005$) across all neighbors (5–15 km). Too few occurrences were present to allow calculation of Ripley's K.

Incisalia augustinus was located at 39 sites (30 muskeg, 8 kettlehole, 1 coastal), which were most frequently encountered in the west and east (Fig. 8). NNSA identified significant segregation (min. $P<0.0005$) from the 22nd–38th nearest neighbors (81–133 km). Ripley's K identified significant aggregation in occurrence at 5 km ($P=0.023$) and from 10–44 km (min. $P<0.0005$), and significant segregation from 61–91 km (min. $P<0.0005$).

Lycaena dorcas was located at 13 muskeg sites, with the majority of populations being found in the eastern half (Fig. 9). NNSA identified significant ($P=0.003$) segregation at the 3rd nearest neighbor (40 km). Ripley's K identified significant aggregation in its occurrence from 16–60 km (min. $P<0.0005$), and significant segregation from 81–82 km (min. $P=0.013$) and 86–91 km (min. $P=0.006$).

Lycaena epixanthe was located at 23 sites (7 muskeg, 7 kettlehole, 9 coastal), with populations sporadically occurring throughout the entire region (Fig. 10). No significant deviations from random were noted by NNSA. However, Ripley's K identified significant segregation (min. $P<0.0005$) in its occurrences from 3 to 21 km.

Oeneis jutta was located at 18 sites (15 muskeg, 3 kettlehole), with populations being noted in the west and south central (Fig. 11). NNSA identified significant aggregation from the 3rd–5th (minimum $p=0.009$; 15–23 km) nearest neighbors. Ripley's K identified significant aggregation from 5–8 km (min. $P=0.008$), 10 km ($P=0.022$), 13 km ($P=0.022$), 16 km ($P=0.024$), and from 18–49 km (min. $P=0.001$).

Comparison of these results across species (Fig. 12) show that significant deviation from random was most apparent at three extents. At <20 km, NNSA identified non-random aggregation for two taxa (*C. freija*, *C. titania*), while Ripley's K identified significant aggregation

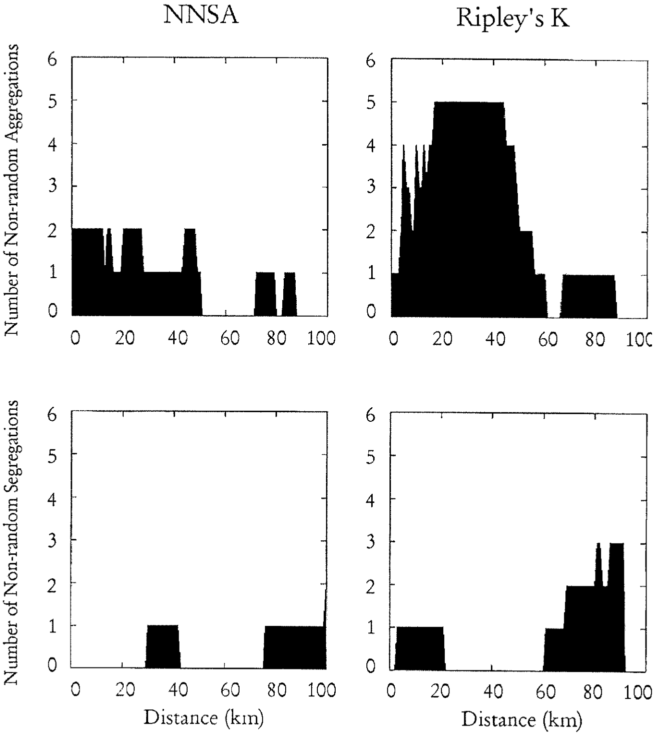

Fig. 12 Frequency of non-random aggregation and segregation patterns from 0–100 km extents for both NNSA and Ripley's K analyses

in four taxa (*C. eunomia dawsonii*, *C. freija*, *I. augustinus*, *O. jutta*). Additionally, Ripley's K identified significant segregation over this range for *L. epixanthe*. From 20–50 km, NNSA identified aggregation for three taxa (*C. eunomia dawsonii*, *C. freija*, *O. jutta*), while Ripley's K identified aggregation for five taxa (*C. eunomia dawsonii*, *C. freija, I. augustinus*, *L. dorcas*, *O. jutta*). Significant segregation was identified at this scale by NNSA for *L. dorcas*. Few non-random occurrence patterns were identified by either method from 50–70 km. However, at larger scales both methods identified significant aggregation in *C. eunomia dawsonii*. Significant segregation at this scale was identified by both methods for *C. freija* and *I. augustinus*, and by Ripley's K for *L. dorcas*.

Discussion

Perhaps the most obvious and important finding from these analyses is the simple realization that in northwestern Wisconsin, across a broad range of spatial scales (0–90 km), most acid-peatland butterflies appear to possess non-random occurrences independent of habitat location and preference.

As we did not sample physical environmental variables from these sites (e.g. soil and water chemistry, local climate, amount and type of plant cover), it is possible that some of these distribution patterns may be related to such factors. If present, however, these factors must be cryptic, as habitats appeared to be homogeneous within each peatland type, possessing similar (if not identical) microhabitats, vascular plant, and bryophyte species. Additionally, given the small total extent of the sample region (ca. 150 × 75 km), it is unlikely that strong climatic gradients exist. Thus, we believe that the patterns of peatland butterfly occurrence are likely related to other factors.

Assuming that peatlands within a given type have approximately similar environments for these butterflies, the existence of non-random occurrence patterns independent of habitat location and preference would be unlikely if dispersal allowed equal access to all suitable sites. The frequent presence of significant non-random occurrence pattern in these species suggests that within this landscape spatial limitation of butterfly dispersal is common.

Inference of spatial process from spatial pattern

The local clustering of occurrences is not surprising as many ecological processes show some degree of spatial autocorrelation over relatively small extents (Shmida and Ellner 1984; Burrough 1986; Okubo and Levin 1989). In particular, limitations on butterfly movement contribute to patchy occurrences in a number of European taxa, including *Clossiana* (*Boloria*) *aquilonaris* (Mousson et al. 1999), *C.* (*Proclossiana*) *eunomia* (Nève et al. 1996a), *Hesperia comma* (Hill et al. 1996), and *Melitaea cinxia* (Hanski et al. 1994). When dispersal limitation is coupled with other aspects of metapopulation dynamics, local aggregations of butterfly occurrence, independent of the physical environment, are often evident. For instance, *M. cinixa* occurrences on the main Åland island in southwestern Finland demonstrate what visually appears to be strong aggregation over 1–10 km extents among appropriate habitat patches (Moilanen and Hanski 1998). Occurrences of *H. comma* in the North Downs, Surrey, UK, also appear to be aggregated over 2–6 km extents within appropriate sites (Hill et al. 1996). The metapopulations of all five edaphically-restricted butterfly taxa of Sierra Nevada (California) serpentine barrens also demonstrate apparent spatial aggregation in their occurrences among known sites (Gervais and Shapiro 1999).

Much of the previous work on occurrence patterns in Lepidoptera has focused on the factors predicting habitat occupancy or vacancy (Ehrlich and Murphy 1987; Thomas et al. 1992; Hanski et al. 1994). While these studies have elucidated the processes influencing individual patches, none have investigated the spatial patterns in occurrence generated by these processes across an entire landscape. Analyzing such patterns may prove a useful tool for identifying those species whose distribution is influenced by spatial processes (Hanski 1999). For instance, *C. eunomia* is known to exist in discrete metapopulations within Belgium and France, with individuals capable of traversing up to 8 km of unfavorable habitat within a season (Nève et al. 1996b). Our analyses demonstrate strong aggregation for this species at relatively small (<50 km) scales. A previous investigation on

Coenonympha tullia (often lumped with *C. inornata*) distribution in Northumberland, UK, documented that occurrences were more strongly related to habitat quality than geographic factors (Dennis and Eales 1999). In northwestern Wisconsin, this species was the only one that exhibited random occurrence patterns at all scales. These examples, in conjunction with our analysis of spatial distribution pattern, illustrate how analyses of spatial pattern can reflect potential processes underlying organism distribution. While Real and McElhaney (1996) note that spatial pattern analysis, alone, cannot distinguish between all processes capable of producing a given pattern, we believe that the analysis of spatial pattern provides an instructive first step that can help improve field experiments or modeling efforts used to evaluate the processes affecting distribution.

It is not clear for the majority of the fauna why aggregation is essentially limited to <50 km extents. This is especially interesting given the fact that many of these species appear to share similar niches: in the region *Clossiana freija*, *C. eunomia*, *C. titania*, *L. dorcas*, and *L. epixanthe* all are obligate cranberry consumers, while *Coenonympha inornata*, *E. discoidalis*, and *O. jutta* appear limited to cottongrass and/or wiregrass (Nekola 1998). While these species might thus be expected to demonstrate some form of competitive exclusion, they instead appear to show largely coincident occurrence patterns at regional scales. Such correspondence between occurrence patterns is likely related to factors that have equally influenced all taxa, such as habitat and host plant distribution. If related to cryptic environmental gradients, the location of colonies may be expected to remain static over time. However, if shifting metapopulation dynamics are responsible, the location of occurrence clusters may change over ecological time scales within the landscape.

Another enigma is the presence of significant small-scale segregation in occurrences of *L. epixanthe*. While it is possible that colonies may have become segregated due to competitive interactions, such processes are generally thought to be limited to small extents within sites (Shmida and Ellner 1984). It is difficult to envision how such mechanisms could operate at distances up to 20 km.

A number of other spatial mechanisms may underlie larger scale (70–150 km) segregated spatial distributions. Migration history may provide one explanation. For instance, migration of *C. eunomia dawsonii* out of Minnesota (beyond the study area boundaries) could help account for its higher occurrence frequencies in the west. Likewise, the absence of species from the center (e.g., *C. freija*, *L. dorcas*, *O. jutta*) could be due to dual migration pathways from peatland-rich landscapes to the west and east. However, these patterns could also be related to cryptic soil and water chemistry or climate gradients that our statistical methods could not control for. In this event, identification of such cryptic gradients would be a useful result, given their difficulty in direct detection.

Teasing apart the historical and environmental influences on distribution at large scales may prove difficult due to covariation between these factors. Population genetics analyses may provide one possible avenue to distinguish between them. If historical factors are responsible for the observed large-scale pattern, it seems likely that significant genetic differences may occur across the study region due to differences in initial population source pools. However, if dispersal is not limiting and contemporaneous environmental gradients are responsible for the observed pattern, differences in allele frequency should be diminished from more thorough genetic mixing.

Conservation implications

Relatively few populations (e.g., <25 stations) of these taxa (except *I. augustinus*) have been previously reported from Wisconsin (Ebner 1970; Masters 1971a, b, 1972; Ferge and Kuehn 1976; Kuehn 1983; Swengel 1995). As acid peatlands are frequent in the northern Wisconsin landscape, it has been generally assumed that these species were simply undercollected and would eventually be found within most appropriate sites (Wisconsin Rare Butterfly Working List 1996). As such, none of these species have been granted endangered or threatened species protection within the state (Wisconsin Endangered Species List 1999).

The existence of complex spatial structure in the occurrence of these taxa suggests that such expectations may be false. The aggregation of most inventoried taxa indicates that, at some scale, high-quality sites will be unoccupied. Modifications to sites within limited areas of occurrence would have profound implications to the long-term survival of those species across the entire landscape. For example, *C. freija* and *C. titania* are essentially restricted to a small cluster of sites in the far west of the study region. Unfortunately, peatlands in this same area were observed to be undergoing the heaviest “all terrain vehicle” abuse within the entire region. Thus, even though appropriate habitat for these species exists throughout the study region, the correspondence of high levels of disturbance in the region where most colonies occur suggests that their continued existence within this landscape may be in jeopardy.

In this region, the vulnerability of peatland butterfly species appears to be generally unrelated to habitat frequency. Such patterns may be common at range edges where increased environmental stress and patch isolation lead to lower habitat occupancy rates (Thomas et al. 1992). When species distribution does not simply mimic habitat abundance, determination of population vulnerability to extirpation can only be assessed by conducting geographically systematic inventories and documenting the actual distribution of taxa. Additionally, repeated monitoring of distribution may be necessary if shifting metapopulations exist.

Comparison of first- and second-order spatial point statistics

Given the different assumptions and algorithms underlying these methods, the general robustness of the results suggests that the underlying patterns are quite strong. Only one species (*L. dorcas*) exhibited a major discrepancy in outcomes, with NNSA identifying segregation in the same 30–40 km extent where Ripley's K showed strong aggregation. Based upon visual inspection of this taxon's occurrences, the Ripley's K result appeared more accurate. Perhaps NNSA was unable to identify aggregation for this species as occurrences were concentrated on a region of widely separated sites.

Comparing results across species, Ripley's K identified more non-random distributions at a given extent, and identified larger regions for non-random distribution, as compared to NNSA. It would thus appear that NNSA is the more conservative of the two tests. However, visual inspection of maps suggests that NNSA might be overly conservative, as it failed to identify areas of apparent aggregation or segregation at some scales (e.g., *C. freija*, *I. augustinus*, *L. epixanthe*, *O. jutta*). A more rigorous comparison of these methods would help to better determine their relative strengths and weaknesses.

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References

Burrough PA (1986) Principles of geographical information systems for land resources assessment. Oxford University Press, New York

Davis JH, Howe RW, Davis GJ (2000) A multi-scale spatial analysis method for point data. Landscape Ecol 15:99–114

Dennis RLH, Eales HT (1999) Probability of site occupancy in the large heath butterfly *Coenonympha tullia* determined from geographical and ecological data. Biol Conserv 87:295–301

Diggle PJ (1983) The analysis of spatial point patterns. Academic Press, New York

Ebner JA (1970) Butterflies of Wisconsin. Milwaukee Public Museum Popular Science Handbook 12, Milwaukee, Wisconsin

Ehrlich PR, Murphy DD (1987) Conservation lessons from long-term studies of checkerspot butterflies. Conserv Biol 1:122–131

Ferge LA, Kuehn RM (1976) First records of *Boloria frigga* (Nymphalidae) in Wisconsin. J Lepid Soc 30:233–234

Gervais BR, Shapiro AM (1999) Distribution of edaphic-endemic butterflies in the Sierra Nevada of California. Glob Ecol Biogeogr Lett 8:151–162

Haase P (1995) Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. J Veg Sci 6:575–582

Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209–219

Hanski I, Kuussaari M, Nieminen M (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762

Hill JK, Thomas CD, Lewis OT (1996) Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. J Anim Ecol 65: 725–735

Kraft CE, Sullivan PJ, Karatayev AY, Burlakova LE, Nekola JC, Johnson LE, Padilla DK (in press) Landscape patterns of zebra mussel inland lake invasions: evaluating dispersal from distribution. J Appl Ecol

Krebs CJ (1985) Ecology. Harper and Row, New York

Kuehn RM (1983) New Wisconsin butterfly records. J Lepid Soc 37:228–235

MacArthur RH (1972) Geographical ecology. Harper and Row, New York

Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman and Hall, New York

Masters JH (1971a) Ecological and distributional notes on *Erebia discoidalis* (Satyridae) in the north central states. J Res Lepid 9:11–16

Masters JH (1971b) First records of *Boloria eunomia* (Nymphalidae) in Wisconsin. J Lepid Soc 25:149

Masters JH (1972) Critical comments on James A. Ebner's "Butterflies of Wisconsin." In: Keuhn RM, Masters JH (eds) Wisconsin butterflies. Mid-Continent Lepidoptera Series 59, pp 5-11

Miller LD, Brown FM (1981) A catalogue/checklist of the butterflies of America north of Mexico. Lepidopterist's Society Memoir 2

Moilanen A, Hanski I (1998) Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503–2515

Mousson L, Nève G, Baguette M (1999) Metapopulation structure and conservation of the Cranberry Fritillary *Boloria aquilonaris* (Lepidoptera, Nymphalidae) in Belgium. Biol Conserv 87:285–293

Nekola JC (1998) Butterfly (Lepidoptera: Lycaeniidae, Nymphalidae, and Satyridae) faunas of three peatland habitat types in the Lake Superior drainage basin of Wisconsin. Great Lakes Entomol 31:27–37

Nekola JC, White PS (1999) The distance decay of similarity in bioigeography and ecology. J Biogeogr 26:867-878

Nève G, Mousson L, Baguette M (1996a) Adult dispersal and genetic structure of butterfly populations in a fragmented landscape. Acta Oecol 17:621–626

Nève G, Barascud B, Hughes R, Aubert J, Descimon H, Lebrun P, Baguette M (1996b) Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). J Appl Ecol 33:14–22

Okubo A, Levin SA (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecology 70:329–338

Real LA, McElhany P (1996) Spatial pattern and process in plant-pathogen interactions. Ecology 77:1011–1025

Ripley BD (1977) Modeling spatial patterns. J R Stat Soc Ser B 39:172–212

Roughgarden J, Gaines SD, Pacala SW (1987) Supply side ecology: the role of physical transport processes. Br Ecol Soc Symp 27:491–518

Saur JD (1988) Plant migration. University of California Press, Berkeley

Shmida A, Ellner S (1984) Coexistence of plant species with similar niches. Vegetatio 58: 29–55

Swengel AB (1995) Butterflies of Northwestern Wisconsin. Madison Audubon Society, Madison

Thomas CD, Thomas JA, Warren MS (1992) Distributions of occupied and vacant butterfly habitats in fragmented landscapes. Oecologia 92:563–567

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Venables WN, Ripley BD (1997) Modern applied statistics with S-Plus. Springer, Berlin Heidelberg New York

Wisconsin Endangered Species List (1999) Wisconsin Department of Natural Resources, Madison

Wisconsin Rare Butterfly Working List (1996) Bureau of Endangered Resources, Wisconsin Department of Natural Resources, Madison

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PALEOREFUGIA AND NEOREFUGIA: THE INFLUENCE OF COLONIZATION HISTORY ON COMMUNITY PATTERN AND PROCESS

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Abstract. Two types of biological refugia (habitats that support populations not able to live elsewhere in a landscape) can be defined from relative refugium age as compared to surrounding matrix age; paleorefugia are now-fragmented relicts of a formerly widespread matrix community, whereas neorefugia have formed more recently than the matrix. This difference should make extinction a relatively more important process in determining species occurrence in paleorefugia, whereas immigration should be relatively more important in neorefugia. Based on these differences, a series of eight a priori predictions relating to the diversity and distribution patterns for the biota of such sites can be generated: (1) the slope of the species–area relationship, and amount of variance explained by it, should be greater in paleorefugia as compared to neorefugia; (2) the negative relationship between habitat isolation and species richness should be stronger in neorefugia as compared to paleorefugia; (3) species richness should be expected to decrease over time in paleorefugia, but to increase over time in neorefugia; (4) the inverse correlation between site distance and community similarity (distance decay) should be stronger in neorefugia as compared to paleorefugia; (5) neorefugia should be enriched in highly vagile species relative to paleorefugia, whereas paleorefugia should be rich in less vagile species relative to neorefugia; (6) geographic factors should be more important predictors of species occurrence for neorefugia than for paleorefugia; (7) paleorefuge sites should possess more and stronger correlations between community composition and environmental covariables (such as soil chemistry, climate, etc.) as compared to neorefuge sites; and (8) the number of competitive co-equivalents held within a system of neorefugia should be greater then the number held within a series of paleorefugia.

The most readily testable predictions (numbers 1, 2, 4, and 5) were evaluated by comparing species-richness and community-composition patterns within two northeastern Iowa refugia: algific talus slopes (paleorefugia) and fens (neorefugia). Results from these tests were consistent with predictions. These results illustrate that colonization history may influence contemporaneous species diversity and community-composition patterns. They also suggest that (1) equilibrium has yet to be achieved in the example systems after 5000–10 000 yr, (2) the ecological-biogeographic debate centered around the mutual exclusivity of vicariance and dispersal is intrinsically flawed, and (3) optimum reserve-design strategies for biodiversity protection within paleorefuge and neorefuge systems will differ.

Key words: biodiversity; biogeography, historical; colonization history, influence on community pattern; conservation biology; dispersal; fens; Iowa (USA), northeastern; island biogeography; refugia, paleorefugia vs. neorefugia; species richness; talus slopes, algific; vicariance.

INTRODUCTION

Past environmental changes have caused repeated fluctuations in species and habitat distributions that can lead to formation of island-like habitats and isolated populations through two contrasting pathways. They may represent remnants of once-more-widespread distributions that have become fragmented, or they may represent the de novo development of habitats or populations in a landscape where they were previously absent. Borrowing terminology used for endemic species (Stebbins and Major 1965, Krukeberg and Rabinowitz 1985), I refer to habitats that have been colonized through these processes, respectively, as ‘‘paleo-

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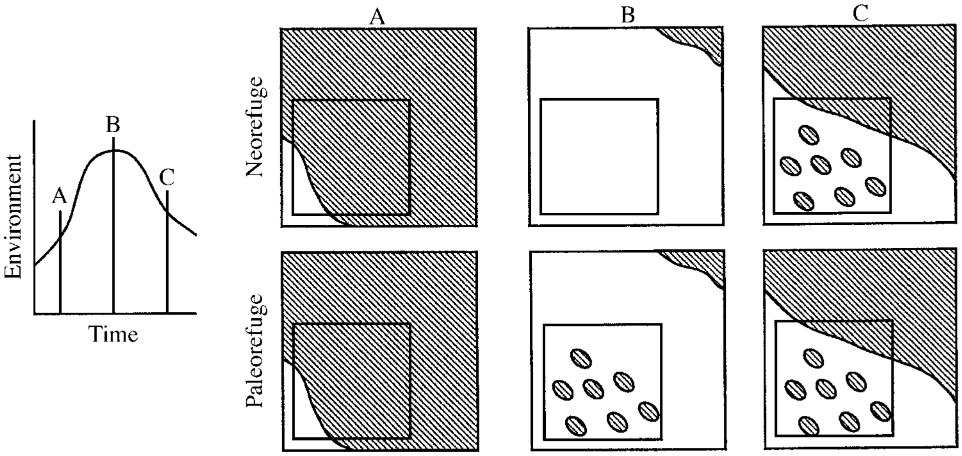

FIG. 1. Diagrammatic representation of the development of paleorefugia and neorefugia. At time period A, environmental conditions are conducive to the existence of a particular habitat (shaded). After critical environmental change (time period B), this habitat has retreated completely from the focal landscape (inner box) in the case of neorefugia but persists as isolated patches in the case of paleorefugia. By time period C, the environment has changed again, allowing the habitat to exist again within portions of its original range. At time period C, paleorefugia are found within essentially the same microenvironmentally buffered patches present at time period B. Neorefugia, in contrast, have formed as appropriate microhabitats develop in isolation from the main habitat area.

refugia'' and ''neorefugia.'' More specifically, paleorefugia represent habitats that are older than the surrounding biological matrix, whereas neorefugia represent habitats that are younger than the surrounding biological matrix. Such habitats are considered refugia as they support communities or populations unable to survive elsewhere in the landscape (i.e., Pielou 1979). As these terms reflect the relative age of a refugium to its matrix, a paleorefugium in one landscape may be of more recent origin than a neorefugium in another. It is also possible that a particular habitat type that developed as a paleorefugium in one landscape may be a neorefugium elsewhere.

In this paper, I ask how such paleorefugia and neorefugia would be expected to differ in their contemporaneous species richness, species distribution, and community-composition patterns. I develop eight predictions about these differences and then investigate the four most easily testable ones with data collected from two types of insular habitats that co-occur in northeastern Iowa.

THE INFLUENCE OF EXTINCTION AND IMMIGRATION

The relative importance of extinction and immigration processes varies greatly between paleorefugia and neorefugia. First, consider the development of paleorefugia sites. Before environmental change, a given community is continuous over a wide geographic extent, harboring a diverse and well-mixed biota potentially near equilibrium with the environment. Following environmental change, the habitat becomes restricted to a few discrete patches in the landscape (Fig. 1). As the community becomes fragmented, habitat size decreases and isolation between fragments increases, leading to increased extinction rates on individual fragments (MacArthur and Wilson 1967, Diamond 1975, Bierrgaard et al. 1992). The richness of individual sites falls, with larger fragments retaining more taxa than smaller ones (Diamond 1975). Although some recolonization from nearby sites undoubtedly occurs (the rescue effect of Brown and Kodric-Brown [1977]), this should not greatly influence large-scale compositional pattern as nearby sites should have been originally colonized from similar species pools.

In contrast, neorefugia sites are created through the development of novel environmental conditions in a landscape (compare time periods B to C in Fig. 1). Consequently, the composition of neorefugia must be a product of immigration. Factors that effect immigration, such as habitat isolation or age, should therefore exert influence on community composition and species richness (Carlquist 1974, Diamond 1975, Bush and Whittaker 1993). Although extinction certainly occurs on these sites as newly recruited populations disappear, this process should be of limited importance as populations can only become extinct if a successful immigration has previously occurred, and as incomplete dispersal between sites will limit rates of competitive exclusion (Shmida and Ellner 1984).

The differential contributions of extinction and immigration have been empirically documented for various insular habitats. Fernald (1925) hypothesized (incorrectly) about the role played by unglaciated nuntacks (reputed paleorefugia) in the development of eastern North American species ranges. Diamond (1973, 1975) noted that the species richness of land-bridge islands (paleorefugia) is primarily determined by extinction rates. Brown (1971) also discussed the role of extinction in shaping rodent faunas of Great Basin montane and alpine communities, which became fragmented following the close of Wisconsinan glaciation (paleorefugia). The importance of immigration in the development of the biota of young volcanic islands (neorefugia) has been shown on Krakatau, Long, and Ritter islands in the eastern Pacific (Diamond 1975, Bush and Whittaker 1993). Similar patterns were demonstrated by Simberloff and Wilson (1969) in their manipulative experiments of mangrove islands. Research on the importance of immigration in shaping community composition and structure has also been referred to as ''supply-side ecology'' (Roughgarden et al. 1987). However, none of these previous works have attempted to compare the contemporaneous ecological patterns of isolated communities that possess different colonization histories and that have, therefore, been exposed to different levels of extinction and immigration.

Predictions about Species Distribution, Species Richness, and Community Composition

My primary assumption is that across a large range of taxonomic groups, extinction will most influence the species composition of paleorefugia, whereas immigration will most influence the species composition of neorefugia. From this assumption, I have developed eight a priori expectations regarding differential species richness, distribution, and community-composition patterns:

(1) All else being equal, the slope of the species–area relationship, and the amount of variance explained by it, should be greater in paleorefugia than in neorefugia. Paleorefugia can be expected to have steeper species–area curves than neorefugia, because for a given-size island the paleorefuge will be approaching equilibrium number through species loss, whereas the neorefuge will be approaching this number through species accretion. Paleorefugia were originally more connected, and presumably once harbored similar numbers of species per unit area. Consequently, differences in species richness should be largely a function of post-fragmentation extinction rates. Such rates are believed to be strongly correlated with habitat size (e.g., Diamond 1975, Bierrgaard et al. 1992). The species richness of neorefugia, however, should also be a function of immigration processes, which are related less to habitat size than to other factors like habitat age and isolation. Consequently, paleorefugia can be expected to have less variance around the species–area curve than neorefugia. This prediction may be violated for neorefugia that have remained isolated over evolutionary time scales, as strong species–area relationships may be generated on island habitats through speciation (Carlquist 1974).

(2) All else being equal, the negative relationship between habitat isolation and species richness should be stronger in neorefugia than in paleorefugia. I expect this as propagule movement (and hence immigration rate) is largely a function of barrier width (Okubo and Levin 1989). Thus, less-isolated neorefugia should have access to a larger propagule pool than more-isolated ones. This result would not be anticipated from paleorefugia as, over limited geographic extents, sites were likely colonized from similar species pools. As such, contemporaneous site isolation should not strongly affect richness. Isolation could influence paleorefugia richness when recolonization from nearby sites (Brown and Kodric-Brown 1977) is important.

(3) Species richness should decrease over ecological time scales in paleorefugia, while increasing over similar time scales in neorefugia. Extinction, or ''relaxation'' (sensu Diamond 1975), should eliminate taxa from paleorefugia, as is typical for land-bridge islands. Such taxa may include those that are not well adapted to local site conditions, that are competitively inferior (e.g., Tilman 1988), or that exhibit area sensitivity (McDonald and Brown 1992). However, as neorefugia form de novo out of a hostile landscape, they will initially be void of species. Over time their richness should increase as taxa from the surrounding species pools immigrate onto sites (Zobel 1997).

It is also possible that over time the species richness of neorefugia and paleorefugia will converge. As time increases, immigration between neorefugia should become more and more complete, thereby increasing the importance of extinction in the structuring of site biotas and strengthening the species–area relationship. On paleorefugia, the stochastic loss of species may eventually lower site richness to levels anticipated for neorefugia. It is not clear what factors will most strongly influence this rate of convergence.

(4) The inverse correlation between site distance and community similarity (distance decay) should be stronger for neorefugia than for paleorefugia. A fundamental principle of geography is the inverse correlation between similarity and intersample distance (Tobler 1970). In the geographical literature this decrease in similarity has been termed ''distance decay'' and been applied to phenomena as diverse as human communication networks, migration patterns (Bennett and Gade 1979, Fotherinham 1981), and spatial interpolation (Burrough 1986). The rate of distance decay among natural communities has been shown to vary with the dispersal strategy of organisms and with the degree of landscape fragmentation (Nekola and White, *in press*).

I expect that the rate of compositional distance decay for paleorefugia should primarily reflect pre-fragmentation rates as long as no strong environmental gradients are present in the current landscape. Consequently, in most cases the rates of compositional distance decay for paleorefugia should be low within regions. However, because immigration is required for development of neorefugia biotas, sites across a region may be colonized through different species pools when source areas or migration corridors differ. As a result, similarity of neorefugia communities should be more strongly correlated with intersample distance.

(5) Neorefugia should be enriched in highly vagile species relative to paleorefugia, whereas paleorefugia should be enriched in less vagile species relative to neorefugia. I expect that species with good dispersal abilities will be more frequently represented in neorefugia, as colonization on such sites is only possible through the crossing of dispersal barriers–effectively eliminating poor dispersers while increasing the relative importance of good dispersers in the neorefugia species pool. Poor dispersers not only can be a component of paleorefugia biotas (as sites were colonized prior to fragmentation), but may be favored over time on these sites if they lose a smaller percentage of propagules beyond site boundaries (Carlquist 1974), and have larger, more competitively fit progeny (Harper 1977). These mechanisms have been suggested by Carlquist (1974) to explain the higher frequency of poorly dispersing plant and animal species on remote oceanic islands.

(6) Geographic factors (such as distance to nearest population) should be more important predictors of species occurrence on neorefugia over ecological time scales. All paleorefuge species (theoretically) had similar access to sites prior to fragmentation. For this reason, contemporaneous geographic factors should be of relatively limited importance in predicting current species distribution. Those environmental factors that directly affect the survival of populations should be of pronounced importance in predicting species occurrence on these sites due to the prolonged competitive sorting that has occurred there. However, the distance to contemporaneous propagule sources should be an important predictor of species occurrence on neorefugia, as the probability of colonization will increase with decreasing dispersal distance. Additionally, direct environmental factors may be less important in predicting species occurrence in neorefugia due to increased habitat breadths that result from limited competitive sorting on these sites and incomplete immigration of potential competitors (Cox and Ricklefs 1977).

(7) The higher levels of competitive sorting in paleorefugia should lead to a stronger tie between environmental and compositional gradients (Peet and Christensen 1988) than in neorefugia. Although community composition within paleorefugia should initially contain more and stronger correlations with environmental covariables than neorefugia, convergence can be expected over ecological time.

(8) The number of competitive co-equivalents held within an archipelago of neorefugia should be greater than that held within a similar set of paleorefugia. The more intense competitive sorting within and the lower levels of pre-fragmentation isolation between paleorefugia should have resulted in similar initial compositions and a strongly competitive environment. As a consequence, there should have been little opportunity for establishment of equivalents with varying fitnesses (Shmida and Ellner 1984). However, the always-isolated nature of neorefugia should allow for less complete intersite dispersal, making it easier for less fit co-equivalents to persist in the landscape.

As is true for many ecological processes that operate over large spatial and temporal extents, collection of data to test these hypotheses may be difficult, or in some cases impossible. And, even if appropriate data exist, it may be equally difficult to control for confounding factors (Brown 1995). This should not imply, however, that hypotheses regarding differential processes between paleorefugia and neorefugia are inherently unfalsifiable. By comparing current ecological patterns between sites within the same geographic region, confounding effects of the local environment, climatic history, and migration history can be at least partially controlled.

The most easily tested hypotheses are those that concern directly quantifiable variables such as current species richness, community composition, habitat size, habitat isolation, and habitat location. Consistency with Hypothesis 1 can be easily tested as it is based on a comparison of species richness to habitat area. Hypothesis 2, which is based on species richness and site-isolation data, can also be readily assessed. Hypothesis 4 can also be easily tested, as it only requires community-composition and geographic-location data. Lastly, Hypothesis 5 can be easily assessed by investigation of the dispersal strategies exhibited for paleorefuge and neorefuge species.

Hypothesis 7 can also be relatively easily tested, as it is based on analysis of how quickly and predictably composition changes over a given amount of environmental-gradient space. Testing of this question is slightly more complex, however, as the documentation of these patterns requires use of multivariate data-reduction procedures such as ordination. It is possible that use of different data-reduction techniques could produce different outcomes. Previous knowledge of which environmental variables are critical in the system may also be necessary.

Hypotheses 6 will be more difficult to test. To assess the effect of geography on species occurrence, it is first necessary to control for variation in distribution related to environmental gradients. Although in some cases it may be relatively easy to quantify this through use of parametric or nonparametric regression techniques (Austin et al. 1990), such analyses will be problematic when environmental variables demonstrate strong spatial autocorrelation or when habitats are clustered in a landscape. In such situations it is difficult to know what the null expectation will be for the effect of geography on species occurrence, independent of environmental variation. While these problems are likely tractable through use of Monte Carlo or other randomization

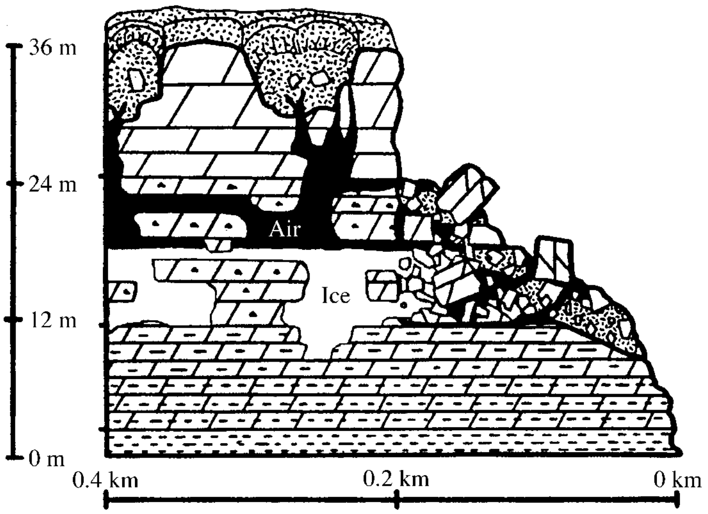

FIG. 2. Cross-section view of a Blanding Formation algific talus slope showing major geomorphological features (adapted from Frest [1991: Fig. 2]). A complete system has small sinks in the forested upland; vertical mechanical karst fissures in the Hopkington Formation; ice reservoirs in mostly horizontal mechanical karst in the thin-bedded Blanding Formation; underlying relatively impervious Tete des Mortes, Mosalem, and/or Maquoketa formations.

techniques (Hilborn and Mangel 1997), the exact form of these tests have yet to be formalized.

Hypotheses 3 and 8 will both be hard to test. Determination of absolute habitat age will be difficult, if not impossible, to measure in most cases. Even when it is possible to age habitats through ^{14}C dating of organically rich basal sediments (peatlands, for example), it would be difficult or impossible to document total species richness over this time period. Hypothesis 8 is difficult to address as it requires determination of which species represent co-competitors. It is not clear how one could adequately assess this without knowing, for a given set of species, all interactions between all potential limiting environmental variables.

Based on these factors, a priori Hypotheses 1, 2, 4, and 5 appear to be the most easily testable. To provide a preliminary assessment for these hypothesized differences, I have used a paleorefugia system (algific talus slopes; Frest 1982) and neorefugia system (fens; Nekola 1994) that co-occur in northeastern Iowa to examine four specific predictions: (1) the species–area relationship is steeper and stronger in algific slopes as compared to fens; (2) the species–isolation relationship is stronger in fens as compared to algific talus slopes; (3) distance-decay patterns are more important in fens as compared to algific talus slopes; and (4) the occurrence frequency of good and poor dispersers varies between algific talus slopes and fens.

METHODS

Study sites

Algific talus slopes.—Algific talus slopes (“algific” coined from the Greek root “algos” and translates to “cold producing”) occur within a deciduous-forest matrix on steep, usually north-facing, carbonate talus slopes where cold air flows out of ice-filled caves (Frest 1981; Fig. 2). These caves developed through ice wedging associated with periglacial activity (Hedges 1972), and have maintained a below-freezing mean annual temperature through thermal buffering provided by overlying cliff-forming carbonates and subtending talus slopes (Frest 1981, 1982). Algific talus slopes are characterized by an unique buffered microclimate where soil temperatures rarely exceed 15° C in the summer (Frest 1982). Approximately 300 algific talus slope sites have been located across a 10-county region of northeastern Iowa (USA) in exposures of Prairie-du-Chien, Galena, Blanding, or Hopkington Formation carbonates (Fig. 3; Frest 1981, 1982, 1983, 1984, 1986*a*, *b*, 1987). A limited number of sites are also known from adjacent portions of Minnesota, Wisconsin, and Illinois, USA (Frest 1991).

Algific talus slope communities range from densely forested to moderately open. Characteristic woody species include *Acer saccharum*, *A. spicatum*, *Abies balsamea*, *Betula lutea*, *B. papyrifera*, *Fraxinus americana*, *Juglans cinerea*, *Pinus strobus*, *Salix bebbiana*, *Sambucus pubens*, *Taxus canadensis*, and *Tilia americana.* The ground layer is typically dominated by a dense bryophyte cover that supports large populations of pteridophytes such as *Cystopteris fragilis*, *Gymnocarpium robertianum*, and *Equisetum scirpoides.* Woody plant cover decreases and bryophyte/pteridophyte cover increases in general with increasing intensity of cold-air seepage. Algific talus slopes harbor populations of over 60 vascular plant species that are disjunct in Iowa from wet woods and bogs in northern or western boreal forests, including *Adoxa moschatellina*, *Carex media*, *Cornus canadensis*, *Linnaea borealis*, *Mertensia paniculata*, *Poa paludigena*, *Pyrola asarifolia*, *Rhamnus alnifolia*, *Ribes hudsonianum*, *Streptopus roseus*, and *Viola renifolia* (Thorne 1964, Frest 1982). At least three near-endemic vascular plant taxa (*Aconitum noveboracense*, *Chrysosplenium iowense*, and *Sullivantia renifolia*) occur on these sites. Algific talus slopes also harbor populations of at least eight

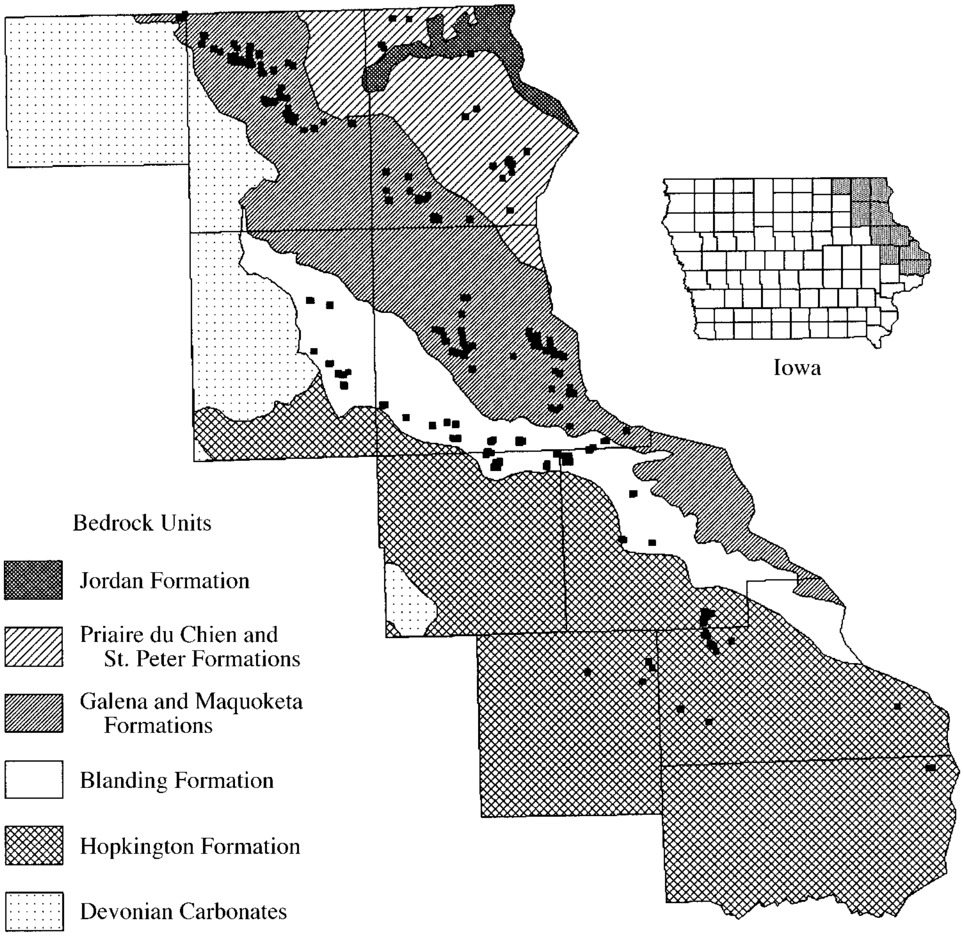

FIG. 3. Distribution of algific talus slopes and major bedrock units in northeastern Iowa, USA.

land snail taxa once thought to have become extinct at the end of the Wisconsinan (Frest 1991). Relict mites in the family Rhagidiidae have also been discovered on these sites (V. Ruzicka, *personal communication*).

These taxa were components of a full-glacial community associated with quasi-maritime climates found south of the ice margin (Frest and Dickson 1986). Populations became restricted to algific talus slopes when this climatic regime disappeared following the retreat of glacial ice from the continental interior (Frest 1981). Due to the microclimatic buffering provided by cold-air seepage, which mimics the full-glacial regional climate, populations were able to persist on algific talus slopes through the Hypsithermal to the cooler and wetter conditions of modern times. Algific talus slopes thus represent paleorefugia whose biota predates the surrounding deciduous forest matrix.

Fens.—In northeastern Iowa, fens occur within a tallgrass-prairie matrix at sites of local groundwater discharge from pre-Illinoian tills, bedrock, aeolian sands, fluvial sands, or oxbow-meander cutoffs (Nekola 1994, Fig. 4). Sites typically occur as hillside terraces, or more rarely as flat expanses in low swales or mounds. The constant issue of groundwater at fen sites creates a buffered habitat somewhat similar to algific talus slopes, with soil temperatures being cooler in the summer, warmer in the winter, and with more constant soil moisture than is otherwise found within the surrounding landscape. Fens are scattered across a 30-county region where at least 2333 sites occurred as recently as 50 yr ago and where 160 sites remain extant (Fig. 5). The bulk of presettlement and extant fens are found on the Iowan Erosional Surface, which was formed during the Wisconsinan through intense periglacial erosion that removed older tills, created a stepped landscape surface, and prevented the accumulation of deep loess deposits (Hallberg et al. 1978, Prior 1991). Similar fen habitats are known from northwestern Iowa (Anderson 1943), Illinois (Moran 1981), Minnesota (Coffin and Pfannmuller 1988), South Dakota (Ode 1985), and Wisconsin (Curtis 1959).

In northeastern Iowa, fen habitats are dominated by a dense sedge turf, which includes *Carex buxbaumii*, *C. interior*, *C. lanuginosa*, *C. lasiocarpa*, *C. prairea*, *C. stricta*, *C. suberecta*, and *C. tetanica*. In discharge zones *Scirpus validus*, *Typha angustifolia*, and *T. la-*

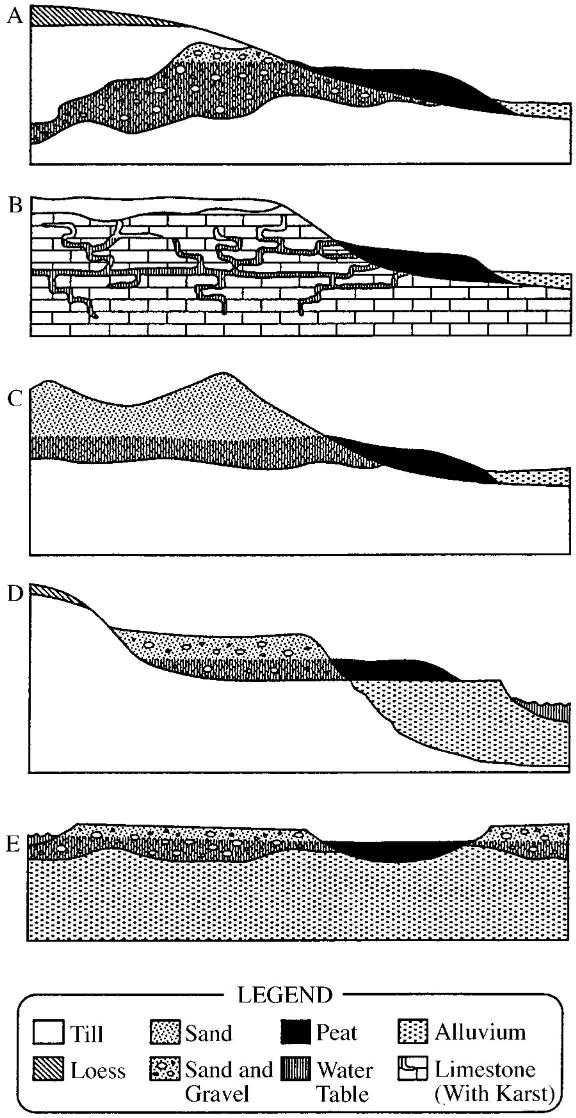

FIG. 4. Cross section of the five geologic features that give rise to fen formation in northeastern Iowa: (A) pre-Illinoian till sites, with groundwater seepage emanating from sand and gravel lenses interbedded between till units; (B) bedrock sites, with groundwater seepage emanating from fractured carbonate, sandstone, or shale units; (C) aeolian sand dune sites, with groundwater seepage emanating from the contact between sand and an impervious till or paleosol; (D) fluvial sand sites, with groundwater seepage emanating from the base of fluvial or outwash terraces; and (E) oxbow sites, which form through hydric succession of cutoff oxbow meanders.

tifolia are often dominant. Scattered clumps of low shrubs are also frequent, and include *Cornus stolonifera, Salix bebbiana, S. discolor, S. petiolaris,* and *S. rigida.* In areas of highest soil saturation, vascular-plant growth often becomes stunted and sparse, with bryophytes becoming dominant. Approximately 50% of the vascular-plant species of these sites are regionally rare (Nekola 1994). Over 80 of these species are disjunct from open peatlands in boreal or northeastern North American, including *Aster junciformis, Betula pumila, Carex sterilis, Epilobium strictum, Eriophorum angustifolium, Galium labradoricum, Gentiana procera, Lobelia kalmii, Menyanthes trifoliata, Mimulus glabratus* var. *fremontii, Parnassia glauca, Rhynchospora capillacea, Salix candida, S. pedicellaris, Solidago uliginosa, Triglochin maritimum,* and *T. palustris.* Northeastern Iowa fens also harbor populations of 19 rare Iowa butterfly and skipper species (Nekola 1994), and seven rare Iowa land snail species (Frest 1990).

^{14}C dates of basal peat layers indicate that northeastern Iowa fens initiated peat development following the end of Hypsithermal warming, less than 6000 yr ago (Thompson 1992). Although a few sites possess basal peat dates extending to 10 000 yr ago (Thompson and Bettis 1994), the presence of oxidized layers within these beds (Hall 1971, Van Zant and Hallberg 1976) indicate that deposition was not continuous, and that during the Hypsithermal even these sites dried out. Thus, although fens may have occurred at modern locations in the late-glacial landscape, the geological record indicates that they did not maintain environmental buffering during the Hypsithermal. Because of this, isolated populations of boreal taxa occurring within these sites cannot represent late Pleistocene or early Holocene relicts, but are instead relatively recent immigrants. In northeastern Iowa, therefore, fens represent neorefugia that are younger than their surrounding tallgrass-prairie matrix.

Data sets

Species richness.—The ecological distance between fen and algific talus slope habitats and the surrounding matrix habitats is not so great as to preclude occurrence of matrix taxa. Such species can colonize sites via short-range dispersal or mass effect (Shmida and Ellner 1984), independent of the colonization history of a given site. As such, inclusion of these ubiquitous or waif species could seriously swamp any potential ecological differences caused by differential colonization histories. By limiting analysis to only those species restricted to fens or algific talus slopes, this source of noise can be filtered out. For this reason, observations of species composition and richness for fen and algific talus slope sites was limited to the universe of vascular-plant taxa restricted (>80% of known northeastern Iowa occurrences) to either of these habitats. In total, 80 restricted vascular-plant species were identified from fens and 51 from algific slopes, based on occurrence records reported in Frest (1982), Howe et al. (1984), and Nekola (1990, 1994), as well as field data collected during this study. The presence or absence of each of these taxa was subsequently noted for all 160 extant northeastern Iowa fens and all 76 extant algific talus slopes in the Blanding Formation outcrop region.

Habitat size.—Sizes of fen sites were estimated through digitization of soil pedons (named variously

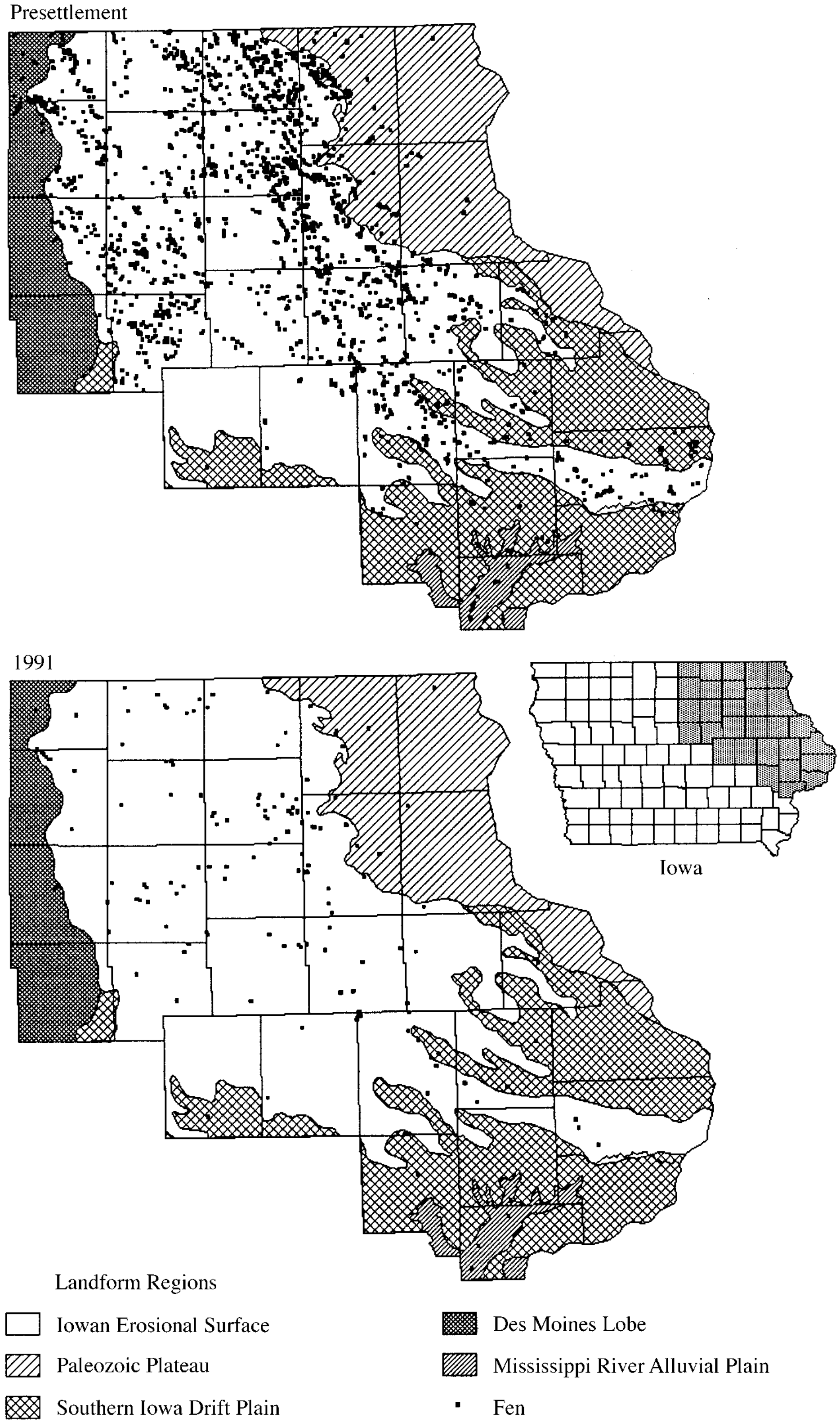

FIG. 5. Presettlement and 1991 distribution of northeastern Iowa fens within major landform boundaries, based on Prior (1991).

as Palms Muck, Houghton Muck, Muck, or Peat soils) associated with fen communities on USDA Soil Conservation Service soil maps. Sizes of algific talus slope sites were determined through digitization of site boundaries recorded from field observations on 7.5-minute U.S. Geological Survey topographic maps.

Isolation.—To quantify the isolation of sites, a weighted summation was calculated for the distance between each site and all others, assuming that the influence of surrounding sites exponentially decreases as intersite distance increases:

$$I = \sum_{i=1}^{n} e^{-cd}$$

where I = isolation index, n = number of other sites in a landscape, d = distance between the reference site and site i, and c = a constant modifying the rate of exponential decay

The smaller the value of this index for a site, the less it is expected to interact with surrounding sites. This index differs from a summed addition of site distances as it down-weights the importance of distant areas to the isolation of a given site. Justification of this form of weighting is based upon theoretical (Okubo and Levin 1989) and quantitative (Preston 1962, Nekola and White, *in press*) studies that have shown that dispersal ability and community similarity tend to exhibit an exponential decay with increasing intersample distance.

No a priori rules exist to suggest the appropriate value of c, the constant that modifies the level of down-weighting of distant sites. To allow a robust test of the effect of isolation on species richness, isolation-index scores were calculated over five different values of c (1.0, 0.5, 0.25, 0.1, and 0.05), corresponding to five different neighborhood radii (roughly equivalent to 3, 6, 12, 30, and 60 km) that demarcate those sites that most strongly contribute to isolation values. Sites that fall outside these neighborhoods contribute very little to the overall isolation-index values for a given location.

Statistical analysis

Prediction 1: The species–area relationship will be steeper and stronger in algific slopes as compared to fens.—The slope of the vascular plant species–area relationship was estimated by multiple least-squares linear regression after both the species-richness and habitat-area values had been log transformed. A double log transform was used as these residuals were more homoscedastic than those generated from untransformed richness vs. log-transformed area. To allow inclusion of sites with zero species, a one was added to the species richness of each site prior to log transformation. Tests for differences between the slopes and intercepts of the two species–area relationships were obtained by analysis of a binary variable representing habitat type that was added into the model following methods outlined in Kleinbaum et al. (1988). The form of this regression model was

$$\begin{aligned} &\ln(\text{species richness} + 1) \\ &\quad = \beta_0 + \beta_1(\ln(\text{habitat size})) + \beta_2(\text{habitat type}) \\ &\qquad + \beta_3(\text{habitat type} \times \ln(\text{habitat size})) + \varepsilon \qquad (1) \end{aligned}$$

where β_0 = intercept for algific slopes, β_1 = slope for algific slopes, β_2 = difference in intercept between algific slopes and fens, and β_3 = difference in slope between algific slopes and fens.

As fens can be significantly larger than algific talus slopes, comparison of species–area slopes and intercepts calculated from the entire data set may lead to inaccurate conclusions (Conner and McCoy 1979). To compensate, the regression analysis was repeated using only those sites falling within the habitat-size overlap between algific talus slopes and fens.

The relative strength of the species–area relationship was determined through comparison of the correlation coefficients generated through separate regressions of log-transformed richness vs. log-transformed area for each habitat. The significance of observed differences between these r values was quantified using the correlation-coefficient homogeneity test (Sokal and Rohlf 1981).

Prediction 2: Species–isolation relationships will be stronger in fens as compared to algific talus slopes.—The significance and amount of extra variance in vascular-plant species richness explained by site isolation was estimated by separately adding each of the five isolation-index values into the previously defined species–area model. The form of this regression model, for each of the isolation-index values, was

$$\begin{aligned} \ln(\text{species richness} + 1) &= \beta_0 + \beta_1(\ln(\text{habitat size})) \\ &\quad + \beta_2(\text{isolation index}) + \varepsilon \qquad (2) \end{aligned}$$

where β_0 = intercept, β_1 = slope of habitat-size relationship, and β_2 = slope of isolation relationship. The amount of additional variance each of the isolation-index values explained was determined through subtraction of r^2 values generated from these models from the r^2 values observed from the species-richness vs. habitat-size regression.

Prediction 3: Distance-decay patterns will be more pronounced in fens as compared to algific talus slopes.—Distance-decay rates in the restricted vascular-plant floras were estimated in both habitats using the procedures outlined in Nekola and White (*in press*). These analyses were conducted at five different sample grain sizes: single sites, plus grid cells of 10, 20, 40, and 80 km on a side laid over the study region. However, 80 × 80 km grid cells were not analyzed for algific talus slopes because of their more limited extent. The flora of a given cell was determined by summing together the floras of all sites whose centroids fell within the boundaries of that cell. The centroid location of each cell was set as the average location of all sites

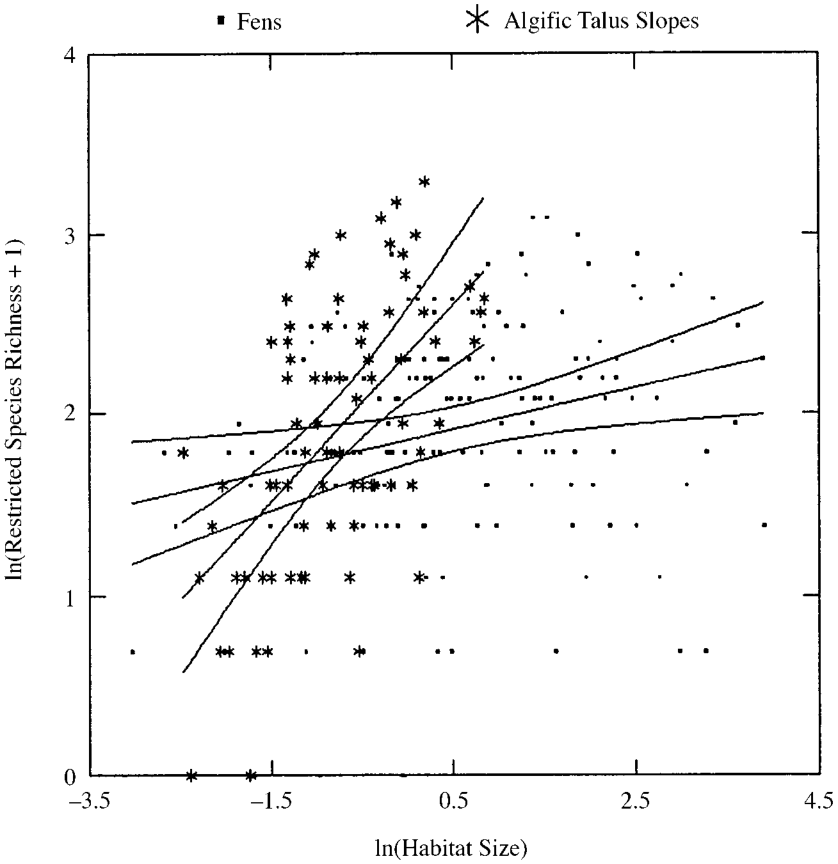

FIG. 6. Species–area curves (Eq. 1). Log-transformed restricted-species richness as a function of log-transformed habitat size for northeastern Iowa algific talus slope and fen habitats. Each group of three curves shows the position of best-fit regression line and 95% confidence interval around the mean of each.

found within that quadrat. Floristic similarity between samples was calculated using Jaccard's index, and distance was calculated as the aerial separation between cell centroids. The amount of variance in similarity explained by distance was estimated through a linear regression of natural-log-transformed similarity vs. untransformed distance (Nekola and White, *in press*). The significance of the similarity–distance relationship was estimated by Mantel matrix randomization tests (RT software package, Manley 1992). All Mantel *P* values were generated using 10 000 replications, as suggested by Jackson and Somer (1989) for biological-data sets.

Prediction 4: The proportional frequency of species with good or poor dispersal abilities will vary between the algific talus slope and fen flora.—Each restricted vascular-plant species found in either of the two habitat types was assigned to one of four dispersal classes expected to differ in their dispersal abilities: (1) macroscopic (>0.1 mm), non-plumose seeds in dry fruits or capsules; (2) fleshy berries, fruits, or nuts; (3) microscopic (<0.01 mm) seeds or spores; and (4) plumose seeds. The frequency of these four categories in the flora of each habitat was determined, and differences tested using the Pearson chi-square statistic.

RESULTS

Prediction 1: The species–area relationship will be steeper and stronger in algific slopes as compared to fens

Both habitats demonstrate a significant positive relationship between species richness and habitat size (Fig. 6, Table 1), with both slope and intercept for algific talus slopes being significantly ($P < 0.0005$) larger than those reported for fens. When this analysis was repeated for only those sites within the range of habitat-size overlap, the slope and intercept were again found to be significantly larger in algific slopes ($P < 0.017$ and $P < 0.0005$, respectively). In both analyses, small algific talus slopes had fewer vascular-plant species than fens of identical size, whereas large algific talus slopes had greater richness than fens of identical size.

The amount of variance explained in these regressions also differed greatly (Table 2). Log-transformed habitat size accounted for 32.6% of observed variance in algific talus slope species richness but accounted for only 6.3% of the variance in fen species richness. This

TABLE 1. Results of multiple-regression analysis of the effect of habitat area and habitat type on restricted vascular-plant species richness in northeastern Iowa fen and algific talus slope habitats (see Eq. 1). Restricted species are those present only in fens or algific talus slopes.

Habitat	N	Value	1 SE	t	P
Algific talus slope sites	76				
Intercept, β_0		2.335	0.102	22.881	<0.0005
Slope, β_1		0.542	0.090	6.003	<0.0005
Difference between algific slopes and fen sites	160				
Intercept difference, β_2		−0.476	0.115	−4.139	<0.0005
Slope difference, β_3		−0.428	0.097	−4.421	<0.0005

Notes: N = no. of observations. There were 160 extant fens and 76 extant algific talus slopes in the Blanding Formation outcrop region.

difference was found to be highly significant ($P = 0.006$).

Prediction 2: Species–isolation relationships will be stronger in fens as compared to algific talus slopes

Isolation was found to be a significant additional predictor of vascular-plant species richness in fens for each of the calculated isolation-index values (P ranging from 0.003–0.027; Table 3). The amount of additional variance explained by isolation in fen habitats varied between 0.026 and 0.053, or between 46% and 84% of the variance explained by log-transformed habitat area. However, for algific talus slopes, isolation was never a significant additional predictor of species richness at any of the isolation-index scores (P ranging between 0.150 and 0.802).

Prediction 3: Distance–decay patterns will be more pronounced in fens as compared to algific talus slopes

In fens, significant ($P = 0.0001$) distance–decay relationships were observed between the restricted species floras at all grain sizes (Table 4). At the largest grain (80 × 80 km regions), this relationship explained over one third of the variance in regional restricted vascular-plant species composition (Table 5). At smaller grains, distance accounted for <5% of observed variance in floristic similarity. In algific slopes, only the distance–decay relationship at the 20 × 20 km sample grain size was found to be significant at the 0.05 level. At this scale, 23% of the observed variance in vascular-plant assemblage similarity was accounted for by intersample distance.

TABLE 2. Significance and r^2 for the restricted vascular-plant species richness vs. habitat-area relationship in northeastern Iowa fen and algific talus slope habitats.

Habitat	No. of observations	P	r^2
Fens	160	0.001	0.063
Algific talus slopes	76	0.000	0.326

Note: Significance of the correlation-coefficient homogeneity test: $P = 0.006$.

Prediction 4: The proportional frequency of species with good or poor dispersal abilities will vary between the algific talus slope and fen flora

The frequencies of dispersal classes differed significantly ($P < 0.0005$) between the two habitats (Table 6). Species with berries, fleshy fruits, or nuts were ~15 times more frequent in algific slopes than fens, whereas species with plumose seeds were ~7 times more frequent in fens than algific slopes.

DISCUSSION

Distinguishing among alternative explanations

In each case the results obtained agree with the a priori hypotheses, which predicted differences between the ecological patterns of paleorefugia and neorefugia and suggest that extinction and immigration have played differing roles in algific talus slope and fen communities (Table 7). However, it is impossible to control for all confounding factors in a natural experiment such as this. By explicitly stating what some of these factors may be, the preliminary nature of these investigations, and potential avenues for future research, may be made more clear.

Two potential confounders stem from the different source pools for the flora of these two habitats, and from the different landscape dynamics of the primary disturbances that effect them. Although the flora of each habitat is a subset of the boreal wetland flora, the species of algific slopes have greater affinity with conifer swamps while the species of fens have greater

TABLE 3. Summary statistics for restricted vascular-plant species richness vs. area and isolation in northeastern Iowa fen and algific talus slope habitats.

Exponential decay coefficient	Algific talus slopes		Fens	
	P	Additional r^2	P	Additional r^2
$c = 1.0$	0.150	0.019	0.027	0.029
$c = 0.5$	0.266	0.012	0.008	0.041
$c = 0.25$	0.497	0.005	0.003	0.053
$c = 0.1$	0.802	0.001	0.003	0.050
$c = 0.05$	0.778	0.001	0.008	0.041

TABLE 4. *P* values for the distance–decay relationships of the restricted vascular-plant floras of northeastern Iowa fen and algific talus slope habitats at differing grain sizes.

Habitat	Grain size (km)				Individual sites
	80	40	20	10	
Fen	0.0002	0.0001	0.0001	0.0001	0.0001
Algific slope	···	0.6245	0.0213	0.2832	0.2339

Note: *P* values were calculated using Mantel tests on distance and similarity matrices for comparisons between each region or site.

TABLE 5. The r^2 values for the distance–decay relationships of the restricted vascular-plant floras of northeastern Iowa fen and algific talus slope habitats at differing grain sizes.

Habitat	Grain size (km)				Individual sites
	80	40	20	10	
Fen	0.335	0.014	0.044	0.034	0.027
Algific slope	···	0.082	0.226	0.005	0.001

Note: The r^2 values were calculated using linear regression on log-transformed data.

similarity with open peatlands (e.g., Curtis 1959). Differences in the composition, coexistence patterns, and dispersal strategies of species in these pools could have contributed to, or created, observed differences. Additionally, algific slopes are occasionally impacted by small-scale talus dislodgement from game trails or individual tree-falls, whereas fens are more often affected by larger-scale events such as fires and regional droughts. Consequently, algific slopes seem more likely than fens to be in a state of successional quasi-equilibrium (Shugart 1984, Turner et al. 1994). This difference could potentially account for the stronger species–area relationship in algific slopes, or for the predominance of vagile species in fens.

Additional research will be necessary to tease apart the effects of these and other factors from effects of colonization history. For example, it would be instructive to extend these analyses of algific slope and fen vascular-plant floras to additional taxonomic groups found on the same sites that possess varying dispersal abilities, such as bryophytes, birds, lepidoptera, or terrestrial gastropods. Such analyses would help document whether the patterns observed for vascular plants in this investigation are general in nature, and whether species groups with different dispersal abilities will respond to identical levels of geographic isolation and patterns of habitat creation in the same way. It is possible that poorly dispersing taxa (snails, for example) may be more influenced by extinction and that more-vagile species (lepidoptera, for example) may be more influenced by immigration processes on the same sites.

Important additional insights may also be garnered if paleorefugia and neorefugia are studied over a more diverse set of environmental situations and landscapes. For instance, comparing identical habitats that have formed at different times in different landscapes (creating a neorefugia in one and a paleorefugia in the other) may be a good way to control for the confounding effects of species source pools or disturbance dynamics. It may also be interesting to study the contrast between these refugia types across a series of landscapes in which sites vary from highly to less isolated. Neorefugia and paleorefugia of very ancient origin may also demonstrate different biogeographic patterns. For instance, some ancient oceanic islands represent neorefugia (like the Hawaiian archipelago, which formed through volcanic eruptions) whereas others represent paleorefugia (like New Zealand and New Caledonia, which were created through fragmentation of continental land masses). As time has been sufficient for speciation to occur, a strong species–area relationship should develop for both. However, the fact that dispersal was originally more important for ancient oceanic neorefugia should allow for stronger species–isolation relationships, and different dispersal-strategy frequencies in their contemporaneous biota as compared to ancient oceanic paleorefugia. Hypotheses regarding paleorefugia and neorefugia are also amenable to some forms of manipulative experimentation for those processes that operate over limited spatial and temporal extents, or to computer simulations for larger-scale patterns. The future research priorities regarding paleorefugia and neorefugia should include more taxa, more habitats, more landscapes, and more times of origin. Through such additional work a clearer understanding of the role of colonization history on contemporaneous ecological pattern can be achieved.

Implications for ecology, biogeography, and conservation

The central question of this paper is whether the historical contingency of habitat formation can have a long-lasting impact on community patterns and processes. The answer to this question has important implications for ecological debates surrounding equilibrium vs. non-equilibrium dynamics, vicariance vs. long-range dispersal, and the delineation of optimum reserve designs for maintenance of biological diversity.

TABLE 6. Frequency of four dispersal classes among restricted vascular-plant species in northeastern Iowa fen and algific slopes. The numbers in parentheses represent the percentage of the total number of species recorded in each habitat contained in each dispersal class.

Habitat	Dispersal class†			
	1	2	3	4
Fen	42 (52.5%)	1 (1.2%)	17 (21.3%)	20 (25.0%)
Algific slope	26 (51.0%)	10 (19.6%)	13 (25.4%)	2 (3.9%)

Note: Chi-square statistic for differences in frequencies for all dispersal classes = 20.998; $P < 0.0005$.

† Dispersal classes: 1 = macroscopic, non-plumose seeds in dry capules; 2 = berry/fleshy fruits; 3 = spore or microscopic seeds; and 4 = plumose seeds.

TABLE 7. Summary outcomes of analysis: observed and predicted differences between algific talus slopes (paleorefugia) and fens (neorefugia) in northeastern Iowa.

Factor	Response		Result†
	Neorefugia	Paleorefugia	
Relative steepness and strength of species–area relationship	Less	Greater	Y
Strength of species–isolation relationship	High	Low	Y
Change in richness over time	Increasing	Decreasing	⋯
Strength of distance-decay relations	High	Low	Y
Dispersal ability of species in habitat	Good	Poor	Y
Relative importance of geography in predicting species occurrence	Strong	Weak	⋯
Strength of community–environment correlation	Weak	Strong	⋯
Relative number of co-competitors in landscape	More	Less	⋯

† Y, relationship found statistically significant and in agreement with a priori predictions; ⋯, not addressed in this analysis.

Equilibrium vs. non-equilibrium dynamics.—Although much classical ecological theory (e.g., MacArthur and Wilson 1967, MacArthur 1972, Tilman 1988) assumes existence of equilibrium conditions, the data presented above suggest that differences in colonization history may still imprint biotas 5000–10 000 yr following habitat development. If ‘‘transient dynamics’’ continue to exist after such time periods, equilibrium conditions cannot be assumed to dominate biogeographic pattern. These results support paleoecological work (Davis 1984) that suggests that disequilibrium between climate and species range may persist over relatively long temporal extents.

Vicariance vs. long-distance dispersal.—The relative importance of vicariance vs. long-distance dispersal in the development of biogeographic pattern has been debated since the times of Wallace, Schimper, Engler, and Hooker (Cain 1944). Many ecologists view dispersal as so efficient that no barriers to movement exist for any species within continental areas, making biogeographic pattern simply the result of physiological limitations and competitive interactions (e.g., Krebs 1985). Saur (1988) has summarized this belief as Beijerinck’s Law: everything is everywhere but the environment selects. However, some cladistic biogeographers have stated that dispersal either does not occur between isolated habitats, or is so unpredictable that it cannot be studied. For these researchers, only the process of vicariance can parsimoniously explain disjunct distributions (e.g., Humphries and Parenti 1986, Brudin 1988).

Analysis of paleorefugia and neorefugia suggest that such absolute positions may be fundamentally flawed as both vicariance and dispersal can operate contemporaneously in the same landscape. Instead of asking which of these processes is responsible for observed biogeographic patterns, it seems more productive to determine how much each has contributed to that pattern. If additional research confirms generality to the patterns attributed above, it may be possible to use similar analyses in additional landscapes to document the occurrence of neorefugia and paleorefugia, and thus the frequency of vicariance and long-distance dispersal.

Conservation of biological diversity.—These preliminary analyses suggest that algific talus slopes are floristically more self-contained than fens, with immigration playing a relatively minor role in the determination of species occurrence. Protection of the vascular flora of these habitats should thus center on those sites that harbor maximum diversity and the internal site dynamics that are responsible for that diversity.

However, these preliminary analyses also suggest that fens are not as self-contained, with immigration from surrounding sites strongly influencing vascular-plant composition. Diversity in these communities varies conversely with isolation, and community composition is strongly influenced by the proximity of source areas. To ensure adequate protection of the processes that gave rise to site diversity in such systems, reserves may have to be chosen to protect not only internal site dynamics, but also the immigration potential between sites. This will be possible only if many sites are protected across the landscape, including those that may not currently support diverse floras. Consequently, neorefugia reserve design may require an integrated, regional strategy.

Unfortunately, the reality of fen destruction in Iowa may make such goals unrealistic. Since European settlement, 93% of northeastern Iowa fens have been destroyed (Nekola 1994; Fig. 5). Even if all remaining sites could be saved, immigration rates cannot be maintained at presettlement levels. The ultimate effect of this will be severely lowered species-immigration rates compared to presettlement times, and low probabilities that species will be able to reestablish themselves following local extinction. If extinction rates are high, strategies to guard fen biodiversity may require not only protection of all remaining sites, but also the physical transport of propagules between sites to reestablish presettlement immigration levels. If this approach is eventually deemed necessary, it would require creation of stochastic immigration models to guide land managers in their attempts to simulate ‘natural’ immigration between sites.

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Literature Cited

Anderson, W. A. 1943. A fen in northwestern Iowa. American Midland Naturalist **29**:787–791.

Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. Ecological Monographs **60**:161–177.

Bennett, D. G., and O. Gade. 1979. Geographic perspectives in migration research. Department of Geography Studies in Geography, Number 12. University of North Carolina, Chapel Hill, North Carolina, USA.

Bierrgaard, R. O., Jr., T. E. Lovejoy, V. Kapos, A. Augusto dos Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments. BioScience **42**: 859–866.

Brown, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. American Naturalist **105**: 476–478.

———. 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology **58**:445–449.

Brudin, L. Z. 1988. Phylogenetic biogeography. Pages 343–370 *in* A. A. Meyers and P. S. Giller, editors. Analytical biogeography. Chapman & Hall, New York, New York, USA.

Burrough, P. A. 1986. Principles of geographical information systems for land resources assessment. Oxford University Press, New York, New York, USA.

Bush, M. B., and R. J. Whittaker. 1993. Non-equilibrium in island theory of Krakatau. Journal of Biogeography **20**: 453–457.

Cain, S. A. 1944. Foundations of plant geography. Harper & Row, New York, New York, USA.

Carlquist, S. 1974. Island biology. Columbia University Press, New York, New York, USA.

Coffin, B., and L. Pfannmuller. 1988. Minnesota's endangered flora and fauna. University of Minnesota Press, Minneapolis, Minnesota, USA.

Conner, E., and E. D. McCoy. 1979. The statistics and biology of the species–area relationship. American Naturalist **113**:791–833.

Cox, G. W., and R. E. Ricklefs. 1977. Species diversity, ecological release, and community structuring in Caribbean land bird faunas. Oikos **29**:60–66.

Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, USA.

Davis, M. B. 1984. Quaternary history and the stability of forest communities. Pages 132–151 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession. Springer-Verlag, New York, New York, USA.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science **179**:759–769.

———. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. Biological Conservation **7**:129–146.

Fernald, M. L. 1925. Persistence of plants in unglaciated North America. Memoirs of the American Academy of Arts and Sciences **15**:241–342.

Fotherinham, A. S. 1981. Spatial structure and distance-decay parameters. Annals of the Association of American Geographers **71**:425–436.

Frest, T. J. 1981. Final report, project SE-1-2 (Iowa Pleistocene Snail). Iowa Conservation Commission, Des Moines, Iowa, USA.

———. 1982. Final report, project SE-1-4 (Iowa Pleistocene Snail). Iowa Conservation Commission, Des Moines, Iowa, USA.

———. 1983. Final report (contract number 30181-1259) northern Driftless Area survey. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA.

———. 1984. Final report, project SE-1-6 (Iowa Pleistocene Snail). Iowa Conservation Commission, Des Moines, Iowa, USA.

———. 1986*a*. Final report, project SE-1-6 number 2 (Iowa Pleistocene Snail). Iowa Department of Natural Resources, Des Moines, Iowa, USA.

———. 1986*b*. Final report, project SE-1-7 (Iowa Pleistocene Snail). Iowa Department of Natural Resources, Des Moines, Iowa, USA.

———. 1987. Final report, project SE-1-8 (Iowa Pleistocene Snail). Iowa Department of Natural Resources, Des Moines, Iowa, USA.

———. 1990. Final report (contract number 65-2454). Field survey of Iowa spring fens. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

———. 1991. Summary status reports on eight species of candidate land snails from the Driftless Area (Paleozoic Plateau), Upper Midwest. Final report (contract number 301-01366). U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA.

Frest, T. J., and J. R. Dickson. 1986. Land snails (Pleistocene-recent) of the Loess Hills: a preliminary survey. Proceedings of the Iowa Academy of Science **93**:139–157.

Hall, S. A. 1971. Paleoecological interpretation of bison, mollusks, and pollen from the Hughes peat bed, Linn County, Iowa. Thesis. University of Iowa, Iowa City, Iowa, USA.

Hallberg, G. R., T. E. Fenton, G. A. Miller, and A. J. Lutenegger. 1978. The Iowan Erosion Surface: an old story, an important lesson, and some new wrinkles. Pages 2.1 to 2.94 *in* R. Anderson, editor. Geology of East-central Iowa, 42nd annual tri-state geological field conference. Iowa Geological Survey, Iowa City, Iowa, USA.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.

Hedges, J. 1972. Expanded joints and other periglacial phenomena along the Niagara Escarpment. Biuletyn Peryglacjalny **21**:87–126.

Hilborn, R., and M. Mangel. 1997. The ecological detective. Princeton Monographs in Population Biology number 28. Princeton University Press, Princeton, New Jersey, USA.

Howe, R. W., M. J. Huston, W. P. Pusateri, R. H. Laushman, and W. E. Schennum. 1984. An inventory of significant natural areas in Iowa. Iowa Conservation Commission, Des Moines, Iowa, USA.

Humphries, C. J., and L. R. Parenti. 1986. Cladistic biogeography. Clarendon Press, Oxford, UK.

Jackson D. A., and K. M. Somer. 1989. Are probability estimates from the permutation model of Mantel's test stable? Canadian Journal of Zoology **67**:766–769.

Kleinbaum, D. G., L. L. Kupper, and K. E. Muller. 1988. Applied regression analysis and other multivariate methods. PWS-Kent Publishing, Boston, Massachusetts, USA.

Krebs, C. J. 1985. Ecology. Harper & Row, New York, New York, USA.

Krukeberg, A. R., and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. Annual Review of Ecology and Systematics **16**:447–479.

Manley, B. F. J. 1992. RT—a program for randomization testing. Version 1.02. The Centre for Applications of Statistics and Mathematics, University of Otago, Dunedin, New Zealand.

MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York, New York, USA.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

McDonald, K. A., and J. H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology **6**:409–415.

Moran, R. C. 1981. Prairie fens in northeastern Illinois: floristic composition and disturbance. Pages 164–168 *in* R. Stuckey and K. J. Reece, editors. Proceedings of the sixth North American Prairie Conference. The Ohio State University, Columbus, Ohio, USA.

Nekola, J. C. 1990. Rare Iowa plant notes from the R. V. Drexler Herbarium. Proceedings of the Iowa Academy of Science **97**:55–73.

———. 1994. The environment and flora of northeastern Iowa fen communities. Rhodora **96**:121–169.

Nekola, J. C., and P. S. White. *In press.*The distance decay of similarity in ecology and evolution. Journal of Biogeography.

Ode, D. J. 1985. Rediscovered plants of fen habitats of South Dakota. Proceedings of the South Dakota Academy of Science **64**:217.

Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecology **70**:329–338.

Peet, R. K., and N. L. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina Piedmont. Pages 233–245 *in* H. J. During, M. J. A. Werger, and J. H. Willems, editors. Diversity and pattern in plant communities. SPB Academic Publishing, The Hague, The Netherlands.

Pielou, E. C. 1979. Biogeography. John Wiley & Sons, New York, New York, USA.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: part II. Ecology **43**:410–432.

Prior, J. C. 1991. Landforms of Iowa. University of Iowa Press, Iowa City, Iowa, USA.

Roughgarden, J., S. D. Gaines, and S. W. Pacala. 1987. Supply-side ecology: the role of physical transport processes. Symposium of the British Ecological Society **27**:491–518.

Saur, J. D. 1988. Plant migration. University of California Press, Berkeley, California, USA.

Shmida, A., and S. Ellner. 1984. Coexistence of plant species with similar niches. Vegetatio **58**:29–55.

Shugart, H. 1984. A theory of forest dynamics. Springer-Verlag, New York, New York, USA.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: a model for insular conservation. Ecology **50**:296–314.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco, California, USA.

Stebbins, G. L., and J. Major. 1965. Endemism and speciation in the California flora. Ecological Monographs **35**:1–35.

Thompson, C. A., and E. A. Bettis III. 1994. Age and development of Iowa fens. Proceedings of the Iowa Academy of Science **101**:73–77.

Thorne, R. F. 1964. Relict nature of the flora of White Pine Hollow Forest Reserve, Dubuque County, Iowa. State University of Iowa Studies in Natural History **20**:1–33.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

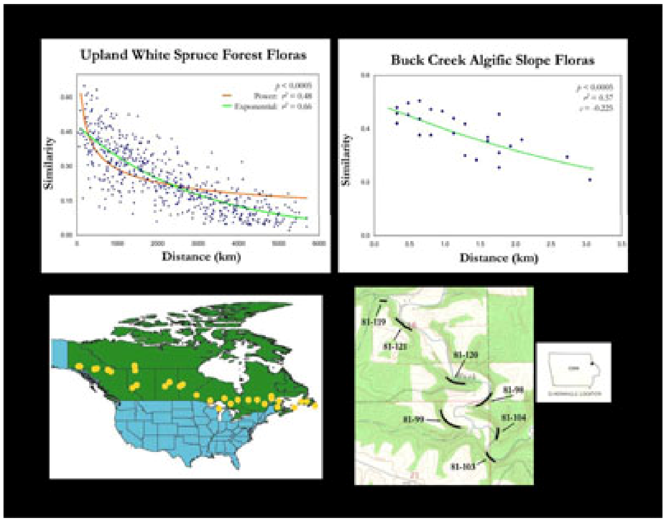
Tobler, W. R. 1970. A computer movie simulating urban growth in the Detroit region. Economic Geography **46**:234–240.

Turner, M. G., W. H. Romme, and R. H. Gardner. 1994. Landscape disturbance models and the long-term dynamics of natural areas. Natural Areas Journal **14**:3–11.

Van Zant, K. L., and G. R. Hallberg. 1976. A late-glacial pollen sequence from northeastern Iowa: Sumner Bog revisited. Iowa Geological Survey Technical Informational Bulletin Series number **3**.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence. Trends in Ecology & Evolution **12**:266–269.

Section IV: Biogeography and Macroecology



The ecological processes that most influence global biodiversity operate at spatial and temporal scales too large for typical manipulative experiments. To understand the impact of such drivers requires observational studies based on multiple sites that encompass large extents and/or represent natural experiments. Identification of general mechanism in biogeography and macroecology requires that pattern and process be investigated over a wide range of organisms representing many different body plans, trophic states, dispersal strategies and reproductive modes. In spite of this, the great majority of work is limited to vertebrates, vascular plants, and a few anthropods (e.g. lepidoptera). Land snails serve as an important potential alternative group because of their very poor active but often excellent passive dispersal abilities and hermaphroditism with common instances of unipartental reproduction. As a result, this group displays a number of unique patterns. Companion articles published in 2014 document that continental (as well as most regional) faunas display strongly bimodal body-size distributions, as opposed to the typical right-skewed pattern. Additionally, they display strong scale-dependence, with site faunas tending to be dominated by small (<5.7 mm^3) species while regional/continental faunas are characterized by large (>90.5 mm^3) taxa. This pattern is more pronounced at lower latitudes and appears driven by a strong inverse correlation between dispersal ability and body size, with small species tending to have much larger ranges and lower levels of allopatric replacement across a given geographic gradient Prior work has also shown that land snail communities demonstrate high levels of microsympatry with up to 25% of a regional fauna co-existing within 0.04 m^2 areas.

My best known contribution in this field is my 1999 paper with Peter White which popularized Distance Decay analyses to the field of Ecology. This work is now considered by many to be a classic in the field with this pattern being one of the major statistics used to test Macroecological hypotheses. I am also interested in documenting the nature and causes of spatial heterogeneity in occurrence patterns, the spread of organisms across landscapes, and continental gradients of body size variation within and between communities. And as intimated in Section III, I am using macroecological pattern to inform about macroevolutionary process in Holarctic land snails.

Representative Publications
[number of citations as of October 27, 2017]

1. Edited Volumes

Cameron, R.A.D., **J.C. Nekola**, B.M. Pokryszko & F.E. Wells. 2005. Pattern and process in land mollusc diversity. *Records of the Western Australian Museum*, Supplement #68.

2. Peer-reviewed Articles

Nekola, J.C. 2014. North American terrestrial gastropods through either end of a spyglass. *Journal of Molluscan Studies*. 80:238-248. **[7]**

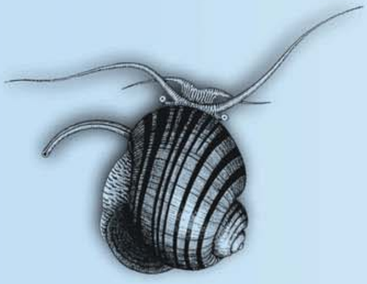
Nekola, J.C. 2013. Biodiversity refuges. pp. 141-148 *in:* MacLeod, N., D.J. Archibald & P. Levin (eds), *Grzimek's Animal Life Encyclopedia: Extinction*. Gale Publishing, Farmington Hills, Michigan. **[6]**

Nekola, J.C., G.M. Barker, R.A.D. Cameron & B.M. Pokryszko. 2013. Latitudinal variation of body size in land snail populations and communities. pp. 62-82 *in*: F. Smith & K. Lyons (eds), *Global Patterns of Body Size*. University of Chicago Press. **[12]**

Nekola, J.C. 2005. Geographic variation in richness, evenness, and shell size of eastern North American land snail communities. *Records of the Western Australian Museum*. Supplement 68:39-51. **[39]**

Nekola, J.C. 2003. Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. *Diversity and Distribution.* 9:55-71. **[52]**

Nekola, J.C. & P.S. White. 1999. Distance decay of similarity in biogeography and ecology. *Journal of Biogeography*. 26:867-878. **[1069]**



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North American terrestrial gastropods through each end of a spyglass

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ABSTRACT

Some suggest that because of scale independence major biodiversity metrics can be estimated at large scales from analysis of a well chosen suite of individual sites. Others have attempted to estimate individual site patterns from analysis of the continental pool. But does such cross-scale extrapolation work? This issue is addressed for the North American terrestrial gastropod fauna by comparison of family representation, species richness and body-size patterns across site to continental scales. These data demonstrate profound differences: while the continental fauna is dominated by large body-size families such as the Polygyridae, Helminthoglyptidae, Oreohelicidae, Succineidae and Urocoptidae, average site faunas are most frequently represented by small body-sized families like the Vertiginidae, Gastrodontidae, Oxychilidae, Euconulidae, Punctidae, Valloniidae, Strobilopsidae and Ellobiidae. Species richness within sites tends to be 2–7 times smaller than random draws of individuals of the same number from regional or continental pools, indicating the potential for strong bias in the construction of site faunas. And, while the body-size spectrum for average site faunas is strongly right-skewed, the continental pool is strongly left-skewed. Thus, although taxa with biovolumes >16 mm^3 dominate the continental fauna (79.4% of total), they make up only a small average fraction (4.1%) of individual site species lists. Within most regions, site faunas are overrepresented in species with biovolumes <4 mm^3 and underrepresented in species with biovolumes >128 mm^3 as compared with the regional pool. As a result, assumptions of self-similarity between observational scales in terrestrial gastropods are inappropriate.

INTRODUCTION

The search for universal patterns and simplifying assumptions is common practice among natural scientists, especially those working in complex systems such as biology. One common form taken by this search is the identification of patterns that are scale-independent, i.e. patterns that remain largely similar across all observational scales. Such relationships are often referred to as expressing 'self-similarity', in which large scale datasets are made up of smaller scale components possessing the same basic properties. In the realm of fractal geometry, for instance, self-similarity across multiple scales has been noted in crystals (Mandelbrot, 1983), clouds (Hentschel & Procaccia, 1984), fluids (Nittman, Daccord & Stanley, 1985) and water drainage networks (Milne, 1988). This assumption also underlies most common algorithms generating fractal artwork, lending aesthetic regularity to the generated images.

However, the assumption of self-similarity has been found to be less useful in biological systems in which the major drivers are themselves scale dependent (Wiens, 1989). For instance, none of the vegetation patterns analysed by Palmer (1988) demonstrated scale independence and self-similarity. Yet, the siren-call of self-similarity has been especially strong in biodiversity analyses as its presence would allow insights regarding patterns and parameters present at one scale to be accurately applied to adjacent scales without the need for empirical observations. Direct measurement of various diversity metrics at tractable (usually single site) scales could thus theoretically be used to generate expectations at regional to global scales where empirical observation may be logistically impossible. Finlay *et al.* (2006), for instance, claimed that self-similarity in various species composition, richness and body-size metrics allows for accurate extrapolation of insect diversity patterns at Hilbre Island and Monks Woods Nature Reserves in England to the entire globe.

Is it really the case that biodiversity patterns appear the same when peering through each end of a spyglass? Can observation of only a few sites allow for accurate estimation of regional to global scale patterns? And, is it also possible that knowledge of regional to global scale patterns informs accurately about relationships within individual sites? These questions will be empirically tested through an analysis of North American terrestrial gastropod species composition, body-size and abundance patterns across site, regional and continental scales.

MATERIAL AND METHODS

Faunistic enumeration

Site scale. Species lists and abundances were considered from 1,574 sites ranging from the Alaskan North Slope and southern California coast east to central Quebec, the Atlantic seaboard and the Florida Keys (Table 1; Fig. 1). These were sampled according to methods presented by Nekola (2010), with individual sample areas being no more than 1,000 m^2. An attempt was made to sample sites from across the entire range of habitats within a given biogeographic region and included 416 bedrock outcrops, 455 upland forests, 335 lowland forests, 126 upland grasslands/shrublands and 242 lowland grasslands/shrublands.

Regional scale. Using the maps of Pilsbry (1948), Burch (1962) and observed community composition patterns as a guide, the continent was subdivided into 21 biogeographic regions with boundaries being set to enclose areas of similar faunistic composition and to also allow each species to occur within at least one region (Fig. 1). The total faunas for each region was then determined through the county-scale distribution maps of Hubricht (1985) for eastern North America (using updates provided by Nekola & Coles, 2010 and J.C. Nekola, unpubl.), with Pilsbry (1948) and various regional lists (e.g. Metcalf & Smartt, 1997; Roth & Sadeghian, 2003; Forsyth, 2004) being used for western North America. The number of survey sites per region ranged from 8 (southern Appalachians) to 252 (western Niagaran Escarpment).

Continental scale. The total North American fauna was based on Nekola (in press). Only species having native or naturalized populations in North America north of Mexico were considered; species only occurring south of the USA boundary are considered to belong to the Central American fauna. The initial point of departure for this dataset is all terrestrial gastropods listed by Turgeon *et al.* (1998). To this were added all subsequently described species as determined via the *Zoological Record*. Additionally, all species listed by Hubricht (1985)—but not by Turgeon *et al.* (1998)—were included, as these represent dead shells limited to drift along the south Texas Gulf Coast that could easily have been sourced from local extant colonies. The list was also expanded to include all subspecies-level entities of Pilsbry (1948) that appear, based on their unique shell features, ranges and/or ecological preferences, to represent valid species-level entities. Finally, 14 undescribed new species encountered by the author during field sampling across North America have also been included, representing six *Vertigo* plus single representatives of *Columella*, *Daedalochila*, *Glyphyalinia*, *Hawaiia*, *Helicodiscus*, *Paravitrea*, *Punctum* and *Succinea*.

Taxonomy and body size

Family assignments for all species were based on those of Bouchet & Rocroi (2005), with the placement of genera into these families generally following Schileyko (2006 and previous works). Generic level assignments generally followed Turgeon *et al.* (1998). Shell/body-size dimensions for each taxon were determined from either the published literature, or in the case of undescribed taxa from lots held in the Nekola collection. Calculation of body volume (in mm^3) was then determined for each species using the formulae presented by McClain & Nekola (2008) and Nekola (in press).

Statistical analyses

All analyses were conducted in the R Statistical Environment with scripts being available upon request.

Family-level composition. The proportional representation of each family within each site was calculated by dividing the total number of species present within each family into the total species richness of that site. This process was repeated across all sites, with the mean proportion for each family then being calculated across all sites. This process was also repeated within each biogeographic region. The proportion of each family within the continental fauna was calculated by dividing the number of species within each family into the continental species richness.

Table 1. Statistical summary for the continental and regional datasets of North American terrestrial gastropods.

Region	No. of sites	Regional richness		Site richness		No. of individuals	
		Reported	Encountered	Median	Maximum	Total	Median/site
Whole continent	1,574	1,204	460	12	39	697,778	237
Churchill	23	17	15	6	12	9,303	261
Central Manitoba	24	53	41	10	21	11,014	288
Laurentian Plateau	48	80	40	8	18	9,729	131
Northwestern Minnesota	192	63	59	15	27	142,305	463
Western Superior Uplands	82	55	44	10	18	5,025	47
Eastern Niagaran Escarpment	73	149	86	16	31	26,804	305
Western Niagaran Escarpment	252	98	84	15	34	92,778	216
New England	194	133	82	13	34	84,661	217
Upper Mississippi Valley	131	103	90	20	39	105,075	587
Ozarks	35	149	88	20	34	20,601	255
Central Appalachians	22	246	86	16	35	7002	219
Southern Appalachians	8	278	42	12	33	2,181	210
Carolinas	38	131	62	8	31	9,298	132
Gulf Coast	37	156	34	3	11	2,260	43
Peninsular Florida	59	130	97	12	28	33,848	301
Southern Plains	14	154	58	12	23	3,379	128
Southern Rockies	161	308	113	7	21	72,116	230
California	30	271	51	5	10	8,219	99
Great Basin	39	76	45	7	13	12,635	206
Pacific Northwest	48	187	64	9	17	13,895	197
Alaskan Interior	64	33	32	7	16	25,644	216

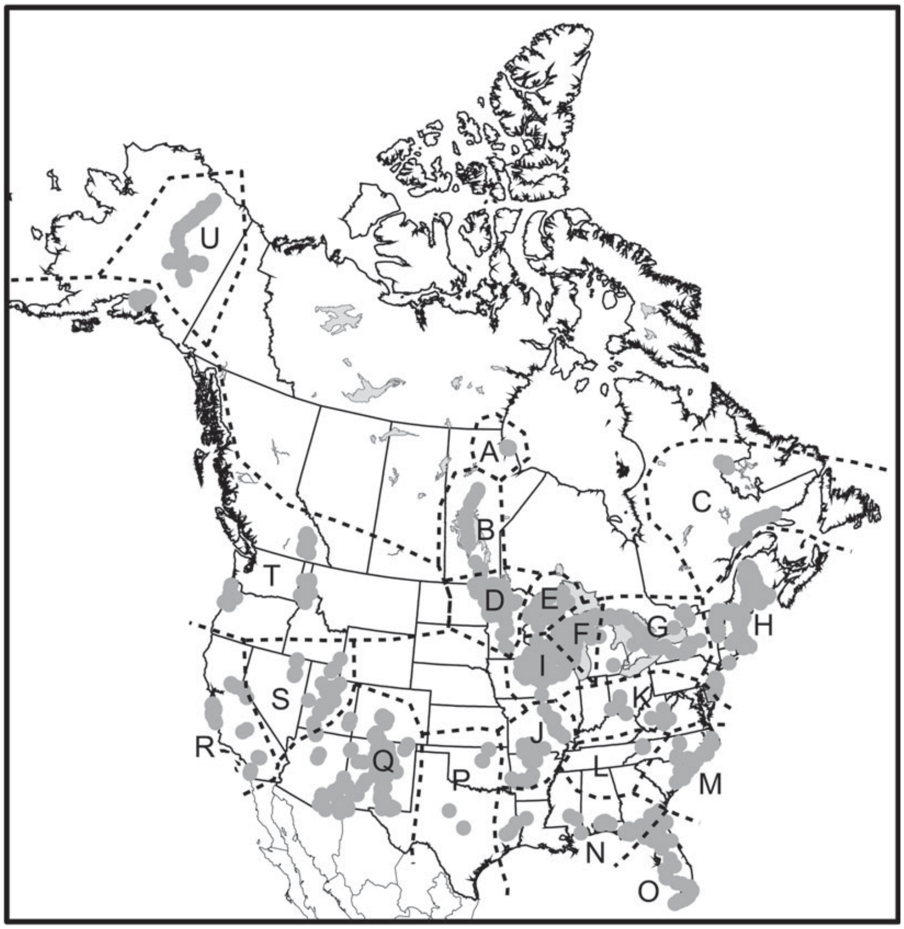

Figure 1. Location of the 1,574 sample sites and 21 biogeographic regions in North America. Regional codes are: A, Churchill; B, Central Manitoba; C, Laurentian Plateau; D, Northwestern Minnesota; E, Lake Superior Uplands; F, Western Niagaran Escarpment; G, Eastern Niagaran Escarpment; H, New England; I, Upper Mississippi Valley; J, Ozarks; K, Central Appalachians; L, Southern Appalachians; M, Carolinas; N, Gulf Coast; O, Peninsular Florida; P, Southern Plains; Q, Southern Rockies; R, California; S, Great Basin; T, Pacific Northwest; U, Alaskan Interior.

This process was also repeated at the regional level. All proportions were multiplied by 100 to give percentage representation.

Statistical significance of the difference between site and regional scale representation was calculated using a sign test for all families occurring in at least 10 regions. The number of cases in which mean site percentage was less than the regional percentage was counted, as was the number of cases in which regional percentage was less than mean site percentage. Under a null expectation of no relationship, these numbers should be equal. The P-value for deviations from this null was calculated using the binomial distribution. Because the test was repeated on 18 different families, the $P = 0.05$ significance threshold was adjusted using a Bonferroni correction to $P = 0.0028$.

Site species richness. The ratio between observed and random expected richness was calculated. Expected random richness was determined by generating a vector representing the species identities of all encountered individuals across either the entire continental dataset or a respective region. For each site, n random individuals were selected from this vector without replacement, where $n =$ the number of all identified individuals from a given site. The number of unique species in the random draw was then reported, with this process being repeated 1,000 times. The mean number of unique species across all random samples was then recorded. This process was repeated across all sites. Observed site richness was then divided into mean random richness. A box plot was then generated showing the variation in observed: random richness across all sites in the continent or respective region. Statistical significance for differences in observed *vs* randomized richness was estimated using the paired Wilcoxon rank-sum test.

Body-size spectra. Observed body-size spectra were determined across all sites by counting the number of species falling within each of 41 $\log_2$ volume classes with bins starting at -2.5 and increasing by 0.5 $\log_2$ units to 18.0. The first bin value ranged from -2.5 to -2.0 ($\sim$0.18 to 0.25 mm^3) and the last bin from 17.5–18.0 (185 363.8 to 262 144 mm^3). The proportion of the total site fauna found within each bin was then determined by dividing the observed bin richness by total site richness. Random expectations were then generated by randomly drawing n species, without replacement, from the continental or respective regional species pool, where $n =$ number of recorded species from that site. The proportion that each bin represented in the random draw was then calculated. This procedure was repeated 1,000 times, with the mean proportion across all randomizations being reported across all 41 bins. This process was repeated for each site. From this, body-size spectra graphs were generated showing across all bins the mean observed site representation and the minimum and maximum mean random values as drawn from the continental or respective regional pool. Regional scale patterns were illustrated through three latitudinal transects: western (Alaskan Interior, Pacific Northwest, Great Basin and southern Rockies), central (Churchill, Northwestern Minnesota, Upper Mississippi Valley and Ozarks), and eastern (Laurentian Plateau, New England, Carolinas, Peninsular Florida).

RESULTS

In all 1,204 species-level taxa are reported from North America, partitioned among 170 genera and 51 families (Nekola, in press). A total of 460 species (38% of the continental total) and 697,778 individuals were recorded from the 1,574 sites (Table 1). Regional faunistic richness ranged from 17 (Churchill) to 308 (Southern Rockies), with encountered species ranging from 15 (Churchill) to 113 (Southern Rockies). Median site richness ranged from 3 (Gulf Coast) to 20 (Upper Mississippi Valley and Ozarks), while maximum richness ranged from 10 (California) to 39 (Upper Mississippi Valley). The total number of encountered individuals ranged from 2,181 (Southern Appalachians) to 142,305 (Northwestern Minnesota), while the median number of individuals encountered per site ranged from 43 (Gulf Coast) to 587 (Upper Mississippi Valley).

Family-level composition

For the entire continental fauna (Table 2), the ten most frequently represented families were the Polygyridae (22.51%), Helminthoglyptidae (14.78%), Vertiginidae (8.64%), Oreohelicidae (6.98%), Pristilomatidae (5.40%), Oxychilidae (4.07%), Succineidae (4.07%), Gastrodontidae (2.91%), Arionidae (2.82%) and Urocoptidae (2.58%). This differs greatly from average site faunas, which were most frequently represented by the Vertiginidae (29.93%), Gastrodontidae (11.19%), Oxychilidae (7.60%), Euconulidae (7.09%), Punctidae (5.44%), Discidae (5.40%), Valloniidae (4.88%), Strobilopsidae (3.23%), Polygyridae (3.20%) and Ellobiidae (2.97%).

Regional species pools demonstrated variability in family-level representation, with the most common family ranging from the Vertiginidae (Churchill, Central Manitoba, Lake Superior Uplands, Laurentian Plateau, New England, Northwestern Minnesota, Eastern Niagaran Escarpment, Western Niagaran Escarpment, Upper Mississippi Valley and Alaskan Interior) to the Polygyridae (Southern Plains, Ozarks, Southern Appalachians, Central Appalachians, Carolinas, Gulf Coast and Peninsular Florida), Oreohelicidae (Pacific Northwest and Great Basin) and Helminthoglyptidae (California and Southern Rockies).

The sign test demonstrates that five families show significant (and another three marginally significant) differences in their representation between site and regional scales (Table 3). The Euconulidae, Punctidae and Vertiginidae all exhibited significantly (Bonferroni adjusted $P < 0.0028$) more instances of mean site fauna proportion exceeding the respective regional species pool proportion than would be expected at random. The Gastrodontidae, Oxychilidae and Strobilopsidae exhibited this pattern to only a marginal ($0.05 < P < 0.0028$) degree. However, the Polygyridae and Succineidae demonstrated significantly more instances of mean site fauna proportion being less than the respective regional pool proportion. Ten families (Agriolimacidae, Cochlicopidae, Discidae, Ellobiidae, Haplotrematidae, Helicodiscidae, Pristilomatidae, Pupillidae, Valloniidae and Vitrinidae) exhibited similar proportional representations between average site faunas and the regional species pool. Because of limited occurrence (<10 regions occupied), statistical power was too low to conduct this test on 25 families. However, among these it should be noted that in all four regions supporting members of the small body-size Thysanophoridae, percent representation within site faunas always exceeded the proportion in respective regional species pools, while in the large body-size Helicidae, Helminthoglyptidae, Humboldtianidae, Hygromiidae, Monadeniidae and Oreohelicidae site fauna representation was always less than the respective regional pool. This was also the case in 75% of the regions supporting large body-size Orthalicidae.

Site richness

Observed site richness values were approximately seven times smaller than random draws taken from the entire continental dataset (Fig. 2). The paired Wilcoxon rank-sum test demonstrated that this difference was highly significant ($P < 0.0000001$). At the regional scale, observed richness generally ranged from 1.85 times smaller than random draws (Lake Superior Uplands) to 6.3 times smaller (Southern Rockies). Observed site faunas were 2.4 and 3.6 times less rich than average random draws from the regional individual pool for Churchill and the Alaskan Interior, respectively. This number ranged from 2.7 to 3.1 for Central Manitoba, the Laurentian Plateau, New England, Northwestern Minnesota, the Eastern and Western Niagaran Escarpments and the Upper Mississippi Valley. In the Southern Plains, Ozarks and Central Appalachians, individual site faunas were 2.6–2.2 times smaller than random draws from their respective regional individual pools. This number ranged from 3.4–3.9 in the Carolinas, Gulf Coast and Peninsular Florida, and 3.1–4.7 in the Pacific Northwest, Great Basin and California. The paired Wilcoxon rank-sum test demonstrated that these differences were all highly significant ($P < 0.0000027$ with a Bonferroni-adjusted P-value threshold of 0.00238). The main exception was the Southern Appalachians, which had observed richness ranging between *c.* 1.3 times larger to 4.2 times smaller than the size of a random draw from the regional individual pool (median = 1.5 times smaller). While sites were generally less rich than random draws from the entire regional individual pool, this difference was only marginally significant ($P = 0.007813$).

Body-size spectra

Observed mean body-size spectra within sites differed strongly from random draws made from the continental species pool (Fig. 3). While observed site faunas were strongly right-skewed with a mode at the 5th $\log_2$ body-size bin (0.71–1 mm^3), random draws of the same richness from the continental species pool were strongly left-skewed, with modal values ranging from the 21st–24th $\log_2$ body-size bin (181–512 mm^3). Site faunas were greatly enriched in species with biovolumes of 5.7 mm^3 or less, and greatly underrepresented in species with biovolumes of 90.5 mm^3 or greater. These differences are highly significant, with the site-scale mode for species with biovolumes <5.7 mm^3 being more than three times larger than the maximum observed randomized mean at that same size class, and the minimum score of the randomized means for species with biovolumes >90.5 mm^3 being at least five times larger than observed scores for these same body-size classes. Species with biovolumes of 5.7–90.5 mm^3 were represented at approximately equal proportions within observed and randomized site faunas.

The enrichment of small species and impoverishment of large species at site scales was also present within most biogeographic regions (Fig. 4). Among the 12 illustrated relationships in Figure 4, the Pacific Northwest, Great Basin, Southern Rockies, Upper Mississippi Valley, Ozarks, Laurentian Plateau, New England and Carolinas all strongly demonstrate this pattern. It is also more weakly exhibited in Northwestern Minnesota and Peninsular Florida. Very similar observed *vs* randomized body-size spectra were noted for the Alaskan Interior and Churchill.

DISCUSSION

These analyses clearly show that family composition, body-size spectra and species richness are not self-similar and scale independent among North American terrestrial gastropods. While the continental fauna is dominated by families with large-sized individuals like the Polygyridae and Helminthoglyptidae,

Table 2. Comparison of terrestrial gastropod family percent representation across observational scales in North America.

Family	Entire Continent		Churchill		Central Manitoba		Lake Superior Uplands		Laurentian Plateau		New England		NW Minnesota		E Niagara		W Niagara		Upper Mississippi		Southern Plains		Ozarks	
	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%
Polygyridae	22.51	3.20					5.46	0.34			12.78	0.50	1.59	0.03	12.08	3.98	8.16	2.78	10.68	6.48	32.47	18.54	29.53	18.40
Helminthoglyptidae	14.78	0.28																						
Vertiginidae	8.64	29.93	64.71	68.11	35.85	31.56	27.27	20.96	26.25	36.93	15.79	30.93	31.75	24.46	15.45	21.86	20.41	28.06	21.36	31.58	12.99	26.55	15.44	23.49
Oreohelicidae	6.98	0.37																						
Pristilomatidae	5.40	2.66			1.89	–	1.82	0.61			2.26	0.47	3.18	3.06	2.69	2.69	3.06	2.66	1.94	4.56	2.60	8.50	6.71	6.40
Oxychilidae	4.07	7.60			3.77	12.05	7.27	11.78	5.00	14.26	9.77	9.17	3.18	9.53	7.38	9.00	8.16	5.11	4.85	5.12	4.55	5.73	6.71	9.11
Succineidae	4.07	2.75	11.77	11.17	13.21	3.34	5.46	1.05	7.50	1.71	6.02	1.96	7.94	4.32	6.71	1.63	9.18	3.62	10.68	2.24	7.14	9.00	6.71	0.52
Gastrodontidae	2.91	11.19			5.66	8.02	9.09	21.71	6.25	7.53	7.52	19.70	6.35	11.92	7.38	16.63	6.12	12.61	5.83	5.66	3.25	5.81	5.37	9.75
Arionidae	2.82	–					3.64	–	11.25	–	6.02	–	3.18	–	6.04	–	4.08	–	3.88	–				
Urocoptidae	2.58	0.18																			1.95	–		
Discidae	2.24	5.40	5.88	–	3.77	13.08	5.46	12.70	3.75	8.66	2.26	3.73	4.76	6.70	4.03	7.90	4.08	7.18	4.85	5.14	1.30	0.99	3.36	2.36
Helicodiscidae	2.08	2.76			3.77	–	3.64	3.74	1.25	0.98	3.01	3.54	3.18	1.76	2.01	3.93	3.06	4.48	3.88	5.95	5.20	5.77	2.69	4.68
Phylomicidae	1.74	–									5.26	–			4.70	–	1.02	–	2.91	–	1.95	–	4.03	–
Haplotrematidae	1.33	0.44									0.75	0.09			0.67	0.29	1.02	0.07	0.97	1.13			0.67	1.70
Orthalicidae	1.33	0.23																			2.60	1.13	0.67	1.35
Monadeniidae	1.33	0.03																						
Pupillidae	1.16	1.88	5.88	2.71	1.89	–			1.25	0.28	1.50	0.41	3.18	0.08	1.34	0.92	2.04	0.05	1.94	1.77	0.65	3.73	0.67	2.50
Valloniidae	1.08	4.88			9.43	4.47	7.27	6.57	8.75	6.71	4.51	4.66	9.52	6.63	4.70	3.47	7.14	3.73	5.83	5.08	3.90	1.56	2.69	1.19
Euconulidae	0.91	7.09	5.88	13.78	3.77	10.25	5.46	5.33	2.50	12.79	3.01	7.25	3.18	7.23	2.69	5.92	4.08	6.33	3.88	5.41	1.95	3.05	2.69	4.40
Ellobiidae	0.91	2.97			3.77	3.73	3.64	2.12	2.50	–	1.50	3.68	3.18	6.33	2.01	4.45	2.04	5.08	1.94	3.98	1.30	0.48	0.67	2.21
Punctidae	0.83	5.44			3.77	6.99	1.82	4.94	2.50	2.74	1.50	7.24	4.76	6.39	2.01	6.06	3.06	5.73	2.91	5.13	0.65	2.44	1.34	4.94
Humboldtianidae	0.83	0.00																						
Helicinidae	0.75	0.63					1.82	0.15									1.02	1.65	0.97	1.73	3.25	1.13	0.67	1.08
Binneyidae	0.75	–																						
Subulinidae	0.66	0.28																			0.65	–		
Helicidae	0.66	0.05							3.75	0.14	3.76	0.03			4.03	0.59	1.02	–			2.60	–	1.34	–
Hygromiidae	0.66	0.02							3.75	–	1.50	0.14			2.69	0.06								
Megomphicidae	0.66	0.01																						
Veronicellidae	0.66	–																						
Agriolimacidae	0.50	1.30	5.88	4.24	1.89	1.96	1.82	0.10	3.75	0.15	1.50	0.96	3.18	1.69	2.01	2.56	2.04	1.73	1.94	3.27	0.65	–	1.34	0.45
Strobilopsidae	0.42	3.23			1.89	1.10	1.82	4.60	1.25	–	3.01	4.17	3.18	4.16	2.01	3.97	3.06	4.89	2.91	4.24	2.60	4.45	2.69	4.44
Thysanophoridae	0.42	0.97																			1.30	–		
Truncatellidae	0.42	0.13																			0.65	–		
Limacidae	0.42	–							2.50	–	3.01	–			3.36	–	1.02	–			1.30	–	2.01	–
Spiraxidae	0.33	0.13																			2.60	0.51		
Pleurodontidae	0.33	0.06																						
Cochlicopidae	0.25	1.99			3.77	2.37	5.46	2.54	2.50	1.77	2.26	1.24	3.18	4.05	2.01	2.84	3.06	3.67	2.91	1.25			1.43	0.22
Vitrinidae	0.17	1.43			1.89	1.10	1.82	0.76	1.25	5.36	0.75	0.15	1.59	1.65	0.67	1.23	1.02	0.42	0.97	0.11				
Pomatiidae	0.17	0.12																						
Pomatiopsidae	0.17	0.07									0.75	–			0.67	0.05	1.02	0.14	1.94	0.18			0.67	0.83
Ferrussaciidae	0.17	0.00																						
Charopidae	0.17	0.09																						
Sagdidae	0.08	0.07																						
Oleacinidae	0.08	0.07																						
Bradybaenidae	0.08	0.03																						
Streptaxidae	0.08	0.02																						
Helicarionidae	0.08	0.01																						
Cepolidae	0.08	0.00																						
Cochlicellidae	0.08	–																						
Milacidae	0.08	–							1.25	–														
Testacellidae	0.08	–							1.25	–					0.67	–								

Family	Southern Appalachians		Central Appalachians		Carolinas		Gulf Coast		Peninsular Florida		Alaskan Interior		Pacific Northwest		Great Basin		California		Southern Rockies	
	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%
Polygyridae	30.22	12.80	23.17	11.07	25.19	4.16	30.13	8.31	14.62	12.70			9.63	4.34			8.86	2.92	17.86	1.93
Helminthoglyptidae													1.07	–			38.75	12.12	24.35	0.51
Vertiginidae	6.12	17.73	9.76	23.49	14.50	36.83	12.82	41.36	13.08	17.53	45.46	59.09	12.30	25.66	19.74	19.83	7.75	22.23	12.66	34.17
Oreohelicidae													14.97	1.10	28.95	7.47	0.37	–	12.34	1.46
Pristilomatidae	12.95	14.39	7.32	7.34	1.53	1.83	3.21	0.52	1.54	3.27			5.88	5.14	1.32	–	2.95	5.98	0.33	4.13
Oxychilidae	12.59	13.82	10.98	11.35	9.16	18.20	8.97	14.20	4.62	4.81	6.06	3.31	3.21	6.43	3.95	1.39	2.21	0.90	1.62	5.75
Succineidae	1.80	–	4.89	1.22	7.63	–	8.33	0.39	6.93	1.30	9.09	9.94	6.42	2.03	13.16	3.59	3.69	1.94	2.27	0.57
Gastrodontidae	8.27	17.92	10.16	10.87	6.11	9.99	7.69	17.30	3.08	2.54			1.60	9.98	2.63	2.48	0.74	11.31	0.65	7.21
Arionidae			2.85	–	2.29	–							14.44	–			7.75	–	0.33	–
Urocoptidae									2.31	3.47									8.44	0.50
Discidae	5.40	0.38	2.85	1.41	2.29	0.36	1.28	–			6.06	3.55	3.21	6.52	2.63	6.94	1.48	2.64	0.65	4.13
Helicodiscidae	5.04	–	4.47	3.55	2.29	2.98	2.56	0.34	3.08	1.54			0.54	0.23			0.37	0.33	0.65	1.12
Phylomicidae	4.68	–	4.89	–	3.05	–	3.21	–	1.54	–									0.33	–
Haplotrematidae	0.72	1.91	0.41	1.94	0.76	1.40	0.64	–					1.60	3.04			4.06	5.56		
Orthalicidae	0.36	–					1.28	–	5.39	3.83									1.62	0.49
Monadeniidae													1.07	0.19			5.90	1.11		
Pupillidae	0.36	–	0.81	0.38	0.76	0.33	0.64	–	1.54	1.97	3.03	5.77	1.07	0.84	6.58	14.95	0.37	0.67	3.90	7.31
Valloniidae	1.08	–	2.03	0.64	2.29	0.64	1.28	1.68	1.54	4.31	6.06	1.34	2.14	4.17	6.58	11.82	0.74	2.39	2.27	8.87
Euconulidae	1.80	6.83	2.03	6.73	3.05	5.36	3.21	6.95	3.85	5.42	9.09	14.27	1.07	8.63	2.63	6.68	0.74	4.20	0.65	6.95
Ellobiidae	2.16	4.24	2.44	4.65	2.29	1.08	1.28	0.25	0.77	0.57			1.60	0.83			0.37	0.33	0.33	0.04
Punctidae	1.44	8.46	1.63	7.77	3.05	6.14	1.28	2.43	0.77	0.24	6.06	0.88	1.60	11.54	1.32	4.97	2.21	20.87	0.97	2.87
Humboldtianidae																			3.25	0.04
Helicinidae	0.72	–	0.41	0.52			0.64	–	2.31	4.77										
Binneyidae													4.28	–			0.37	–		
Subulinidae			0.41	–	1.53	0.29	1.28	–	6.15	7.17							0.37	–	0.33	–
Helicidae			1.63	0.44	1.53	–	2.56	–	1.54	–			1.60	–	1.32	–	2.58	0.48	0.65	–
Hygromiidae					2.29	–	0.64	–	0.77	–							0.37	–		
Megomphicidae													1.60	0.35			1.85	–		
Veronicellidae									6.15	–										
Agriolimacidae	0.72	–	0.81	1.31	1.53	0.91	0.64	0.34	0.77	0.13	3.03	1.34	2.67	0.31	2.63	1.09	1.11	1.22	0.97	0.31
Strobilopsidae	1.08	–	1.63	3.19	2.29	9.09	2.56	5.61	2.31	2.86										
Thysanophoridae									1.54	4.31			1.07	6.19	1.32	4.68			0.65	4.78
Truncatellidae									2.31	3.40							0.74	–		
Limacidae	0.72	–	1.63	–	1.53	–	1.92	–					2.14	–	1.32	–	1.48	–	0.65	–
Spiraxidae					0.76	–	0.64	0.34	0.77	3.04										
Pleurodontidae									3.08	1.62										
Cochlicopidae	1.08	0.95	0.81	1.28	0.76	0.42					3.03	0.13	1.07	0.12	1.32	0.20	0.37	–	0.33	2.41
Vitrinidae			0.41	–							3.03	0.39	0.54	1.15	1.32	13.65	0.37	2.81	0.33	3.99
Pomatiidae									1.54	3.34										
Pomatiopsidae	0.72	–	0.81	0.85	0.76	–	0.64	–												
Ferrussaciidae			0.41	–					1.54	0.07										
Charopidae													0.54	1.20	1.32	0.26			0.33	0.45
Sagdidae									0.77	1.77										
Oleacinidae									0.77	1.93										
Bradybaenidae									0.77	0.69										
Streptaxidae							0.64	–	0.77	0.62										
Helicarionidae									0.77	0.33										
Cepolidae									0.77	0.07										
Cochlicellidae					0.76	–											0.37	–		
Milacidae			0.41	–									0.54	–			0.37	–	0.33	–
Testacellidae													0.54	–			0.37	–		

R%, the percentage of species in the continental/regional fauna occurring within that family. S%, the percentage representation of that family within an average site within that region. Dashes indicate families that are present in the respective fauna but have not yet been encountered within sites.

Table 3. Comparison of family representation at regional *vs* site scales for terrestrial gastropods in North America.

A. 10 or more regions

Family	R > S	S > R	*P*-value
Agriolimacidae	14	5	0.063568
Cochlicopidae	11	5	0.210114
Discidae	6	12	0.237885
Ellobiidae	11	8	1.0
Euconulidae	**1**	**20**	**0.000021**
Gastrodontidae	*3*	*16*	*0.004425*
Haplotrematidae	3	7	0.343750
Helicodiscidae	7	9	0.803619
Oxychilidae	*5*	*15*	*0.041389*
Polygyridae	**16**	**0**	**0.000031**
Pristilomatidae	7	9	0.803619
Punctidae	**2**	**18**	**0.000402**
Pupillidae	10	7	0.629059
Strobilopsidae	*1*	*12*	*0.003418*
Succineidae	**17**	**2**	**0.000729**
Valloniidae	12	7	0.359283
Vertiginidae	**3**	**18**	**0.001490**
Vitrinidae	6	7	1.0

B. <10 regions

Family	R > S	S > R
Bradybaenidae	1	0
Cepolidae	1	0
Charopidae	1	2
Ferrussaciidae	1	0
Helicarionidae	1	0
Helicidae	5	0
Helicinidae	3	5
Helminthoglyptidae	2	0
Humboldtianidae	1	0
Hygromiidae	2	0
Megomphicidae	1	0
Monadeniidae	2	0
Oleacinidae	0	1
Oreohelicidae	3	0
Orthalicidae	3	1
Pleurodontidae	1	0
Pomatiidae	0	1
Pomatiopsidae	3	2
Sagdidae	0	1
Spiraxidae	2	1
Streptaxidae	1	0
Subulinidae	2	1
Thysanophoridae	0	4
Truncatellidae	0	1
Urocoptidae	1	1

R > S represents the number of regions in which family representation in the regional pool exceeded the representation on an average site. S > R represents the number of regions in which family representation within an average site exceeded the representation in the regional pool. Assuming the null of R > S = S > R, *P*-values for families present in at least ten regions are based on the bionomial sign test. Families with $P < 0.0028$ have been highlighted in bold font; families with $0.05 < P < 0.0028$ have been highlighted in *italic* font.

typical site faunas are dominated by families with small-sized individuals like the Vertiginidae and Gastrodontidae. Likewise, while the continental fauna demonstrates a left-skewed body-size spectrum dominated by species with biovolumes >90.5 mm^3, average site faunas are right-skewed and dominated by species with biovolumes <5.7 mm^3. Random draws representing the same number of individuals from the entire continental dataset contained on average at least seven times more species than the actual number observed at that site.

These discrepancies were generally also observed between sites and their respective biogeographic regions. Typically, families with small-sized individuals (Euconulidae, Gastrodontidae, Oxychilidae, Punctidae, Strobilopsidae, Thysanophoridae and Vertiginidae) were overrepresented in typical site faunas as compared to their respective regional species pool, while families with large-sized individuals (Helminthoglypidae, Monadeniidae, Oreohelicidae, Polygyridae and Succineidae) were underrepresented. This bias is demonstrated across most regions (e.g. Pacific Northwest, Great Basin, Southern Rockies, New England and Carolinas). However, both arctic regions tended to show little discrepancy between typical site body-size spectra and the regional pool. Site richness also generally ranged from two to six times smaller than would be expected from random draws from the respective regional individual pool. Even in the case of the Southern Appalachians, where the eight sampled sites were only collected across a 20-km extent and only 42 total species were encountered (15% of the entire regional fauna) the majority of sites were still found to have fewer species than would be expected from a random draw of all encountered individuals. As more samples are made across a larger extent within this region and more of this regional fauna is encountered, the distribution of observed to random ratio scores will be lowered and made to fall in line with other regions.

These analyses indicate that site faunas are not a simple random sample drawn from the continental or regional pool. Rather, important biases are present. The most important of these are not only the predictable filtering of species along environmental gradients (principally soil architecture, moisture and acidity; Nekola, 2003, 2010) but also purely geographic filtering caused by dispersal limitation and other forms of spatial constraint (Nekola & White, 1999; Hubbell, 2001).

As a result, it is not possible to extrapolate accurately these macroecological metrics across scales for North American terrestrial gastropods. Rather, the fauna looks considerably different depending upon whether one is looking down from continental scales, or up from site scales. From the continental-scale perspective, the fauna is generally dominated by families with large-sized individuals. However, from the site scale the fauna is dominated by a series of families with small body-sized individuals. Documenting the faunas of a few individual sites will thus not allow for an accurate portrayal of the continental fauna and knowledge of the continental fauna informs little about what one would expect within individual sites.

The lack of self-similarity within the North American terrestrial gastropod fauna appears to be principally caused by a strong inverse correlation between body and range size. In this fauna, many small species (especially within the Euconulidae, Gastrodotidae, Oxychilidae, Punctidae, Strobilopsidae and

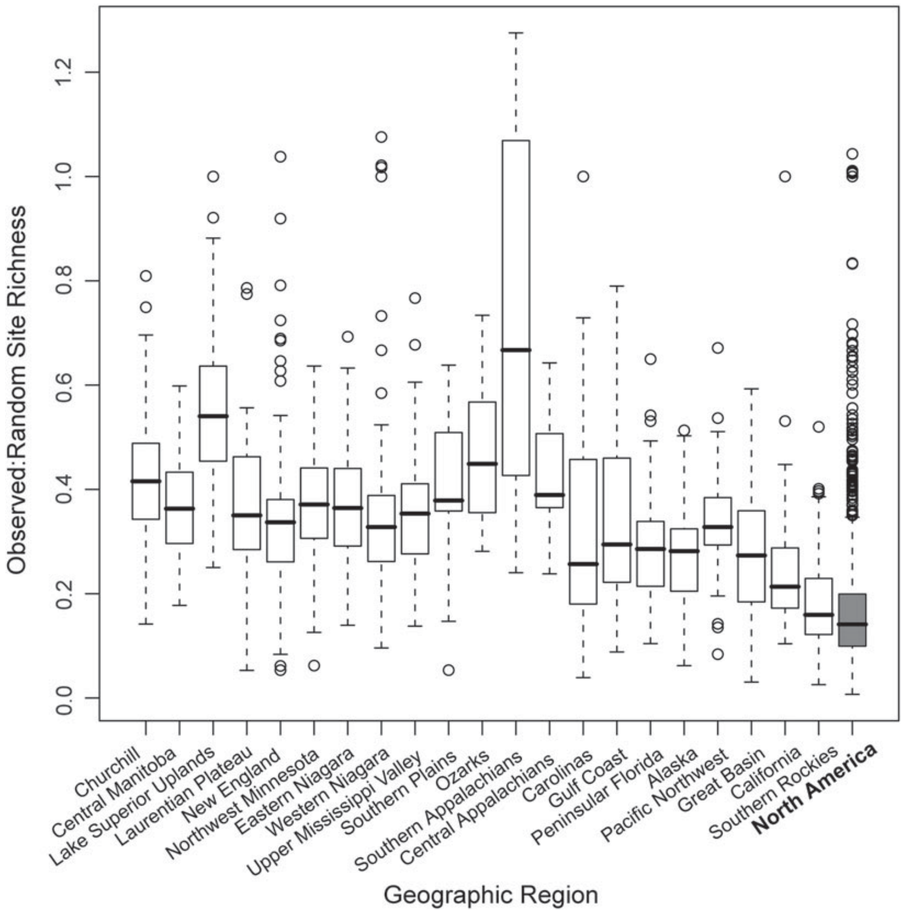

Figure 2. Box plot showing distribution of observed site richness *vs* randomized expectations from the regional/continental individual pool of terrestrial gastropods in North America. The site *vs* continental-scale comparison is identified by grey fill.

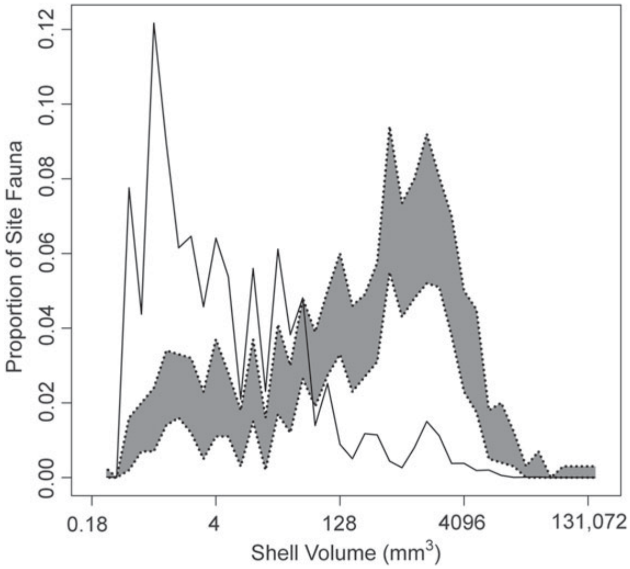

Figure 3. Site *vs* continental body-size spectra for terrestrial gastropods of North America as represented by 41 $\log_2$ body-size classes. The solid line represents the observed average for individual sites. The upper and lower dashed lines represent the maximum and minimum mean scores (respectively) observed for that size class across 1,000 random samples drawn per site from the continental pool. The range between these extremes has been filled with grey.

Vertiginidae) tend to have component species harboring extensive ranges. Examples include *Euconulus fulvus* (Müller, 1774), *E. alderi* Gray, 1840, *Punctum minutissumum* (I. Lea, 1841) and *Vertigo arthuri* von Martens, 1884, which range across the entire continent north of 38°N, while also extending south along the crest of the Rockies to the Mexican border. *Gastrocopta pellucida* (Pfeiffer, 1841), *Glyphyalinia umbilicata* (Singley, in Cockerell, 1893), *Hawaiia miniscula* (A. Binney, 1840) and *Straitura meridionalis* (Pilsbry & Ferriss, 1906) likewise extend across much of North America south of 35°N. And, both *Strobilops labyrinthica* (Say, 1817) and *Strobilops aenea* Pilsbry, 1926 range across most of the southeastern quarter of the continent. A number of genera with large body-sized species, however, demonstrate significant levels of allopatric replacement and local endemism. These are especially pronounced within the Polygyridae (e.g. *Ashmunella*, *Daedalochila*, *Stenotrema*, *Inflectarius*, *Patera*, *Triodopsis*, *Trilobopsis* and *Vespericola*), Helminthoglyptidae (e.g. *Helminthoglypta*, *Micrarionta* and *Sonorella*), Oreohelicidae (e.g. *Oreohelix* and *Radiocentrum*), Urocoptidae (e.g. *Holospira* and *Coelostemma*), Monadeniidae (*Monadena*) and Humboldtianidae (*Humboldtiana*), with it being uncommon for species within these genera to be sympatric at the site scale.

It seems likely that the combined effects of body size on passive dispersal and uniparental reproduction rates help explain this counter-intuitive pattern. Because terrestrial gastropods are among the poorest active dispersers known among terrestrial animals, with individuals moving perhaps no more than 1–10 m over their lifetime (Schilthuizen & Lombaerts, 1994) and populations being unable actively to cross barriers of only 100–1,000 m (Baur, 1988; Schilthuizen & Lombaerts, 1994),

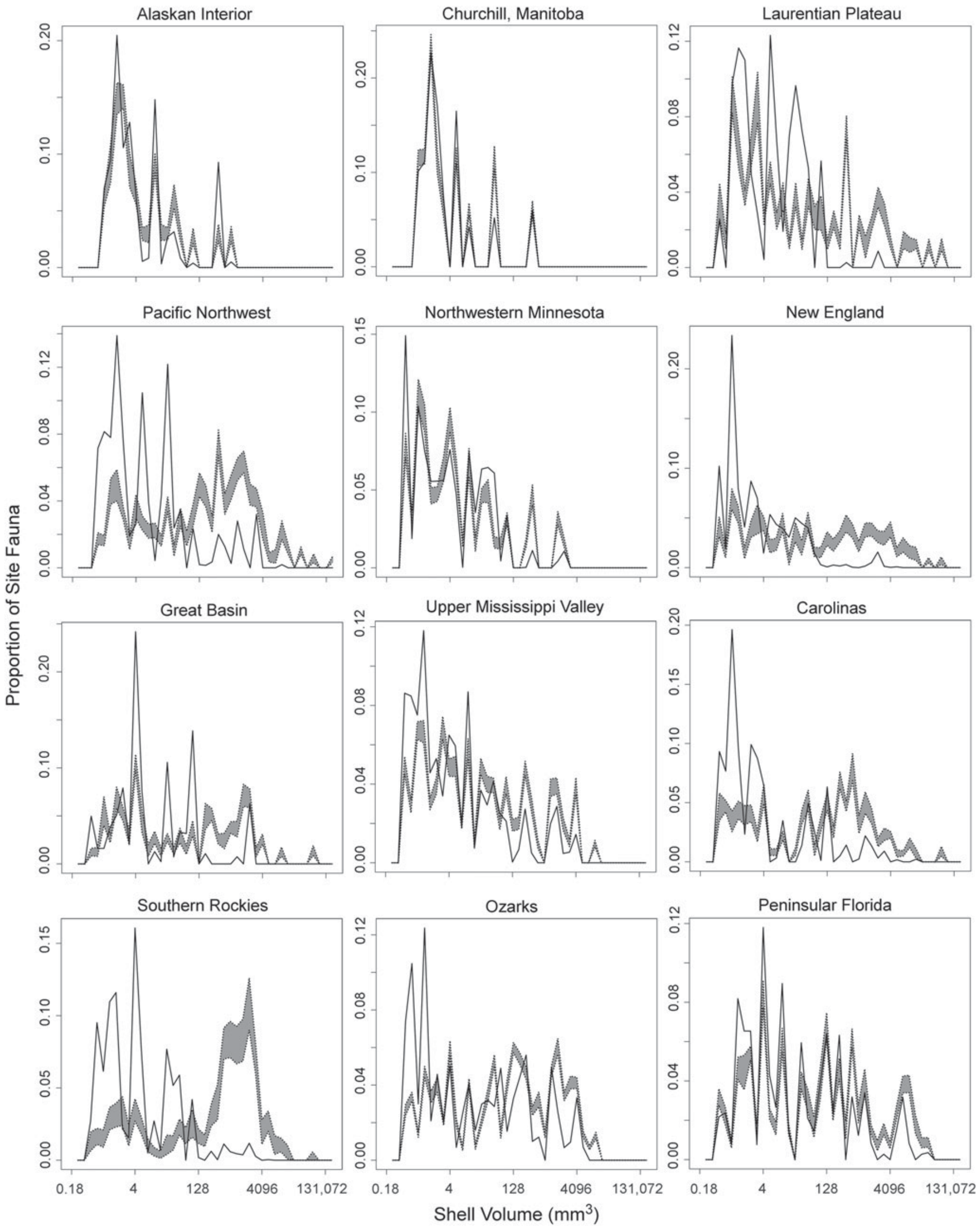

Figure 4. Site *vs* regional body-size spectra of terrestrial gastropods in North America, as represented by 41 $\log_2$ body-size classes across twelve selected biogeographic regions. Panels are arranged in three columns (western, central and eastern North America) from most northern (top) to most southern (bottom). In each panel, the solid line represents the observed average for individual sites in that region. The upper and lower dashed lines represent the maximum and minimum mean scores (respectively) observed for that size class across 1,000 random samples drawn per site from the respective regional pool. The range between these extremes has been filled with grey.

passive dispersal takes precedence in determining population movement and species range size. Small snails/slugs are much more easily moved via passive vectors than larger ones, because small-sized individuals are less likely to be pulled off by gravity or fluid mechanics during movement. Additionally, a number of North American genera with species of small body-size contain some that are capable of uniparental reproduction (Pokryszko, 1987; Bulman, 1990). For these, movement of only a single unmated individual is required to found a new population, greatly increasing the effectiveness of long-range dispersal events in causing range expansion. DNA sequence data illustrate, for instance, that members of the genus *Balea* have been repeatedly carried across 9,000 km of open sea in the eastern Atlantic Ocean by migrating birds (Gittenberger *et al*., 2006). Species within the *Vertigo gouldii* group in North America may possess ranges exceeding 5,000 km in extent even though their modern ranges were covered by continental ice as recently as 12,000 yr BP (Nekola, Coles & Bergthorsson, 2009). This is not a universal pattern, however, with many Pristilomatidae and Helicodiscidae exhibiting local endemism in the eastern USA (e.g. *Helicodiscus*, *Paravitrea*, *Pilsbryna* and *Polygyriscus*). Comparison of the breeding systems and ecology between large-range *vs* small-range small body-sized species will undoubtedly document important differences. For instance, many locally endemic *Helicodiscus*, *Paravitrea* and *Polygyriscus* species tend to be restricted to highly insular rock talus habitats, perhaps making it easier for their populations to become isolated and speciate.

Because similar analyses have not yet been performed in other regions, it cannot be conclusively stated whether strong scale-dependence is a general phenomenon or is unique to North America terrestrial gastropods. Because a strong inverse correlation between body and range size (Pokryszko & Cameron, 2005; Cameron, Pokryszko & Horsák, 2010, 2012) in combination with an overabundance of small individuals and large species (Nekola *et al*., 2013) exists in the European fauna, it seems likely that scale-dependence also occurs there. Preliminary investigations of the New Zealand fauna (Nekola *et al*., 2013), however, show apparent strong coupling in species richness and individual abundance across the body-size spectrum. Given that this fauna, as well as that of eastern Australia (Stanisic *et al*., 2007, 2010), also harbours many narrow-range endemics of small body size (especially in the Charopidae and Punctidae), self-similarity within these faunas is possible. Yet, the commonness in western Australia of large body-size camaenids demonstrating strong alloptaric replacement with smaller species demonstrating extensive ranges (Solem, 1988; Cameron, 1992) suggests that at least parts of this continental fauna may behave in a fashion similar to that in North America.

Lastly, it is important to point out that at least some of the ‘self-similar’ patterns reported by Finlay *et al*. (2006) are almost certainly not rooted in ecological mechanisms. For instance, S-shaped species-abundance distributions along a rank-abundance axis and power-law species-area relationships have both been shown to be common expectations across a wide variety of complex systems spanning not only the physical, biological and social sciences but also the arts (Nekola & Brown, 2007). As a result, the similarity of these patterns across scales only means that these systems have remained complex across these scales—and no more. Given that complex systems typically demonstrate nesting, with a given system being made up of complex parts, while at the same time being a component of even larger-scale complex systems (Brown, 1994; West, 2006), these findings are to be expected and are likely mathematically trivial.

Because of scale-dependence, no easy mathematical short-cut exists for documenting the North American terrestrial gastropod fauna. It is not only impossible to look at a few sites and be able accurately to assemble continental or most regional scale biodiversity patterns, but it is also equally impossible to deduce the makeup of site faunas given knowledge of the continental or regional pool. This fauna can only be accurately known by looking at many sites spread across all biogeographic regions and then summarizing these data to allow for expression of emergent properties. The only way this can be accurately accomplished is thus through extensive, time consuming and expensive fieldwork.

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REFERENCES

BAUR, B. 1988. Microgeographical variation in shell size of the land snail *Chondrina clienta*. *Biological Journal of the Linnean Society*, **35**: 247–259.

BOUCHET, P. & ROCROI, J.-P. 2005. Classification and nomenclator of gastropod families. *Malacologia*, **47**: 1–397.

BROWN, J.H. 1994. Complex ecological systems. In: *Complexity: metaphors, models, and reality* (G.A. Cowan, D. Pines & D. Melzer, eds), pp. 419–449. Santa Fe Institute Studies in the Science of Complexity, Proceedings Volume XVIII. Addison-Wesley, Reading.

BULMAN, K. 1990. Life history of *Carychium tridentatum* (Risso, 1826) (Gastropoda: Pulmonata: Ellobiidae) in the laboratory. *Journal of Conchology*, **33**: 321–333.

BURCH, J.B. 1962. *The eastern land snails*. W. C. Brown Co., Dubuque, IA.

CAMERON, R.A.D. 1992. Land snail faunas of the Napier and Oscar Ranges, Western Australia: diversity, distribution and speciation. *Biological Journal of the Linnean Society*, **45**: 271–286.

CAMERON, R.A.D., POKRYSZKO, B.M. & HORSÁK, M. 2010. Land snail faunas in Polish forests: patterns of richness and composition in a post-glacial landscape. *Malacologia*, **53**: 77–134.

CAMERON, R.A.D., POKRYSZKO, B.M. & HORSÁK, M. 2012. Forest snail faunas from Crimea (Ukraine), an isolated and incomplete Pleistocene refugium. *Biological Journal of the Linnean Society*, **109**: 424–433.

FINLAY, B.L., THOMAS, J.A., McGAVIN, G.C., FENCHEL, T. & CLARKE, R.T. 2006. Self-similar patterns of nature: insect diversity at local to global scales. *Proceedings of the Royal Society B*, **273**: 1935–1941.

FORSYTH, R.G. 2004. *Land snails of British Columbia. Royal British Columbia Museum handbook*. Royal British Columbia Museum, Victoria.

GITTENBERGER, E., GROENENBERG, D.S.J., KOKSHOORN, B. & PREECE, R.C. 2006. Molecular trails from hitch-hiking snails. *Nature*, **439**: 409.

HENTSCHEL, H.G.E. & PROCACCIA, I. 1984. Relative diffusion in turbulent media: the fractal dimension of clouds. *Physics Review A*, **29**: 1461–1470.

HUBBELL, S.P. 2001. *The unified neutral theory of biodiversity and biogeography. Monographs in Population Biology 32*. Princeton University Press, Princeton, NJ.

HUBRICHT, L. 1985. The distributions of the native land mollusks of the eastern United States. *Fieldiana, New Series*, **24**: 1–191.

McCLAIN, C. & NEKOLA, J.C. 2008. The role of local-scale on terrestrial and deep-sea gastropod body size distributions across multiple scales. *Evolutionary Ecology Research*, **10**: 129–146.

MANDELBROT, B. 1983. *The fractal geometry of nature*. W.H. Freeman, San Francisco.

METCALF, A.L. & SMARTT, R.A. 1997. *Land snails of New Mexico*. New Mexico Museum of Natural History and Science, Albuquerque, New Mexico.

MILNE, B.T. 1988. Measuring the fractal geometry of landscapes. *Applied Mathematics and Computation*, **27**: 67–79.

NEKOLA, J.C. 2003. Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. *Diversity and Distribution*, **9**: 55–71.

NEKOLA, J.C. 2010. Acidophilic terrestrial gastropod communities of North America. *Journal of Molluscan Studies*, **76**: 144–156.

NEKOLA, J.C. in press. Overview of the North American terrestrial gastropod fauna. *American Malacological Bulletin*.

NEKOLA, J.C., BARKER, G.M., CAMERON, R.A.D. & POKRYSZKO, B.M. 2013. Latitudinal variation of body size in land snail populations and communities. In: *Global patterns of body size* (F. Smith & K. Lyons, eds), pp. 62–82. University of Chicago Press, Chicago.

NEKOLA, J.C. & BROWN, J.H. 2007. The wealth of species: ecological communities, complex systems, and the legacy of Frank Preston. *Ecology Letters*, **10**: 188–196.

NEKOLA, J.C. & COLES, B.F. 2010. Pupillid land snails of eastern North America. *American Malacological Bulletin*, **28**: 29–57.

NEKOLA, J.C., COLES, B.F. & BERGTHORSSON, B. 2009. Evolutionary pattern and process in the *Vertigo gouldii* (Mollusca: Pulmonata, Pupillidae) group of minute North American land snails. *Molecular Phylogenetics and Evolution*, **53**: 1010–1024.

NEKOLA, J.C. & WHITE, P.S. 1999. Distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**: 867–878.

NITTMAN, J., DACCORD, G. & STANLEY, H.E. 1985. Fractal growth of viscous fingers: quantitative characterization of fluid instability phenomenon. *Nature*, **314**: 141–144.

PALMER, M.W. 1988. Fractal geometry: a tool for describing spatial patterns in plant communities. *Vegetatio*, **75**: 91–102.

PILSBRY, H.A. 1948. *Land Mollusca of North America (north of Mexico)*. Academy of Natural Sciences of Philadelphia Monograph, 1(1)–2(2).

POKRYSZKO, B.M. 1987. On aphally in the Vertiginidae (Gastrocopta: Pulmonata: Orthurethra). *Journal of Conchology*, **32**: 365–375.

POKRYSZKO, B.M. & CAMERON, R.A.D. 2005. Geographical variation in the composition and richness of forest snail faunas in northern Europe. *Records of the Western Australian Museum, Supplement*, **68**: 115–132.

ROTH, B. & SADEGHIAN, P.S. 2003. Checklist of the land snails and slugs of California. *Santa Barbara Museum of Natural History Contributions in Science*, **3**: 1–81.

SCHILEYKO, A.A. 2006. Treatise on recent terrestrial pulmonate molluscs, Part 13. Helicidae, Pleurodontidae, Polygyridae, Ammonitellidae, Oreohelicidae, Thysanophoridae. *Ruthenica*, **Suppl. 2**: 1765–1906.

SCHILTHUIZEN, M. & LOMBAERTS, M. 1994. Population structure and levels of gene flow in the Mediterranean land snail *Albinaria corrugata* (Pulmonata: Clausiliidae). *Evolution*, **48**: 577–586.

SOLEM, A. 1988. Maximum in the minimum: biogeography of land snail from the Ningbing Ranges and Jeremiah Hills, north-east Kimberly, Western Australia. *Journal of the Malacological Society of Australia*, **9**: 59–113.

STANISIC, J., CAMERON, R.A.D., POKRYSZKO, B.M. & NEKOLA, J.C. 2007. Forest snail faunas from S.E. Queensland and N.E. New South Wales (Australia): patterns of local and regional richness and differentiation. *Malacologia*, **49**: 445–462.

STANISIC, J., SHEA, M., POTTER, D. & GRIFFITHS, O. 2010. *Australian land snails Volume 1: a field guide to eastern Australian species*. Queensland Museum, Brisbane.

TURGEON, D.D., QUINN, J.F., BOGAN, A.E., COAN, E.V., HOCHBERG, F.G., LYONS, W.G., MIKKELSEN, P., NEVES, R.J., ROPER, C.F.E., ROSENBERG, G., ROTH, B., SCHELTEMA, A., THOMPSON, F.G., VECCHIONE, M. & WILLIAMS, J.D. 1998. *Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks*. Edn 2. American Fisheries Society Special Publication 26. Bethesda, MD.

WEST, B.J. 2006. Thoughts on modeling complexity. *Complexity*, **11**: 33–43.

WIENS, J.A. 1989. Spatial scaling in ecology. *Functional Ecology*, **3**: 385–397.

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The distance decay of similarity in biogeography and ecology

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Abstract

Aim Our aim was to understand how similarity changes with distance in biological communities, to use the distance decay perspective as quantitative technique to describe biogeographic pattern, and to explore whether growth form, dispersal type, rarity, or support affected the rate of distance decay in similarity.

Location North American spruce-fir forests, Appalachian montane spruce-fir forests.

Methods We estimated rates of distance decay through regression of log-transformed compositional similarity against distance for pairwise comparisons of thirty-four white spruce plots and twenty-six black spruce plots distributed from eastern Canada to Alaska, six regional floras along the crest of the Appalachians, and six regional floras along the east–west extent of the boreal forest.

Results Similarity decreased significantly with distance, with the most linear models relating the log of similarity to untransformed distance. The rate of similarity decay was 1.5–1.9 times higher for vascular plants than for bryophytes. The rate of distance decay was highest for berry-fruited and nut-bearing species (1.7 times higher than plumose-seeded species and 1.9 times higher than microseeded/spore species) and 2.1 times higher for herbs than woody plants. There was no distance decay for rare species, while species of intermediate frequency had 2.0 times higher distance decay rates than common species. The rate of distance decay was 2.7 times higher for floras from the fragmented Appalachians than for floras from the contiguous boreal forest.

Main conclusions The distance decay of similarity can be caused by either a decrease in environmental similarity with distance (e.g. climatic gradients) or by limits to dispersal and niche width differences among taxa. Regardless of cause, the distance decay of similarity provides a simple descriptor of how biological diversity is distributed and therefore has consequences for conservation strategy.

Keywords
Similarity, spatial dependence, distance decay, biological diversity, boreal forest.

INTRODUCTION

The similarity between two observations often decreases or decays as the distance between them increases, a pattern long recognized in the geographical literature and once called 'the first law of geography' (Tobler, 1970). That early interest in the distance decay of similarity led subsequently to formal analyses of spatial autocorrelation and eventually to the field of geostatistics, a field that has grown tremendously in the last decade (Cressie, 1993).

While ecologists and biogeographers have rarely referred to distance decay *per se*, a negative relationship between distance and similarity is implicit in several ecological and evolutionary phenomena. For example, species turnover along spatial environmental gradients produces a decrease of similarity with distance (e.g. Whittaker, 1975; Cody, 1985). Mass effect (Shmida & Ellner, 1984), source-sink dynamics in metapopulations (Hanski & Gilpin, 1991), and supply side ecology (Roughgarden, Gaines & Pacala, 1987) have stressed the importance of dispersal and therefore distance in explanations

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of population dynamics and community composition (Palmer, 1988). Studies in island biogeography have found a decrease in percent species saturation of oceanic or habitat islands as a function of their distance from a source pool of immigrants (Vuilleumier, 1970; Kadmon & Pulliam, 1993), producing a decrease in the similarity of species lists with distance. Dispersal, migration, and gene flow produce geographic patterns in the distribution of genetic variation and in the distribution of species that result from vicariance and adaptive radiations (Meyers & Giller, 1988; Briggs, 1991), leading to spatially autocorrelated distributional patterns that were described in the early biogeographic literature under the age and area and centre of origin hypotheses (Cain, 1944; Willis, 1922).

These examples suggest two very different causes of biological distance decay. On the one hand, a decay of similarity results from a simple decrease in environmental similarity with distance (e.g. movement along a topographic or climatic gradient). In this case, the underlying explanation is competitive sorting of species with different physiological abilities; composition, at least after sufficient time has elapsed, is predictable from environment. We term this source of biological distance decay the niche difference model.

The second cause of distance decay is that the spatial configuration (the size and isolation of habitats), spatial context (the nature of the matrix surrounding the habitats), and time influence species and gene movement across landscapes. Variation in distance decay rates among landscapes occurs in this case because different landscapes have different resistances to the movement of organisms. Variation in distance decay rates among different species groups will also arise if the groups have different dispersal abilities—in essence, different species will perceive a given spatial configuration of habitats differently. Variation in landscape resistance to movement and in dispersal abilities suggest an interaction between the spatial template and time: the greater the resistance to movement or the less vagile the organism, the greater the amount of time required for the organism to cross a given spatial template. As a result, the nature of the spatial configuration of habitats will affect how long the effects of historic events persists in terms of distributional patterns of species. When time or dispersal are limiting, current environmental conditions will not fully explain species distributions or local composition. We term this source of distance decay the model of temporal and spatial constraint: history and the nature of the spatial template explain species distributions. At large scales of space and time, the imprint of past events has been termed historic biogeography (Schluter & Ricklefs, 1993).

In this paper we explore distance decay as a descriptor of compositional variation. We first discuss scale dependence in the detection of distance decay and develop a conceptual framework for distance decay. We then examine distance decay rates in boreal and montane spruce-fir forests, comparing the rate of similarity decay in several species groups (vascular plants, mosses, species abundance classes, growth form classes, and dispersal classes) across the same set of plots. Finally, we discuss the implications of distance decay perspective for community composition, biogeographical pattern, and conservation.

DISTANCE DECAY OF BIOLOGICAL SIMILARITY: CONCEPTUAL FRAMEWORK

Distance decay and geostatistics

Our approach to the distance decay of similarity is parallel to, but methodologically different from, geostatistical approaches to the analysis of spatial autocorrelation (Cressie, 1993). It is now standard practice to use semi-variograms to characterize the relationship of variance of a parameter to intersample distance or lag (Ripley, 1988), a critical step in the optimal interpolation technique called kriging (Burrough, 1986; Webster & Oliver, 1990). To construct a semi-variogram, variance is calculated by comparing values of the parameter at two locations of known distance apart. The statistic we model here, similarity, is a parallel concept to variance in the sense that it results from comparison of two observations from different locations. In our case the observations consist of species lists; similarity is a complex function of the occurrence of many species (Faith, Minchin & Belbin, 1987). By contrast, variance is calculated for univariate factors (e.g. soil pH, rainfall, or abundance of a single species).

Variance and similarity both measure differences between samples and can be modelled as a function of intersample distance. In this paper, we use linear regression to model that relationship. The intercept of this model is similar to the nugget effect (residual intersample variance as distance decreases to zero) in semi-variograms. The shape of the similarity-distance relationship can be examined for evidence of a range and sill which, in semi-variograms are, respectively, the distance at which variance becomes independent of further increases in distance and the amount of variance at that distance. Regression of similarity against distance has the advantage in our case of producing a direct estimate of the rate of distance decay and thus the rate of composition change through space. One of our purposes is to ask whether species with different dispersal types or growth forms show different rates of compositional change.

Scale dependence and distance decay

Grain, extent and related geostatistical concepts

Observations of distance decay will show scale dependence. Ecologists have divided scale into grain and extent (Allen & Hoekstra, 1991; Weins, 1989). Grain, which is similar to the concept of support or resolution in the geostatistical literature (Odland, 1988; Webster & Oliver, 1990; Cressie, 1993), is the contiguous area over which a single observation is made (e.g. quadrat, plot, or pixel). In this sense it is a special case of support, which is defined as an *n*-dimensional volume within which a linear averaged value of a regionalized value may be computed (Olea, 1991). Spatial extent, called area in the geostatistical literature (Cressie, 1993), is the space over which observations are made.

The grain size or support of samples will effect observed similarities, a phenomenon known as the support effect in the geostatistical literature. Consider two areas with identical species lists. If a small quadrat is sampled from each area, species-area relationships dictate that these quadrats will have only a subset of the possible species and will contain identical species lists only a portion of the time. If we increase grain size, however, species lists will become more complete until, at a grain size that is equivalent to the size of the study areas, all possible species will be contained and the observed similarity will equal the real similarity. If two regions have a similarity greater than zero, small samples, by chance, can have either higher or lower similarity than the real similarity. The distribution of sample scores will vary with the distribution of individuals among species, the spatial pattern of species and individuals, the sampling design, and that component of the species-area relationship that we term the species-grain relationship (Palmer & White, 1994). In general, we expect that the variation in observed similarities among samples will increase as grain size decreases, assuming that the real similarity is a positive value. This effect of change in support or grain size on sample statistics has been well discussed in the geographical literature as the modifiable areal unit problem (Openshaw, 1983). It has generally been found that variation increases as support or grain size decreases.

Although distance decay proposes that similarity decreases with extent, natural periodicities in the environment may cause a lack of distance decay at some scales of observation (Fig. 1). Geostatisticians have treated similar patterns of variance as the problem of non-stationarity (Webster & Oliver, 1990). For example, if extent is only large enough to include a mountain crest and its adjacent valley, distance decay will likely occur as a result of the strong environmental gradient that is present. However, if extent is increased to include the next mountain crest, similarity of community composition will likely increase in relation to the first mountain summit. If extent is increased further still to include a large number of mountain crests and valleys, distance decay will likely re-emerge from either climatic gradients or the presence of dispersal barriers between places with similar environments.

The detection of distance decay requires that the variation due to small grain size or support be less than the variation due to spatial extent. Increasing the grain size or support of a sample will decrease variation, and may allow detection of weak distance decay trends. Alternatively, increasing extent while holding sample grain or support constant may allow identification of distance decay trends because the variation due to distance will be larger than the noise present from small grain size or support. The strongest distance decay relationships should be observed when the variation due to sampling error is minimized (with large sample grains or support) and the variation due to distance decay is maximized (with large sample extents).

A conceptual model for variation in distance decay rates

The rate of distance decay will vary with the strength of environmental gradients and will differ among taxa and between landscapes of different spatial configurations and histories. More formally, we suggest that the rate of decay in biological similarity will be correlated with two characteristics of the environment (environmental distance and the nature of the spatial template) and two characteristics of the organisms under study (niche-breadth and dispersal ability). The effects of each of these factors are discussed below.

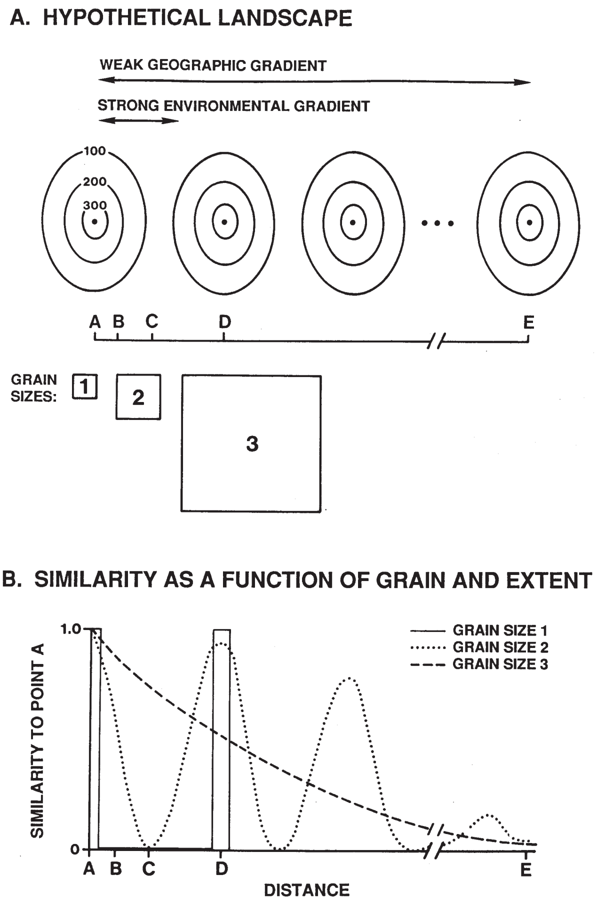


Figure 1 The influence of sample grain and extent on the observation of distance decay. A, A hypothetical landscape with spatial periodicities in similarity controlled by strong environmental gradients (elevation contours); B, the distance decay of similarity as detected by samples of differing grain and extent.

Environmental distance

For a fixed spatial distance, the steeper the rate of environmental change, the more rapid the turnover in species composition and the higher the expected rate of distance decay. Ecologists often have assumed that composition is solely a function of environment (e.g. MacArthur, 1972; Tilman, 1988). For the rate of distance decay to be solely controlled by environmental distance, all species must have access to all appropriate habitats and time must be sufficient to allow competitive interactions to sort species as a function of environment. In essence, this summarizes Beijerinck's Law: everything is everywhere but the environment selects (Saur, 1988). Niche characteristics and competition determine composition.

The spatial template

Characteristics of the spatial template (habitat size, isolation, and the nature of the matrix) will effect the rate of distance decay, all else being equal. The more isolated the habitat, the less efficient dispersal will be. Some species will not locate all available habitats (Huffaker, 1958; Shmida & Ellner, 1984), leading to lower levels of species overlap among sites and higher rates of distance decay. Factors which would effect distance decay rates are: the unfavourability of the matrix (which would affect rates of movement), the favourability of the habitat patches (which would affect size, reproduction, and persistence of the populations), and the presence of corridors or stepping stone connections. In a sense, these measure the resistant to movement of the landscape. The percolation coefficient is an example of a measure of the affect of spatial characteristics on movement. This coefficient represents the permeability of a given landscape to unidirectional organism movement (Gardner *et al*., 1989).

Niche breadth and overlap

The wider the average niche breadth and overlap for a group of organisms, the lower the rate of distance decay which will occur over a fixed amount of environmental distance. Realized niche breadth and overlap may decrease over successional time as species sort along gradients (Werner & Platt, 1976; Christensen & Peet, 1984).

Dispersal ability

Highly vagile species will be less affected by barriers and will be able to locate most or all of the appropriate habitats in a landscape (Bush & Whittaker, 1991; Dzwonko & Loster, 1992) and such dispersal may compensate for low persistence rates (e.g. as suggested by the source-sink population model and the rescue effect, Brown & Kodric-Brown, 1977). More vagile taxa should therefore show lower rates of distance decay over a given landscape. Species with poorer vagilities will be unable to cross barriers, leading to their absence from potential sites (Weddell, 1991), contributing to higher distance decay rates.

DISTANCE DECAY IN SPRUCE-FIR FORESTS

The boreal and montane spruce-fir forests of eastern and northern North America have similar structures over large areas (Cogbill & White, 1991). Two data sets were constructed from published studies of these forests. In the first, the vascular plants and bryophytes of the North American boreal forests were analysed from data in LaRoi (1967) and LaRoi & Stringer (1976). These papers present species lists for nine hectare plots (300 × 300 m) distributed from Newfoundland to Alaska in two community types: upland white spruce forests (thirty-four plots containing 252 vascular plant species and 118 bryophyte species) and lowland black spruce forests (twenty-six plots containing 195 vascular plant species and seventy-nine bryophyte species). Similarity and distances were calculated for all pairwise combinations of plots within these two habitat types (a total of 561 values for white spruce stands and 351 for black spruce stands). These data sets were chosen because they allow us to examine distance decay for relatively homogeneous forests (each of the habitats is dominated by the same tree species throughout) in relatively unbroken topography across a large geographic extent.

The second data set consisted of regional vascular plant lists for the boreal forest and Appalachian montane spruce-fir. While the boreal forest exists in a relatively continuous band from Alaska to Newfoundland, montane spruce-fir is restricted to the highest peaks, with the areas dominated by spruce and fir separated from one another as a series of island-like clusters (Cogbill & White, 1991). Species lists for six boreal and six Appalachian spruce-fir forest regions were compiled from the literature and corrected to a common nomenclatural base (Crandall, 1958; Curtis, 1959; Grigal, 1968; Lakela, 1965; LaRoi, 1967; Maycock, 1961; Maycock & Curtis, 1960; McIntosh & Hurley, 1964; Nicholson, Holway & Scott, 1969; Ohmann & Ream, 1971; Oosting & Billings, 1951; Ramseur, 1960; Siccama, 1974; White, 1982; White & Miller, 1988). Similarity was calculated between all pairwise comparisons of these regions within both groups. This data set has a larger support (each list is a regional flora) than the one from LaRoi (1967).

We addressed several questions using these data sets: Does community similarity decrease with distance and, if so, what statistical model best describes this relationship? Do isolated habitats (Appalachian mountain summits and slopes) have a higher rate of distance decay than more contiguous ones (boreal forest)? Do data sets with larger grain size or support (the regional floristic lists), because they have more complete species lists, have higher overall similarities and lower distance decay rates than data sets with smaller grain size or support (boreal forest plot data)? Do wind-dispersed species (bryophytes and wind-dispersed vascular plants) have higher rates of distance decay than less vagile species? Do taller and dominant species (which may have broader environmental tolerances) have lower distance decay rates than smaller and understory species?

We addressed the questions about dispersal, dominance, and frequency by using data from a single set of plots, thus holding spatial configuration and environmental distance constant for all groups compared. The distance decay rates for bryophytes and vascular plants were compared with data from both white spruce and black spruce plots. Comparisons among vascular plant classes were made with data from white spruce plots only. The following paragraphs describe the questions addressed with white spruce plots in more detail.

The contribution of species in different frequency classes to distance decay rate

Species were divided into three classes: species found on one to three plots (139 species), four to fourteen plots (eighty-four species), and fifteen to thirty-four plots (twenty-nine species). We also summed the last two classes to produce a fourth class, those species found on four to thirty-four plots (113 species). Common species are shared by many plots and therefore decrease the overall rate of distance decay (in the extreme, for species found in all plots, intersample similarity is always 1.0 and is independent of distance). Species found in only one plot would lower the similarity between any two plots but would not contribute to a spatial trend in similarity at this scale (similarity based on these species would be zero at all distances). We therefore hypothesized that species with intermediate frequency would show the steepest rate of distance decay.

Variation in distance decay rate among growth forms

Casual observation suggested that trees in the boreal forest have wider geographic distributions than plants with other growth forms. This suggests wider environmental tolerances and a lower distance decay rate. We therefore investigated whether there were systematic differences in distance decay rates for plants with different growth forms. Species were divided into five classes: trees (nineteen species), tall shrubs (twenty-two species), low shrubs (thirty-five species), subshrubs (sixteen species), and herbs (160 species). We also compared the bryophyte data to the data from these vascular plant growth form classes.

Variation in distance decay rate among dispersal classes

More vagile species should have lower distance decay rates than less vagile species. Species were divided into three major and five total dispersal classes: wind dispersed species (a total of sixty-three species, comprised of two subcategories, twenty-eight spore/microseed species and thirty-five plumose seed species), berry-fruited/nut-bearing species (sixty-four species), and species with other dispersal types (125 species). We also compared the bryophyte data to the data from these vascular plant dispersal classes.

Similarity index

We used Jaccard's Index (Mueller-Dombois & Ellenberg, 1974) due to its simplicity, its widespread use, its accessibility through common statistical packages, and its use of presence/absence data. We chose a presence-absence metric because it represents a more conservative measure of community similarity than ones based on species abundance data which are more sensitive to disturbance and local environmental differences.

Data analysis

For the largest empirical data sets (white spruce and black spruce stands of the boreal forest), similarity and distance were calculated and then log-transformed. Linear regression was used to calculate distance decay rates or all four combinations of these transformed and untransformed variables. Inspection of the plots and regression residuals were used to determine which formulation most closely approximated a linear relationship over most intersample distances.

Because the values in the matrices (561 for white spruce stands, 351 for black spruce stands) are not independent, randomization tests were used to establish the significance of regression models and to make comparisons of distance decay rates among various subsets of the data. Mantel tests with 10,000 replications (Jackson & Somer, 1989) were used to estimate significance of each model (Manly, 1991).

The comparison of distance decay rates among various subsets of the data was done with a randomization test developed by Blake Weiler of the Ecology Curriculum at the University of North Carolina at Chapel Hill. Our objective was to compare the slopes of the distance decay relationship between two data subjects (e.g. trees *v.* herbs) across all plots. The method followed this outline: (1) all non-zero similarities based on the two data subsets to be compared were assembled (we used non-zero values because we were interested in the slope of the distance decay relationship over those distances that have a measured similarity—presumably similarity falls to zero at some distance and then is independent of distance thereafter); (2) after testing the difference in mean similarity for the two data subsets, similarity values within each subset were rescaled to a common mean (we sought to test the difference in slopes of the distance decay relationships independent of differences in the means); (3) for each pair of sites, the two similarity values (one for each of the two data subsets to be compared) were randomly reassigned to the two data subsets; (4) after this randomization had been carried out for all pairs of sites, linear regression was used to determine the slope of the distance decay relationship for each of the randomized subsets; (5) step four was repeated to produce 10,000 values for the slope of the distance decay relationship for randomized subsets; (6) finally, the absolute difference between the slopes in each of the 10,000 randomizations was compared to the difference between the observed slopes based on the original data (and thus the true assignments to data subset categories) and we calculated how many times (out of 10,000 trials) randomization produced a difference in slope between the subsets that was at least as great as the observed difference in slope based on the original data. If correct assignment to data categories is significant (if the categories are indeed different in slope), then the observed difference should exceed the randomized differences a high percentage of the time. We used this percentage as the *P* value for our tests.

RESULTS

Distance decay in spruce-fir forests

In all data sets except for rare species in white spruce stands, similarity decreased significantly with distance (Figs 2–6, Table 1). The most linear relationship and the most heteroscedastic regression residuals were found in models that used the log transformation of similarity and untransformed distance. A semi-log model was thus used in all of the regression models presented here. This implies an exponential rate of distance decay. For the boreal forest plot data, the rate of similarity decay ranged from -0.17 (black spruce bryophytes; units are in ln (similarity) per 1000 km of distance) to -0.55 (white spruce vascular plants of intermediate frequency) and r^2 values ranged from 0.24 (black spruce bryophytes) to 0.71 (common vascular plants on white spruce plots). For the regional floras, the rate of similarity decay ranged -0.25 (boreal forest, $r^2 = 0.54$) and -0.67 (Appalachian montane forest, $r^2 = 0.80$). All of these relationships are fit well by a straight line in log-linear space (Figs 2–6), with no obvious sill (i.e. no distance at which the data imply a change of slope for the regression). Our closest observations are not close enough for a detailed analysis of the intercept value for the regressions, which is analogous to the nugget effect in semi-variograms, although we make a few comments on that parameter below.

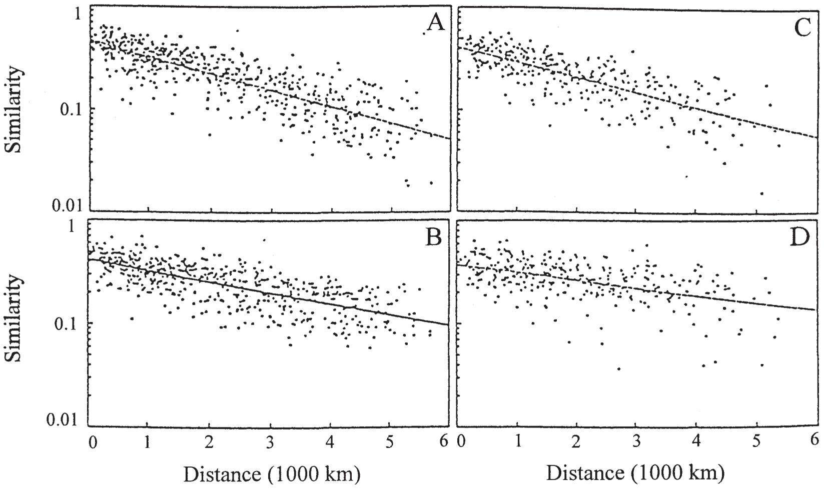


Figure 2 The log of similarity plotted against distance for all pairwise comparisons of plots sampled across the boreal forest based on data in LaRoi (1967) and LaRoi & Stringer (1976). A, Vascular plants in thrity-four white spruce stands; B, bryophytes in thirty-four white spruce stands; C, vascular plants in twenty-six black spruce stands; D, bryophytes in twenty-six black spruce stands.

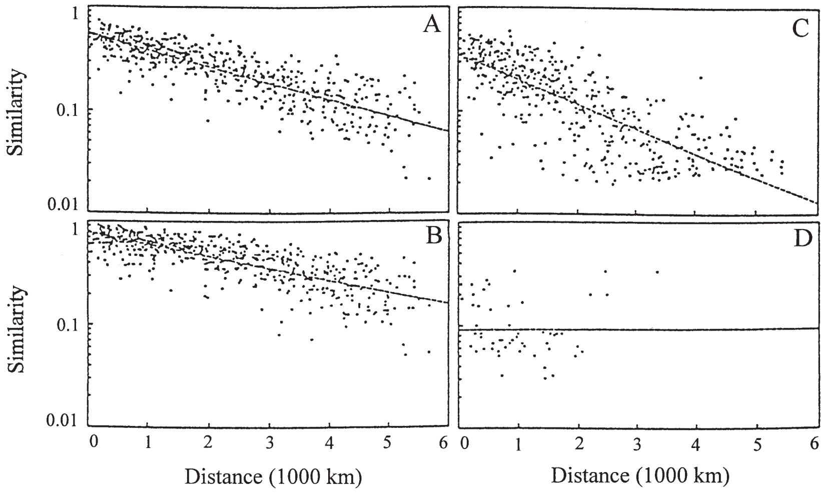


Figure 3 The log of similarity plotted against distance for species frequency classes (white spruce stands only; data from LaRoi, 1967). A, Vascular plants found in four or more plots; B, vascular plants found in fifteen to thirty-four plots; C, vascular plants found in four to fourteen plots; D, vascular plants found in three or fewer plots.

The effect of frequency, growth form, dispersal type, and habitat isolation on distance decay rates

Species frequency

When rare species (those occurring in three or less of the 34 white spruce plots) were eliminated from the data set, the rate of distance decay was unaffected (Fig. 3A; Table 1), but similarities were generally higher, the intercept was closer to unity (complete similarity at a distance of 0), and the r^2 value was higher. Thus, rare species lower overall similarity but do not affect the rate of distance decay. As might be expected from this analysis, the rare species themselves showed no decay of similarity as a function of distance (Fig. 3B).

The species occurring in four or more plots were divided into two groups: common species (fifteen or more plots) and intermediate species (four to fourteen plots). The common species had a higher intercept value than intermediate species and a rate of distance decay (-0.27) that was only one half as great as the rate for intermediate species (-0.55) (Fig. 3C–D; Table 1).

The influence of rare species can also be seen by comparing distance decay rates for regional floras (Fig. 6) with those for plot data (Fig. 2). Both include data taken over the geographic extent of boreal forest, but the floristic lists include rare species that are at their range limits at each location, whereas the plots are less likely to sample species that are very rare in the landscape as a whole. The fuller regional species lists (and larger support) of the floristic data set lowers the observed rate of similarity loss per unit distance. In a sense, the larger support reduces the observed rarity of species. Thus, the rate of distance decay for boreal forest plot data was 1.5 times higher than that for boreal forest floristic lists across the same geographical extent (Table 1).

Growth form

In the white spruce plots, herbs had 1.7–2.1 times higher distance decay rate than woody plant classes ($P < 0.005$–0.0001; Tables 1 and 2, Fig. 4). The higher distance decay rate for the smallest vascular plants was reversed for the contrast between vascular plants and bryophytes: herbs had 1.6 times the rates for bryophytes in the same plots (Fig. 2, Table 1). Interestingly, bryophytes had similar rates of distance decay to tall woody

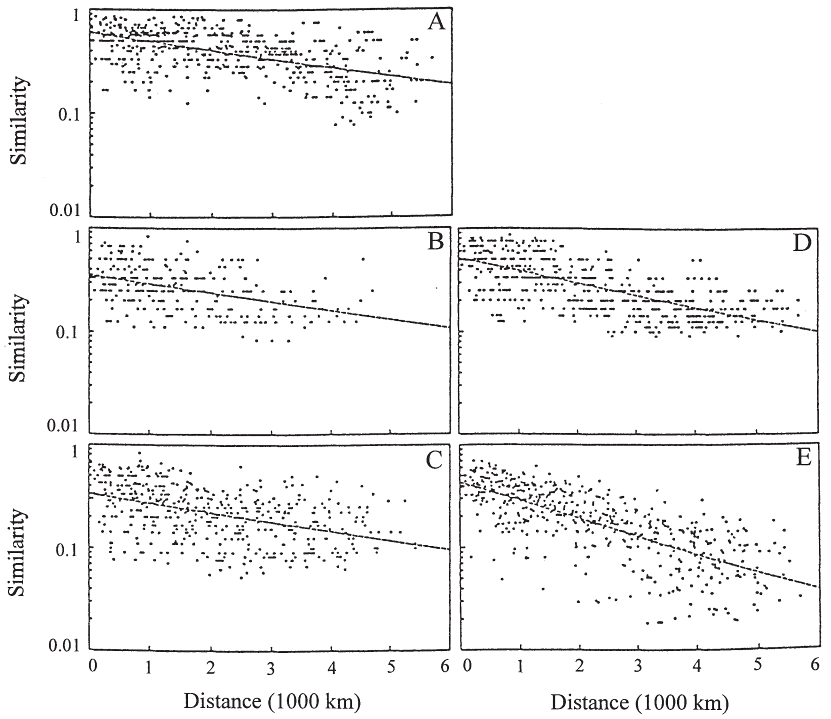


Figure 4 The log of similarity plotted against distance for growth form classes (white spruce stands only; data from LaRoi, 1967). A, Trees; B, tall shrubs; C, low shrubs; D, subshrubs; E, herbs.

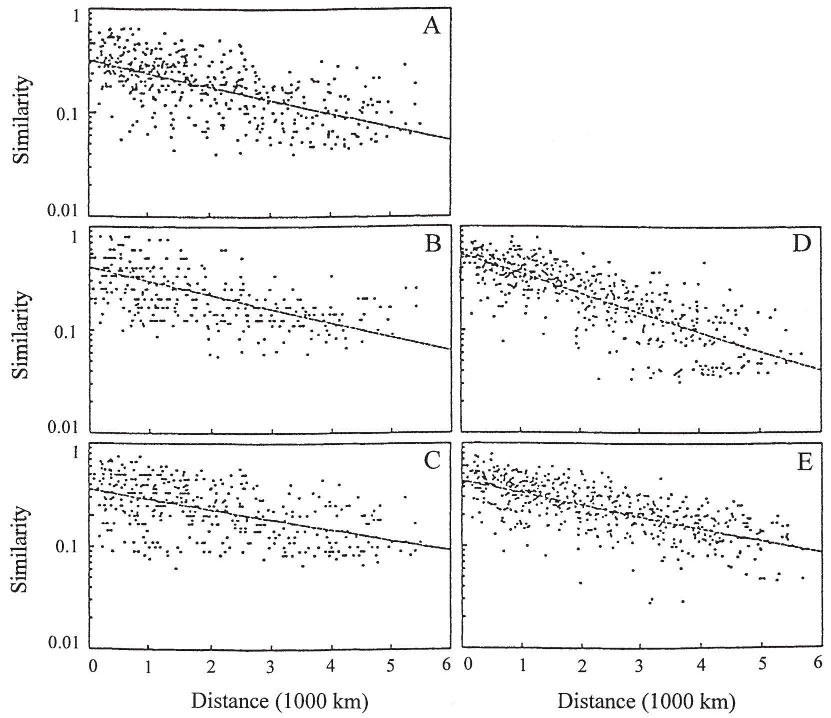


Figure 5 The log of similarity plotted against distance for dispersal classes (white spruce stands only; data from LaRoi, 1967). A, Wind-dispersed species; B, species with plumose seeds; C, species with spores or microscopic seeds; D, species with nuts or fleshy berries; E, species with other types of seeds.

plants on the same plots; they also had similar rates to wind-dispersed vascular plants (see below). Vascular plants as a group had 1.5 (white spruce plots) and 1.9 (black spruce plots) times higher distance decay rates than bryophytes of the same plots (comparisons significant at the $P < 0.001$ level; Table 1).

Dispersal type

For vascular plants on white spruce plots, berry-fruited and nut-bearing species had nearly twice the rate of distance decay shown by spore/microseed and plumose seed species (-0.43 *v.* -0.23 and -0.25, $P < 0.001$; Tables 1 and 2, Fig. 5B, C, and

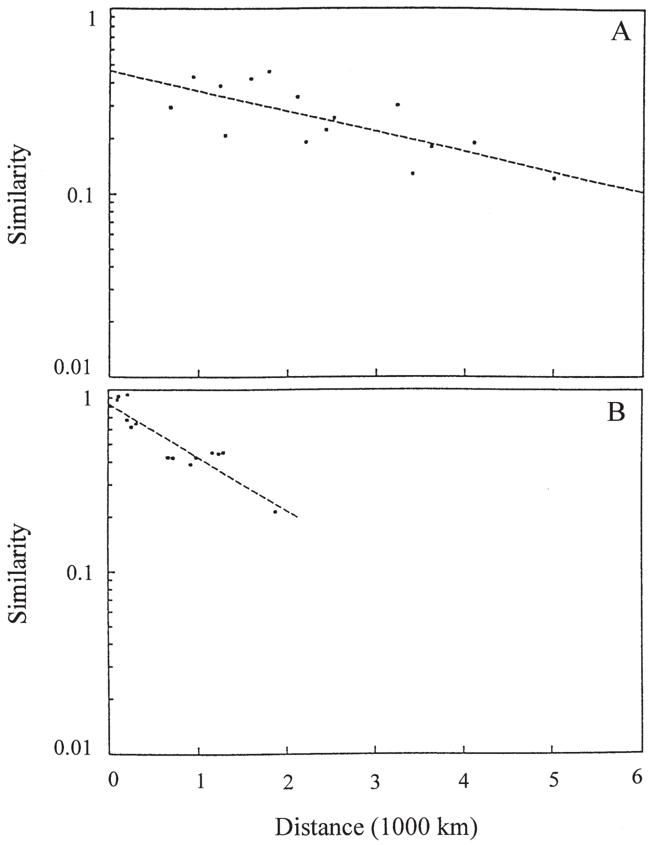


Figure 6 The log of similarity plotted against distance for all pairwise comparisons of vascular plant floras from six regions across the northern boreal forest [data modified from Curtis (1959), Grigal (1968), Lakela (1965), LaRoi (1967), Maycock (1961), Maycock & Curtis (1960) and Ohmann & Ream (1971)] and six areas along the crest of the Appalachian mountains [data modified from Crandall (1958), LaRoi (1967), McIntosh & Hurley (1964), Nicholson, Holway & Scott (1969), Oosting & Billings (1951), Ramseur (1960), White (1982)]. A, Boreal spruce-fir forests; B, Appalachian spruce-fir forests.

Table 1 Regression statistics for the decay of similarity with distance in spruce-fir data sets. The sample size (*n*) is the number of similarity values and distances in each matrix. The number of plots or areas are as follows: white spruce plots, 34; black spruce plots, 26; boreal spruce-fir areas, 6; Appalachian montane spruce-fir areas, 6. For the three data subsets of the white spruce plots, the sample size is sometimes lower than 561 because of the removal of plot pairs with a similarity of zero. Intercepts are in units of ln(similarity). Slope values are in units of ln(similarity) per 1000 km distance.

Data set	Species	*n*	Intercept	Slope	r^2	*P*
White spruce vascular plants	252	561	−0.75	−0.37	0.67	0.0001
White spruce bryophytes	118	561	−0.87	−0.25	0.53	0.0001
Black spruce vascular plants	195	351	−0.88	−0.33	0.57	0.0001
Black spruce bryophytes	70	351	−0.98	−0.17	0.24	0.0001
Data subsets (white spruce plots only)						
Frequency class:						
4–34 plots	113	561	−0.57	−0.37	0.71	0.0001
15–34 plots	29	561	−0.24	−0.27	0.59	0.0001
4–14 plots	84	467	−1.04	−0.55	0.66	0.0001
1–3 plots	139	63	−2.40	−0.006	0.00	n.s.
Growth form:						
Trees	19	555	−0.51	−0.19	0.30	0.0001
Tall shrubs	22	271	−1.21	−0.20	0.17	0.0001
Low shrubs	35	472	−1.09	−0.21	0.20	0.0001
Subshrubs	16	528	−0.66	−0.28	0.45	0.0001
Herbs	160	554	−0.84	−0.40	0.52	0.0001
Dispersal class:						
Wind	63	485	−1.14	−0.29	0.38	0.0001
Plumose	35	329	−1.09	−0.25	0.31	0.0001
Spore/microscopic	28	408	−1.02	−0.23	0.28	0.0001
Fleshy fruits, nuts	64	532	−0.62	−0.43	0.62	0.0001
Other	125	561	−0.84	−0.27	0.48	0.0001
Boreal forest regions	250	15	−0.76	−0.25	0.54	0.0039
Appalachian spruce-fir	226	15	−0.18	−0.67	0.80	0.0018

Table 2 Significance levels for differences in slopes for the growth form and dispersal classes.

A. Growth form	Tall shrubs	Low shrubs	Subshrubs	Herbs
Trees	0.05	0.05	0.0001	0.0001
Tall shrubs		(0.18)	0.01	0.005
Low shrubs			0.005	0.0001
Subshrubs				0.0001

B. Dispersal class	Plumose	Spore/micro.	Fleshy	Other
Wind	(0.0649)	0.0001	0.0001	0.004
Plumose		(0.645)	0.0001	(0.79)
Spore/microseeded species			0.0001	(0.306)
Fleshy fruited, nut-bearing species				0.0001

E). Berry-fruited and nut-bearing species had the highest r^2 values among the dispersal types (Table 1). These data suggest that wind-dispersed species are both more widely dispersed and more variable in their occurrences. Bryophytes had similar distance decay rates to spore/microseeded and plumose seeded vascular plants on the same plots (Table 1).

Habitat isolation

Appalachian forest communities had a rate of similarity decay 2.7 times that observed for the continuous northern boreal forest (Fig. 6, Table 1).

DISCUSSION

Form of the distance decay model

In the geographic literature, a distance effect on the interaction between human populations has been modelled with a power or gravity function (Bennett & Gade, 1979):

$$I = A^{*}d^{-c}$$

where I is interaction, A is a constant, d is distance, and c is the friction coefficient (correlated with technologies for communication and barriers to movement over a given distance). This model implies an ever decreasing effect of a unit distance as distance becomes larger and a linear relationship only under double log transformation.

The finding that a semi-log model showed the most linear relationships suggests similarity could in fact be related to distance through an exponential model:

$$S = S_0 e^{-cd}$$

where S is similarity at distance d; S_0 is initial similarity or similarity at distance 0; c is a constant for the rate of distance decay; and d is distance. Exponential decay models have previously been used in biogeography and ecology to model plant dispersal (Okubo & Levin, 1989) and to describe the relationship between spatial distance and floristic similarity in the Galapagos (Preston, 1962). The exponential model, in contrast to the power model, implies a constant proportional change in similarity per unit distance. This is attractive because it suggests that the processes underlying the distance decay relationship vary only with environmental distance, spatial configuration, and organism attributes but not with distance independent of these factors. Hubbell (1995) has produced a simulation model of species colonization and extinction that results in just such a decrease in similarity with distance.

Variation in distance decay rates

The rate of distance decay varied among species groups in expected ways: on the same plots, spore/microseeded and plumose species had lower rates of distance decay than larger fruited species. Trees, other woody plants, wind dispersed, and more frequent species raised overall similarity and lowered the rate of distance decay, while herbaceous plants, heavy fruited, and less frequent species lowered the rate. Further, the more fragmented montane forests dominated by the same genera of trees as the boreal forest had much higher rates of distance decay than the more contiguous boreal forest itself. We will consider alternative explanations for these patterns.

While it can be suggested that due to their small propagule size bryophytes should be more vagile and possess wider ranges along geographic gradients than vascular plant species (Saur, 1988), other explanations are reasonable. The smaller size of bryophytes compared to vascular plants may allow persistence in microsites not available to vascular plants, thus increasing geographic range. Bryophytes may have broader physiological tolerances and higher persistence rates because they can cycle rapidly between active and dormant states.

In light of these possibilities, it is interesting to note that herbs, which are the smallest vascular plants (thus sharing, with bryophytes, environments that have less fluctuating air temperatures), showed the highest rates of similarity loss with distance of all groups. By contrast, wind-dispersed vascular plants had very similar rates of distance decay to bryophytes on these plots regardless of plant stature. Tall vascular plants had as low or lower distance decay rates than bryophytes.

In terms of the comparison of wind and non-wind dispersed species, dispersal type could be correlated with other traits that influence the rate of geographic turnover. For example, wind-dispersed species could have wider niche breadth (as has been argued for early successional species generally), thus showing a lower rate of distance decay. On the other hand, wind-dispersed species often have small seeds and may therefore have a lower probability of establishment from a given dispersal event, particularly in undisturbed forest studies here (i.e. the probability of establishment in late successional stands could be correlated with seed size). It is unclear how this would influence distance decay; a simple expectation is that it would tend to make similarity more variable at any distance.

The higher rate of distance decay in the Appalachian montane spruce-fir forests could be due to less efficient dispersal among fragmented habitats, but it could also be the result of history (the southern and northern Appalachian spruce-fir forest may have had access to different refugial populations after climatic warming started 15,000 years BP) and/or steeper rate of environmental change with distance. In terms of environmental distance, montane spruce-fir forests have very similar growing season temperatures across the wide range of latitudes covered in the data set (a mean July temperature of 17°C is correlated with their lower elevational boundaries), but are exposed to increasingly low winter temperatures northward (Cogbill & White, 1991).

Sorting out the relative importance of environment and niche-based explanations from spatial configuration and dispersal-based ones is a difficult challenge. Explanations of species composition based on environmental factors and competition are old ones in ecology. However, explanations based on history and dispersal have also been proposed from the beginning. Gleason (1923) suggested that in the Midwest passive dispersal of propagules was the major factor explaining community composition. Palmgren (1926) found that many plant species of the Åland Archipelago, Finland, were absent from seemingly suitable sites, and suggested that dispersal limitation was responsible for this pattern.

When species do not disperse to all appropriate sites, composition will be constrained by the spatial configuration of sites and dispersal abilities of species. At one extreme (if all species had the same dispersal abilities), community composition would be a stochastic subset of the species which can occupy that habitat. Shmida & Ellner (1984) and Shmida & Wilson (1985) have shown how such conditions may lead to the coexistence of co-competitive species in a landscape, which are allowed to co-exist only because populations are spatially separated from each other at any given moment. At the other extreme (if species have a graded series of dispersal abilities), community composition at each location would be a nested subset (varying with habitat isolation) of the full species list. Hierarchical nesting of species lists has been much discussed in the context of habitat area and area-sensitive species (Patterson, 1987); similarly, there may be isolation-sensitive species. Presences explained not by local environment but by continued dispersal has been termed mass effect (Shmida & Wilson, 1985); here we add that absences can be the result, not of local environment, but of dispersal limitations and of stochastic patterns of original colonizing populations (e.g. the imprint of initial refuge competition and migration routes).

Regardless of whether we can evaluate causes, the decay of similarity with distance is a relatively simple descriptor of variation in species composition and has consequences for how we conserve biological diversity. Whether because of environmental distance decay or spatial and historical factors, the distance decay paradigm suggests a natural world that is, at some scales, everywhere unique. Distance decay rates describe the rate of turnover that underlies this uniqueness.

Simberloff & Abele (1970) argued that the theory of island biogeography was silent on preserve design; that is, this theory could not be used to argue whether one large area would have more species than several smaller areas that summed to the same total area. They suggested that the critical factor was the degree of overlap (i.e. the similarity) among the smaller areas. Shafer (1990) showed that whether one area or several small areas of the same total area had more species or not was dependent on two factors: the slope of the log(species)-log(area) relationship and the similarity among the smaller areas. We add here that if the smaller areas (which are by definition non-contiguous and thus spatially dispersed compared to one contiguous area) are more different from one another as a function of the distance between them (see also Palmer & White, 1994), then the decay of similarity with distance is a central explanation of why some investigators (e.g. Stohlgren & Quinn, 1991) find that smaller dispersed conservation areas collectively have more species than large conservation areas. In essence, conservation strategy requires both grain size for population persistence (Shoenwald-Cox, 1983; Newmark, 1987) and spatial extent (for capturing areas dissimilar to one another). The SLOSS (single large or several small) debate can never be resolved because size (grain) and subdivision (extent) maximize different aspects of how biological diversity is distributed. The distance decay of similarity, in this sense, provides a metric and a conceptual base for such efforts as GAP analysis that seek to identify habitats and species left out of existing conservation areas (Davis *et al*., 1990).

REFERENCES

Allen, T.F.H. & Hoekstra, T.W. (1991) Role of heterogeneity in scaling of ecological systems under analysis. *Ecological heterogeneity* (ed. by J. Kolasa and S.T.A. Pickett), pp. 47–68. Ecological Studies 86. Springer-Verlag, New York.

Bennett, D.G. & Gade, O. (1979) *Geographic perspectives in migration research*. University of North Carolina at Chapel Hill Department of Geography Studies in Geography, Number 12.

Briggs, J.C. (1991) Historical biogeography: the pedagogical problem. *J. Biogeogr.* **18**, 3–6.

Brown, J. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.

Burrough, P.A. (1986) *Principles of geographical information systems for land resources assessment*. Oxford University Press, New York.

Bush, M.B. & Whittaker, R.J. (1991) Cracked: colonization patterns and hierarchies. *J. Biogeogr.* **18**, 341–356.

Cain, S.A. (1944) *Foundations of plant geography*. Hafner Publishing Co., New York.

Christensen, N.L. & Peet, R.K. (1984) Secondary forest succession on the North Carolina Piedmont. *Forest succession: concepts and* *application* (ed. by D.C. West, H.H. Shugart and D.B. Botkin), pp. 230–245. Springer-Verlag, New York.

Cody, M.L. (1985) Towards a theory of continental species diversities. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 214–257. Harvard University Press, Cambridge, Mass.

Cogbill, C.V. & White, P.S. (1991) The latitude-elevation relationship for Appalachian spruce-fir. *Vegetatio*, **94**, 153–175.

Crandall, D.L. (1958) Ground vegetation patterns of the spruce-fir area of the Great Smoky Mountains National Park. *Ecol. Monogr.* **28**, 337–360.

Cressie, N.A. (1993) *Statistics for spatial data*. John Wiley & Sons, New York.

Curtis, J.T. (1959) *The vegetation of Wisconsin*. University of Wisconsin Press, Madison.

Davis, F.W., Stoms, D.M., Estes, J.E., Scepan, J. & Scott, J.M. (1990) An information systems approach to the preservation of biological diversity. *Int. J. Geogr. Info. Syst.* **4**, 55–78.

Dzwonko, Z. & Loster, S. (1992) Species richness and seed dispersal to secondary woods in southern Poland. *J. Biogeogr.* **19**, 195–204.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, **69**, 57–68.

Gardner, R.H., O'Neill, ??, Turner, M.G. & Dale, V.H. (1989) Quantifying scale-dependent affects of animal movement with simple percolation models. *Landscape Ecol.* **3**, 217–227.

Gleason, H.A. (1923) The vegetation history of the middle west. *Ann. Assoc. Am. Geogr.* **12**, 39–85.

Grigal, D.F. (1968) *The relationship between plants communities and soils in northeastern Minnesota*. PhD Dissertation, University of Minnesota, Minneapolis.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linn. Soc.* **42**, 3–16.

Hubbell, S.P. (1995) Towards a theory of biodiversity and biogeography on continuous landscapes. *Preparing for global change: a midwestern perspective* (ed. by G.R. Carmichael, G.E. Folk and J.L. Schnoor), pp. 173–201. Academic Publishing bv, Amsterdam.

Huffaker, C.B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, **27**, 343–383.

Jackson, D.A. & Somer, K.M. (1989) Are probability estimates from the permutation model of Mantel's test stable? *Can. J. Zool.* **67**, 766–769.

Kadmon, R. & Pulliam, H.R. (1993) Island biogeography: effect of geographical isolation on species composition. *Ecology*, **74**, 977–981.

Lakela, O. (1965) *A flora of northeastern Minnesota*. University of Minnesota Press, Minneapolis.

LaRoi, G.H. (1967) Ecological studies in the boreal spruce-fir forests of the North American taiga. I. Analysis of the vascular flora. *Ecol. Monogr.* **37**, 229–253.

LaRoi, G.H. & Stringer, M.H. (1976) Ecological studies in the boreal spruce-fir forests of the North American taiga. II. Analysis of the bryophyte flora. *Can. J. Bot.* **54**, 619–643.

MacArthur, R.H. (1972) *Geographical ecology*. Harper and Row, New York.

Manly, B.F.J. (1991) *Randomization and Monte Carlo methods in biology*. Chapman and Hall, New York.

McIntosh, R.P. & Hurley, R.T. (1964) The spruce-fir forests of the Catskill Mountains. *Ecology*, **45**, 314–326.

Maycock, P.F. (1961) Botanical studies on Mont St. Hilaire, Rouville County, Quebec. *Can. J. Bot.* **39**, 1293–1325.

Maycock, P.F. & Curtis, J.T. (1960) The phytosociology of boreal conifer-hardwood forests of the Great Lakes region. *Ecol. Monogr.* **30**, 1–35.

Meyers, A.A. & Giller, P.S. (1988) Process, pattern, and scale in biogeography. *Analytical biogeography* (ed. by A.A. Meyers and P.S. Giller), pp. 3–12. Chapman and Hall, New York.

Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. John Wiley and Sons, New York.

Newmark, W.D. (1987) A land-bridge perspective on mammalian extinctions in western North American parks. *Nature*, **325**, 430–432.

Nicholson, S., Holway, J.G. & Scott, J.T. (1969) *A floristic comparison of undisturbed spruce-fir forests of the Adirondacks with four other regions*. Atm. Sci. Res. Center, State U. of N.Y. at Albany. Rept. 92.

Odland, J. (1988) *Spatial autocorrelation*. SAGE Publications, Newbury Park, California.

Ohmann, L.F. & Ream, R.R. (1971) Wilderness ecology: virgin plant communities of the Boundary Waters Canoe Area. *North Central For. Exp. Sta. Rept.* NC-63. St. Paul, Minnesota.

Okubo, A. & Levin, S.A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, **70**, 329–338.

Olea, R.A. (1991) *Geostatistical glossary and multilingual dictionary*. Oxford University Press, Oxford, England.

Oosting, H.J. & Billings, W.D. (1951) A comparison of virgin spruce-fir in the northern and southern Appalachian systems. *Ecology*, **32**, 84–103.

Openshaw, S. (1983) *The modifiable areal unit problem*. Concepts and Techniques in Modern Geography No. 38. Geobooks, Norwich, England.

Palmer, M.W. (1988) Fractal geometry: a tool for describing spatial pattern of plant communities. *Vegetatio*, **75**, 91–102.

Palmer, M.W. & White, P.S. (1994) Scale dependence and the species-area relationship. *Am. Nat.* **144**, 717–740.

Palmgren, A. (1926) Chance as an element in plant geography. *Proceedings of the International Congress of Plant Sciences, Ithaca, New York* (ed. by B.M. Duggar), pp. 591–602. George Banta Publishing Company, Menasha, Wisconsin.

Patterson, B.D. (1987) The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* **1**, 323–334.

Preston, F.W. (1962) The canonical distribution of commonness and rarity: parts I and II. *Ecology*, **43**, 185–215; 410–432.

Ramseur, G.S. (1960) The vascular flora of the high mountain communities of the southern Appalachians. *J. Elisha Mitchell Sci. Soc.* **76**, 82–112.

Ripley, B.D. (1988) *Statistical inference for spatial processes*. Cambridge University Press, Cambridge.

Roughgarden, J., Gaines, S.D. & Pacala, S.W. (1987) Supply side ecology: the role of physical transport processes. *Organization of communities: past and present* (ed. by J.H.R. Gee and P.S. Giller), pp. 491–518. Blackwell Scientific, Oxford.

Saur, J.D. (1988) *Plant migration*. University of California Press, Berkeley.

Schluter, D. & Ricklefs, R.E. (1993) Species diversity: an introduction to the problem. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 1–10. University of Chicago Press, Chicago.

Schoenwald-Cox, C. (1983) Guidelines to management: a beginning attempt. *Genetics and conservation* (ed. by C. Schoenwald-Cox, S.M. Chambers, B. MacBryde and W.L. Thomas), pp. 414–446. Benjamin/Cummings Publishing, New York.

Shafer, C. (1990) *Nature reserves: Island theory and conservation practice*. Smithsonian Institute Press, Washington, DC.

Shmida, A. & Ellner, S. (1984) Coexistence of plant species with similar niches. *Vegetatio*, **58**, 29–55.

Shmida, A. & Wilson, M.V. (1985) Biological determinant of species diversity. *J. Biogeogr.* **12**, 1–20.

Siccama, T.G. (1974) Vegetation, soil, and climate on the Green Mountains of Vermont. *Ecol. Monogr.* **44**, 325–349.

Simberlof, D.S. & Abele, L.G. (1976) Island biogeography and conservation practice. *Science*, **191**, 285–286.

Stohlgren, T.J. & Quinn, J.F. (1991) Evaluating the contribution of northern California National Park areas to regional biodiversity. *Proceedings of the Symposium on Biodiversity of Northwestern California*, 226–232.

Tilman, D. (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton.

Tobler, W.R. (1970) A computer movie simulating urban growth in the Detroit region. *Econ. Geogr.* **46**, 234–240.

Vuilleumier, F. (1970) Insular biogeography in continental regions. 1. The northern Andes of South America. *Am. Nat.* **104**, 378–388.

Webster, R. & Oliver, M.A. (1990) *Statistical methods in soil and land resource survey.* Oxford University Press, Oxford.

Weddell, B.J. (1991) Distribution and movement of Columbian ground squirrels (*Spermophilus columbianus* (Ord)): are habitat patches like islands? *J. Biogeogr.* **18**, 385–394.

Weins, J.A. (1989) Spatial scaling in ecology. *Funct. Ecol.* **3**, 385–397.

Werner, P.A. & Platt, W.J. (1976) Ecological relationships of co-occurring Goldenrods (Solidago: Compositae). *Am. Nat.* **110**, 959–971.

White, P.S. (1982) *The flora of the Great Smoky Mountains National Park: an annotated checklist of the vascular plants and a review of previous floristic work*. USDI, National Park Service, Southeast Regional Office, Res./Resource Manage. Rept. SER-55.

White, P.S. & Miller, R.I. (1988) Topographic models of vascular plant richness in the southern Appalachian high peaks. *J. Ecol.* **76**, 192–199.

Whittaker, R.H. (1975) *Communities and ecosystems*. MacMillan Publishing, New York.

Willis, J.C. (1922) *Age and area: a study in geographical distribution and origin of species*. Cambridge University Press, Cambridge.

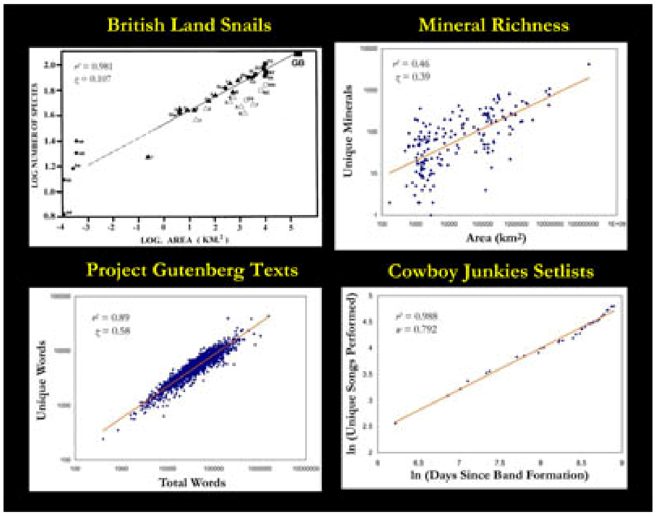
BIOSKETCHES

Jeffrey C. Nekola received his Ph.D. in Ecology from the University of North Carolina at Chapel Hill in 1994. His previous work includes the documentation of the effect of colonization history on community composition and the spatial distribution of rare vascular plant and butterfly species within and between isolated habitats. He is currently investigating species-rich land snail communities at scales ranging from 1 to 10,000 m.

Peter S. White is Professor, Department of Biology, University of North Carolina at Chapel Hill and Director of the North Carolina Botanical Garden. His work ranges from studies of biogeography, rare species, exotic species invasions, and species richness to vegetation dynamics and disturbance.

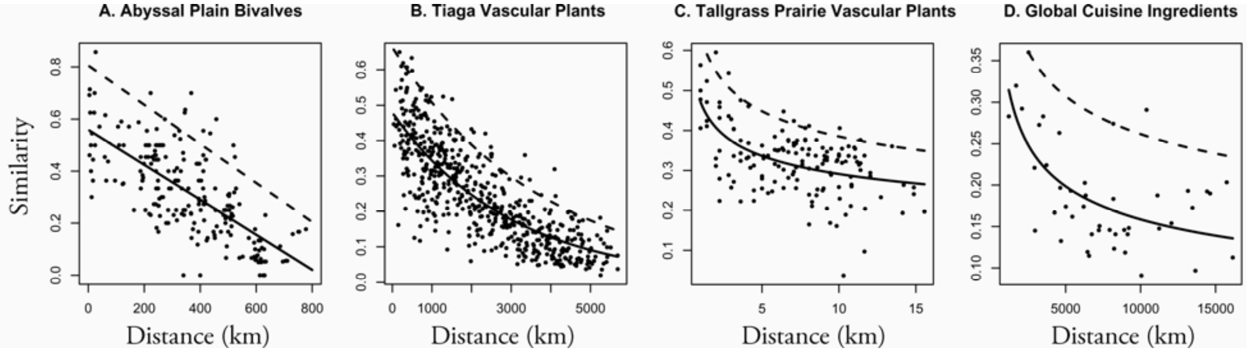
Section V: Ecological Theory and Modeling

Without the context provided by theory, ecological research may become bogged down in trivial detail. However, pure theory may easily become untethered from reality unless it is constantly informed by real-world observations. For this reason, I have chosen actively pursue theoretical issues while also maintaining an active research program spanning multiple frames of reference across multiple taxa groups. There are a number of biodiversity patterns which appear to be universal across multiple scientific disciplines. For instance, rarity-enriched Species Abundance Distributions, power-law Species Area/Time Relationships, and non-linear Distance Decay patterns appear ubiquitous across a wide array of complex systems, including not only ecology but also meteorology, geoscience, materials science, economics, sociology, and even the arts. Determining the common mechanisms underlying the distribution of trees in tropical forests, the longevity of drink tumblers in restaurants or of song performance frequencies in Cowboy Junkies setlists will help ecologists and others understand what patterns are caused by statistical mechanics rather than disciplinary mechanisms such as birth, death, immigration, or competition for limiting resources. All disciplines must begin this search for such fundamental mechanisms which are both more universal and less explicitly mechanistic than those typically sought. In this way we will be able to define the rigid rules for life's sonnet, within which there is an infinity of detail.



A particular foci for my theoretical interests is consideration of the role played by spatial or temporal distance. In particular, I am interested in applying Tobler's First Law of Geography: "Everything is related to everything else, but near things are more related to each other" to biogeographic analysis and modeling. For instance, this premise can be used, via gravity models, to predict the spread of organisms. Such models offer an important counterpoint to diffusion models as they assume landscape heterogeneity and do not require organisms to migrate via a moving wavefront. Gravity models provide a much more accurate portrayal of Zebra Mussel movement through small lakes of the upper Midwest USA than are possible via diffusion models.

My latest contribution in this general topic area derives this relationship from individual species occurrences and then illustrates that the functional form is related to sample scale, with power-law decay dominating within and exponential-decay dominating between communities. It also documents why distance decay is a universal expectation across a wide range of physical, social, artistic and biological systems. There are perhaps a dozen or more other diversity metrics that likewise appear to be universal statistical expectations, with rarity-enriched species abundance distributions and power-law species area/ time relationships serving as classic examples. As a result, the mere existence of these patterns likely say little about specific mechanism (e.g. neutral vs. deterministic community assembly) other than illustrating that the system consists of many quasi-independent parts. Thus, before we attempt to discern underlying mechanism we must: **A.** determine which patterns are simply cross-disciplinary expectations derived from statistical mechanics and thus say little *per se* about explicit ecological mechanism; **B.** determine what parameters of these relationships, if any (e.g. functional form or rate of change), are most likely to reflect differences in underlying ecological mechanism; **C.** investigate variation in these parameters to determine their utility in differentiating competing ecological models.



Examples of linear, exponential, and power-law distance decay showing the best-fit regression to the mean and the upper threshold (95% percentile).

Representative Publications
[number of citations as of October 27, 2017]

Nekola, J.C. & B. McGill. 2014. Scale dependency in the functional form of the distance decay relationship. *Ecography*. 37:309-320. **[18]**

McGill, B. & **J.C. Nekola**. 2010. Mechanisms in macroecology: AWOL or purloined letter? Towards a pragmatic view of mechanism. *Oikos*. 119:591-603. **[57]**

Nekola, J.C., A.L. Šizling, A.G. Boyer & D. Storch. 2008. Artifactions in the log-transformation of species abundance distributions. *Folia Geobotanica*. 43:259-468. **[21]**

Moses, M.E., C. Hou, W.H. Woodruff, G.B. West, **J.C. Nekola**, W. Zuo & J.H. Brown. 2008. Revisiting a model of ontogenetic growth: estimating model parameters from theory and data. *The American Naturalist.* 171:632-645. **[98]**

Nekola, J.C. & J.H. Brown. 2007. The wealth of species: ecological communities, complex systems, and the legacy of Frank Preston. *Ecology Letters.* 10:188-196. **[101]**

Bossenbroek, J.M., C.E. Kraft & **J.C. Nekola.** 2001. Prediction of long-distance dispersal using gravity models: Zebra Mussel invasion of inland lakes. *Ecological Applications.* 11:1178-1788. **[226]**

Research

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Scale dependency in the functional form of the distance decay relationship

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We examine a novel mathematical approach which posits that the decay of similarity in community composition with increasing distance (aka distance decay) can be modeled as the sum of individual species joint-probability vs distance relationships. Our model, supported by analyses of these curves from three datasets (North American breeding birds, North American taiga plants, and tropical forest trees), suggest that when sampling grain is large enough to avoid absences due to stochastic sampling effects, and/or sampling extent is large enough to generate species turnover through the deterministic crossing of environmental and/or geographical range limits, species joint-probability over increasing distance will generally exhibit exponential decay. However, at small scales where occurrence is driven more by stochastic sampling effects, species joint-probability curves exhibit a power-law decay form. Lacking a theoretical prediction of how individual species joint-probability relationships combine to generate community distance decay, we also performed a meta-analysis of 26 ecological and 4 human-system datasets, using non-linear regression to mean and quantile non-linear regression at tau = 0.95 for linear, exponential, and power-law decay forms. These analyses demonstrate that the functional form of community distance decay – as shown by comparison of AIC ranks – is largely determined by observational scale, with power law decay prevailing within domains where the species pool remains constant, while exponential decay prevails at larger scales over which the species pool varies, paralleling the patterns predicted in our mathematical approach.

The decay of compositional similarity with increasing inter-observation distance (aka distance decay) is a ubiquitous pattern found across a wide array of physical, biological, social and other complex systems (Tobler 1970, Nekola and Brown 2007). It has garnered considerable interest within the fields of community ecology (Condit et al. 2002, Green et al. 2004, Soininen et al. 2007), macroecology (McKnight et al. 2007, Blanchette et al. 2008, Qian et al. 2009) and conservation biology (Bell 2003, Steinitz et al. 2005), and has been suggested to shed important insights into underlying fundamental mechanisms (Nekola and White 1999, Hubbell 2001, Tuomisto et al. 2003, Gilbert and Lechowicz 2004).

In spite of this interest, controversy exists regarding its expected functional form. While a number of empirical analyses have firmly established exponential decay (Nekola and White 1999, Qian et al. 2005, 2009, Jobe 2007), linear (Blanchette et al. 2008, Perez-del-Olmo et al. 2009) and power law (Harte et al. 1999, Condit et al. 2002, Green et al. 2004) forms have also been documented. In spite of this, all theoretical derivations of the distance decay relationship (Harte and Kinzig 1997, Hubbell 2001, Chave and Leigh 2002, Houchmandzadeh 2008, Morlon et al. 2008) generate power-law or power-law-like forms.

Here we begin to develop analytical underpinnings for a theory of community distance decay based on joint-probabilities for individual species. We show that: 1) expectation of exponential or power-law forms for individual species joint-probability curves is a function of sampling scale, and 2) the community distance decay curve is a sum of single species joint-probability curves. Because a theoretical prediction for the shape of community distance decay curves from individual species joint-probability curves is not analytically tractable (except in a few specific cases), we consider this issue through empirical meta-analysis of 26 community datasets collected over both spatial and temporal extents, covering a large range of ecosystems (simulated data to abyssal plain to continental mountains, arctic tundra to tropics), taxa groups (including mammals, birds, lepidoptera, robber flies, land snails, vascular plants, bryophytes), sample grains (100 m^2 – subcontinental and daily-yearly) and total extent (3–9000 km and 1–25 yr). Four human system examples are also considered (1 spatial, 3 temporal; Nekola and Brown 2007) to identify if general patterns in community distance decay functional forms exist.

Individualistic model of distance decay

Single species distance decay

We begin with consideration with the decay of joint-probability (Palmer 2005) for a single species/agent/event with increasing inter-observation distance. Specifically, if comparing two plots L and M of the same size A at distance d apart (Fig. 1) for species i, then:

$$p_i(d_{LM}) = \text{Prob}\{\text{species } i \text{ present at } M \mid \text{species } i \text{ present at } L\} \qquad (1)$$

or more generally:

$$p_i(d) = \text{Prob}\{\text{species present at any site distance } d \text{ from a site where species } i \text{ is present}\} \qquad (2)$$

While this definition has a clear relationship to the occupancy function used by numerous authors (Harte et al. 1999, He and Legendre 2002), in these previous formulations p has been a function of the plot area, A, rather than the distance, d, from reference plot L. Thus, our approach is the first to explicitly consider spatial structure.

It is clear that under biologically realistic conditions where species have finite ranges, $p_i(d)$ needs to fit the following criteria: 1) $p_i(0) = 1$; 2) $p_i(\infty) = 0$; 3) $p_i(d_{AB}) = p_i(d_{BA})$ (i.e. isotropy or direction does not matter); 4) $p_i(d_1) \geq p_i(d_2)$ if $d_1 < d_2$ (i.e. p_i monotonically decreasing); 5) $p_i(d_1 + d_2) = g(p(d_1), p(d_2))$ for some functional form g if d_1 and d_2 are linear and contiguous as shown in Fig. 1 (i.e. decomposability with distance). Note that 1, 2 and 4 combined can be used to show that $0 \leq p_i(d) \leq 1$ if $0 \leq d \leq \infty$.

There are an infinite number of functional forms that fit these criteria. Three that have been commonly used to analyze community distance decay (Nekola and White 1999, Soininen et al. 2007) include the linear $[p_i(d) = 1 - cd]$, exponential $[p_i(d) = \exp(-cd)]$, and power law $[p_i(d) = d^{-c}]$. Additionally, Harte (2011) suggests a logarithmic decay $[p_i(d) = 1 - c^*\log(d)]$ form. All contain a single parameter, c, which denotes decay rate. Note that the power law form violates criterion 1, the linear form violates criterion 2, while the logarithmic form violates both. As a result, these functional forms can in practice be used only over limited intervals: $[0, d_{max}]$ where $d_{max} = d$ at which $p_i(d) = 0$ for the linear, $[\epsilon, \infty]$ for the power law, and $[\epsilon, d_{max}]$ for the logarithmic. While Palmer (2005) calculated $p_i(d)$ for tropical trees at the La Selva Biological Station in Costa Rica, he did not propose that it take on any particular mathematical form. However, his plot of $p_i(d)$ across all species and sites appears to demonstrate an exponential trace.

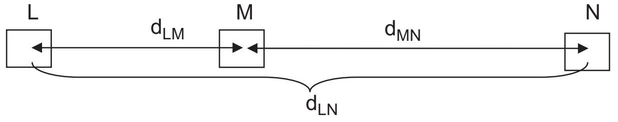

Figure 1. Heuristic diagram demonstrating the relationship between sample plots and distances used in the theoretical model.

What form should g in criterion 5 take? This function describes how p_i should behave when a long distance d is decomposed into two smaller distances d_1 and d_2 (where $d_1 + d_2 = d$ and lie along a straight line; Fig. 1). Clearly it should be commutative and associative. The most obvious, simple forms are $g(x,y) = x + y$ or $g(x,y) = x^*y$. However, the additive form violates criterion 4 [e.g. $p(6) = p(4 + 2) = p(4) + p(2) > p(4)$ but $p(6) < p(4)$] and can easily produce $p_i > 1$. The multiplicative form fits well with our intuitive sense of how similarity decays [i.e. $p_i(d_1 + d_2) = p_i(d_1)^*p_i(d_2)$], and is essentially the law of independent probabilistic events [P(A and B) = P(A)*P(B)]. Note that $p_i(d_1 + d_2) = p_i(d_1)p_i(d_2)$ can only be satisified by $p_i(d) = \exp(cd)$ with criteria 1 and 2, requiring that $c < 0$. A negative exponential form for the decay of joint occurrence probability with increasing distance thus conforms well to criteria 1–5.

It is instructive to proceed with a more rigorous examination of the form of g. Considering the straight line connecting L to M to N in Fig. 1, via the law of total probability (Karlin and Taylor 1975):

$$\begin{aligned} &\text{P(present at N} \mid \text{present at L)} \\ &\quad = \text{P(present at N} \mid \text{present at M)} \\ &\qquad \times \text{P(present at M} \mid \text{present at L)} \\ &\qquad + \text{P(present at N} \mid \text{NOT present at M)} \\ &\qquad \times \text{P(NOT present at M} \mid \text{present at L)} \end{aligned} \qquad (3)$$

or:

$$p_i(d) = p_i(d_2)p_i(d_1) + X(d_2)(1 - p_i(d_1)) \qquad (4)$$

where: $X(d)$ is the probability of a species being present at one point conditioned on it NOT being present at another point [note this is not simply $1 - p_i(d)$].

More simply:

$$p_i(d) = p_i(d_1)p_i(d_2) + Y(d_1,d_2) \qquad (5)$$

where $Y(d_1,d_2) = \text{Prob}\{\text{present at N, absent at M} \mid \text{present at L}\}$ or essentially the probability of encountering an 'occurrence hole' (sensu Rapoport 1982, Hurlbert and White 2007) within the range of species i. $Y = 0$ when species i is never absent at M if present at L and N. In such cases, we have the multiplicative form for g and $p_i(d) = \exp(-cd)$. If $Y \neq 0$, then g is more complex, and $p_i(d)$ is not a simple exponential.

Community distance decay

Assuming $p_i(d)$ is exponential for one species, then what distance decay form should be expected across a community assemblage? As is common in theoretical ecology, we will work with the Sørenson similarity measure due to its tractable mathematics (Plotkin and Muller-Landau 2002, Morlon et al. 2008). Let S_{LM} be the number of species found in both plots L and M, while S_L is the number of species found in plot L and similarly for S_M. We assume approximately $S = S_L = S_M$. because systematic changes in richness will lead to bias in parameter estimation (Jobe

2007). Then Sørenson (d_{LM}) = Sørenson (L,M) = S_{LM}/average (S_L,S_M). If we sum the probability that a species is present in M over all species present in L, this gives:

$$\text{Sørenson }(L,M) = \sum_{i=1}^{S_L} p_i(d_{LM}) \Big/ S = \frac{1}{S}\sum_{i=1}^{S} \exp(-c_i d) = E_i \exp(-c_i d) \tag{6}$$

where E_i is the expectation (or averaging) operator taken with respect to i or over all species. We call this the community aggregated distance decay function. This makes the strong assumption that the joint probability decay is independent between all species.

A sum of exponentials as found in Eq. 6 can take on a vast variety of shapes, dependent entirely on the distribution of c_i values. If we treat c_i as a random variable, C, from which the c_i are drawn and using the tools for calculating the expected value of a function of a random variable (Lindgren 1976 p. 113) we have:

$$\text{Sør}(d) = E_i \exp(-c_i d) = \int \exp(-xd) f(x)\,dx \tag{7}$$

Where $f(x)$ is the pdf of the random variable describing the distribution of C. A uniform distribution for C across [0, c] yields $1 - [\exp(-c{*}d))/(c{*}d)]$. In the limiting case of c having a Dirac delta distribution (i.e. c_i is constant with no variation), then Eq. (6) and (7) give community Sørenson similarity as an exponentially decaying function of distance. Assuming C is distributed according to an exponential distribution yields Sør$(d) = c/(c+d)$ while assuming C is distributed according to a power law yields Sør$(d) = \Gamma(c)c/(b^{c}{*}d^{c})$. However, as will be shown in the results, C is strongly right-truncated, making a Beta distribution the most likely. While this does not yield an analytically solvable integral, a partial understanding can realized by taking a Taylor-series expansion of $E_i \exp(-c_i d)$. Let C now be the mean value of c_i ($C = \bar{c}_i$) and $\Delta_i = c_i - C$, with the expansion around C:

$$E_i \exp(-c_i d) = E_i \exp(-(C+\Delta_i)d) = \exp(-Cd)E_i\left[1 + \frac{(\Delta_i d)^2}{2!} - \frac{(\Delta_i d)^3}{3!} + \frac{(\Delta_i d)^4}{4!} - \frac{(\Delta_i d)^5}{5!} + \ldots\right] \tag{8}$$

The infinite series inside the brackets is a function of d that alternates in sign, with $k^n/n!$ converging to zero for large enough n (where $k = \Delta_i d$). Thus, while the series does converge, it occurs in a way that depends on Δ_i and d. In particular if $\Delta_i d$ is > 1 over much of the range of interest for d, the possibility exists for very slow convergence and strong deviations from $\exp(-Cd)$. Nothing further can be said about this situation without a detailed knowledge of the distribution and magnitude of Δ_i relative to d. After examining empirical distributions in the Results, we will present further analysis in the Discussion as to when convergence on $\exp(-Cd)$ may be expected.

Equation 6 can be expanded for the case where the evaluated species pool is not just the species present at L but includes all taxa in the regional pool. To do this, we redefine S to be the richness of the regional species pool, with w_i being the occupancy rate for species i (i.e. the fraction of sites supporting species i) or equivalently the probability that species i is found at site L. Then we have:

$$\text{Sør}(d) = \frac{1}{S}\sum_{i=1}^{S} w_i \exp(-c_i d) = E_i w_i \exp(-c_i d) \tag{9}$$

We call this the weighted community aggregate distance decay function. This curve should closely approximate the traditional community-level decay of similarity curve which is generated by calculating pairwise similarity between samples (Nekola and White 1999).

Model assumptions

Two main assumptions underlie our approach. First, to produce an exponential decay of joint-probability over increasing distance for a single species we assumed that Y(d_1,d_2) = 0 or equivalently that a species must occur at M if present at L and N. In effect Y informs about the probability that a sample plot falls inside an occurrence hole within a species range. The value of Y should show strong scale dependence: if sample grain is small with significant sampling error and extent does not exceed the environmental and/or geographic range limits of species within the pool, then it is likely that the main reason for compositional turnover will be sampling effects (Nekola and White 1999). In such instances Y≠0, and because in such situations $p_i(d)$ is not exponential, this form will also not provide a good fit to the community data. The expected shape in such cases should initially show a more rapid decrease in joint-probability than the exponential expectation because of occurrence holes, but will then ultimately asymptote > 0 because the probability of a given species within the pool is also > 0. Although not a rigorous proof, at a minimum the above demonstrates that a more power-law like than exponential form would result from cases where Y≠0. Multiple theoretical distance decay models assuming such small grains and uniform species pools have all produced power law decay forms (Harte and Kinzig 1997, Chave and Leigh 2002, Houchmandzadeh 2008, Morlon et al. 2008).

When sample grain is large relative to the organism/agent/event (making for guaranteed detection), with extent being large enough to pass beyond species environmental and/or geographic range limits (allowing the community pool to vary across the sample), then the main cause of species turnover will be the exceeding of species distributional limits, minimizing the chance that a species will be absent at M but present at L and N. In these situations Y = 0, and the exponential form should represent a good approximation. Note that these conditions may be met at various absolute scales. For instance, if strong local spatial or temporal gradients exist, even over very limited extents the community pool will not be uniform and the exponential form should occur.

The second major assumption is that the decay of each species joint-probability is independent of that exhibited by others. This allows summing of individual decay curves to produce Eq. 6. Such an assumption of independence between co-occurring species is one of the foundational bases of modern community ecology (Gleason 1926, Curtis 1955, Whittaker 1975) that accurately reproduces a number of community patterns (McGill 2010, 2011, He and Legendre 2002, Green and Plotkin 2007). Although species pairs can be identified which clearly show non-independent distributions (e.g. red bellied woodpecker and red-headed woodpecker – Root 1989; American beach and its obligate parasite beachdrops – Voss 1985), these interactions represent such a small fraction of all possible pairwise interactions (Barker and Mayhill 1999) that the assumption of independence is a valid approximation.

Summary of model predictions

1) Individual species will exhibit exponential decay in their joint-probability with increasing distance if and only if observational scale is large enough to allow a varying species pool and to avoid quasi-stochastic occurrence holes.

2) The Sørenson decay of community similarity is equivalent to the occupancy-weighted community average of the individual $p_i(d)$ curves in the regional species pool.

3) The weighted community aggregate curve (Eq. 8) will fit better than the unweighted curve in cases where species are not equally likely across the species pool (or equivalently that the species pool changes over the extent studied), but will fit worse when the species pool is constant across sites.

4) The functional form for community distance decay [$Sør(d)$] depends on the distribution of c_i, the decay rates of for individual joint-probability curves. Unfortunately this distribution has never been studied and we have no empirical knowledge of its shape, making impossible the prediction of community distance decay functional form. Even when all single species joint-probability curves are exponential, community decay curves of innumerable forms can be produced.

Methods

Test of model predictions

Three different datasets were used to test the general accuracy of our approach. The first is the vascular plant data of LaRoi (1967), which was sampled from 34 nine-ha (300 × 300 m) mature, undisturbed upland white spruce forest plots at relatively equal distances across boreal North America. A total of 220 vascular plant species were encountered, with individual plot richness ranging from 19–56. The second is the North American Breeding Bird Survey (BBS), which is run annually at over 2000 routes across the continental US and southern Canada (Sauer et al. 2011). A 3-min point count is taken every half mile (approximately 0.8 km) for 50 stops along a transect of 25 miles (approximately 40 km). An individual route typically has 50–100 bird species detected and overall almost 600 species of birds have been observed at least once. To avoid issues with detection error and year-on-year variability, we took average abundance over the years 2003–2007, and used only the 1430 routes that had a quality code reflecting appropriate weather and observer ability for all five years. Thus, a bird was counted as being present at a given route if it appeared at least once in five years. The third dataset was the Barro Colorado Island tree plot containing 225 species (Condit et al. 2000). Every tree >10 cm DBH was recorded within each of the 50 one hectare plots. Distance was recorded between hectare midpoints.

Due to their continental extents, we a priori expect the LaRoi and BBS datasets to have individual site compositions drawn from varying species pools. Decay of individual species joint-probabilities in these data should thus generally take on an exponential form. However, because the BCI dataset covers only a 1 km extent, all samples are likely to be drawn from only two nested species pools (young within old forest; Svenning et al. 2004). In this situation, species absences are likely due to stochastic sampling effects and/or disturbance history, with a power-law like decay-form prevailing. In all three cases the community distance decay curve should be the sum of the individual species decay curves, although the fit should be worse for the BCI data because of the greater impact of stochastic sampling errors. While no explicit prediction can be made for the functional form of the community distance decay curve, the heuristic considerations given above suggest that an exponential form may be more likely at large grains and/or extents which sample across varying species pools. We also predict the weighted community aggregate curve should perform better for the La Roi and BBS data since they have large enough extents/strong enough gradients to exceed the limits of individual species, while conversely the BCI data should be better fit by an unweighted curve.

To test the individual species portion of the model (prediction 1), for each dataset we fit an exponential decay curve to the each species joint-probability by calculating similarity (1 if the species was present in both plots; 0 of not) and distance between each occupied site and all others. Because calculations were only conducted from occupied sites, we constrained similarity to equal 1 at the origin and fit only a single parameter to the decay function. Other functional forms (e.g. linear, power law, logarithmic) were not fit because of their violations of criteria 1 and/or 2. We then calculated mean similarity across distance bins of 200 km (LaRoi and BBS) or 200 m (BCI). Due to the computational challenges in the 1403 site × 600 species BBS data (reflecting a total potential number of $\sim 6 \times 10^8$ calculations), prior to model fit we randomly removed absent sites in order to generate occupancy rates of approximately 10%. We then sampled 10 000 individuals from all site by site pairs. We recorded the c and r^2 value for each species. To calculate the community aggregated curve (Eq. 6), we predicted values every 200 km or 200 m, took their average, and plotted a line through the data. We calculated the weighted community aggregate curve (Eq. 7) similarly except that each species was weighted by its observed occupancy. Because singleton and doubleton species do not possess enough degrees of freedom to accurately fit an exponential model (singletons are points in space while doubletons can only demonstrate linear patterns), we also calculated a community aggregate curve in which each species was equally weighted ($w_i = 1/S$) after removal of singletons and doubletons. We term this the filtered community aggregate curve.

The traditional community distance decay curve was also calculated for each dataset. Because of its use in model formulation, Sørenson similarity was used. Since the total BBS data would represent almost 2 000 000 pairwise comparisons, we limited analysis to 10 000 randomly-drawn pairs. To these data we then fit a linear decay curve using ordinary least squares (OLS) regression and an exponential and power-law decay curves using non-linear least squares (NLS) regression. Note that under the assumption of normal errors, OLS and NLS give maximum likelihood estimates allowing the use of the Akiake information criteria (AIC), which we used to compare the three models. We also plotted a LOESS line on these plots to allow for easy visual comparison of the central tendency in the empirical data vs the community aggregated curves.

Meta-analysis of community similarity datasets

Lacking a theoretical prediction for the functional form of community distance decay, we also conducted a meta-analysis of 26 ecological and 4 human-system datasets. Two datasets represent simulated community turnover data using COMPAS (Minchin 1987), with composition lists being generated for 50 randomly-spaced sites along a single gradient containing 20 species. Two different turnover scenarios were used: constant turnover where all species possess the same modal abundance, standard deviation, and are equally spaced along the gradient, and lognormal turnover, where species modes, standard deviations, and gradient placement follow a lognormal distribution. The remaining data are empirical, represent examples of both spatial and temporal decay, and attempt to maximize ecosystem range, taxa groups, sample grains, and extents. Information regarding the habitat type, taxa group, maximum extent, sample grain, number of samples, and additional notes on these datasets is found in Table 2. These data include: Galapagos Islands vascular plant flora (Preston 1962); North America upland taiga vascular plants (LaRoi 1967) and bryophytes (LaRoi and Stringer 1976); fen-restricted vascular plants in northeastern Iowa (Nekola 1994); Martha's Head to Bermuda abyssal plain bivalves (Allen and Sanders 1996); Belize terra firma tropical forest (Bird 1998); entire vascular plant floras for all algific talus slope sites along Buck Creek, Clayton County, Iowa (Nekola 1999); Peruvian and Panamanian terra firma forest (Condit et al. 2002); Barro Colorado Island terra firma forest (Condit et al. 2000); New Zealand land snails (Barker 2005); eastern North American and Asian vascular plants (Qian et al. 2005); Iowa county butterfly faunas (Schlicht et al. 2007); small rodent and winter annuals plants at Portal, Arizona (Ernest et al. 2009); eastern North American rock outcrop, Atlantic coastal plain acidophile, and southwestern USA montane land snail faunas (Nekola 2010); North American Breeding Bird Survey (Sauer et al. 2011); southern Flint Hills tallgrass prairie vascular plants (McGlinn and Palmer 2011); seasonal butterfly and skipper emergences at the Rock Island Preserve, Linn County, Iowa (F. Olsen pers comm.); and seasonal robberfly emergences at the Sevilleta LTER (H. Lease pers. comm.). Representative human-system datasets include: concert setlists for Cowboy Junkies (<www.setlist.com>) and Phish (<www.ihoz.com/PhishStats.html>) performances; all commercially available garden vegetable varieties in the US and Canada as reported by the Garden Seed Inventory of the Seed Savers Exchange; all ingredients reported for the cuisines of Ethiopia, Hungary, India, Iran, Ireland, Korea, Mexico, Norway, Puerto Rico, and Thailand (Smith 1990). The Cowboy Junkies setlist, Garden Seed Inventory, and global cuisine distance decay analyses were previously reported in Nekola and Brown (2007).

For each of these datasets, Jaccard similarity was calculated between each pairwise combination of samples, while distance was calculated as the linear difference in space or time between observations. The Jaccard metric was employed because of its common use in distance decay analyses (Nekola and White 1999). The Jaccard and Sørenson indices differ only slightly in their denominator values, and perform in a highly similar (and for all intents, identical) fashion. These data were then subjected to non-linear regression to the mean using the 'nls' routine in R, and quantile regression using the 'nlrq' routine in R with tau = 0.95. Quantile regression was used because the central tendency may not be as important in the distance decay relationship as the shape of the upper bound (Rocchini and Cade 2008). For each of these regression approaches three different functional forms were fit to the data: $S_d = S_i - cd$ (linear decay); $S_d = S_i\ e^{-cd}$ (exponential decay) and $S_d = Ad^{-c}$ (power-law decay) where S_d = intersample similarity at distance d; S_i = initial similarity or nugget (Nekola and White 1999); A = arbitrary intercept; d = intersample distance; c = rate of similarity change. We did not fit logarithmic decay [$S_d = a - c(\log(d))$] because we found it to neither outperform power-law fits in the three intensively studied datasets (LaRoi, BBS, BCI) nor in those data which appeared by eye to most likely to express the logarithmic functional form (Tallgrass Prairie Preserve, Iowa Butterfly County occurrences, Portal rodents, and Cowboy Junkes setlists).

AIC values were calculated for each regression and ranked from 1 (least) to 3 (largest) across the three functional forms for each dataset. We then constructed a contingency table for each of the regression methods, showing 1st, 2nd, and 3rd AIC ranks vs linear, exponential, and power-law fits. A Fisher-exact test was conducted on these tables to determine if cell frequency violated null expectations.

Results

Model test

All three model predictions were confirmed across the three datasets. In general, the exponential decay form was found to be a good approximation for taiga vascular plant and continental bird species joint-probabilities with increasing observational distance (Fig. 2). While the vast majority of LaRoi and BBS species were fit by an exponential model

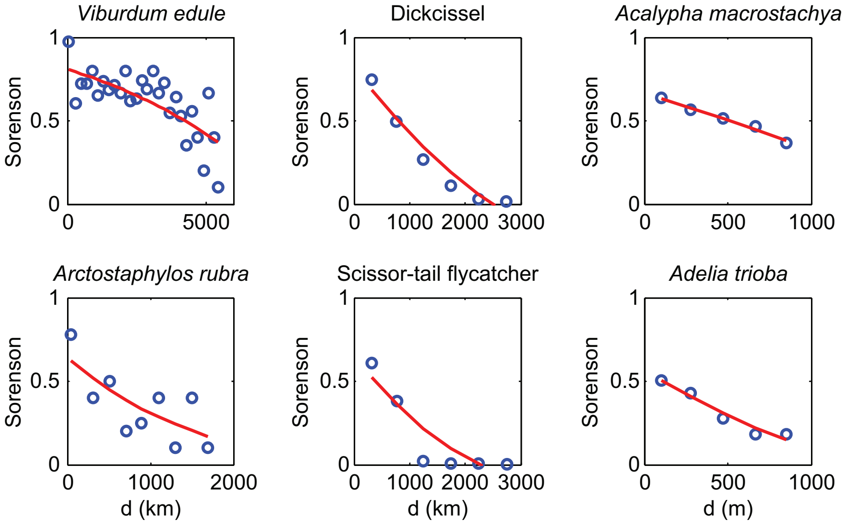

Figure 2. Individual species joint-probability decay with distance [$p_i(d)$] curves for arbitrary species. Blue dots are observed similarities. Red line is LOESS smoothed regression. Left column represents two species from the LaRoi dataset. Middle column represents two species from the Breeding Bird Survey dataset. Right column represents two species from the Barro Colorado Island dataset. Note that for a few species (like *Viburnum edule*) exponential decay is a poor fit. However, as seen in the bottom row of Fig. 3 there only a few such species.

with $r^2 > 0.9$, a noticeably higher frequency of poor fits were noted in the BCI data (Fig. 3). These results confirm prediction 1. It should be noted, however, that six BBS species (1% of total), present at only a handful of sites, demonstrated increasing similarity with distance. These were removed from subsequent analysis. The distribution of c_i values was unimodal with a strong right truncation, making exponential and power law distributions for C a poor description of the empirical data (Fig. 3). Visual comparison of the weighted community aggregate vs the LOESS line for the true Sørenson decay (Fig. 4) shows a remarkable convergence in the LaRoi and BBS data, confirming prediction 2. Table 1 also demonstrates that the community weighted aggregate produces exponential decay parameters that are very close to the observed true community decay values. This is quite remarkable given that no parameters in the weighted community aggregate curve were adjusted to make them fit the true Sørenson decay curve. Although no community aggregate curve provides a good fit to the empirical BCI community decay data, the unweighted curve is a better fit, confirming prediction 3. Linear, exponential and power law forms were then fit to the empirical Sørenson community distance decay (Fig. 4). Community distance decay in the LaRoi and BBS data are best fit by the exponential form, while the BCI data is best fit by a power law (Table 1).

Meta-analyses

All 26 ecological and 4 human-system datasets demonstrated a negative relationship between community similarity and

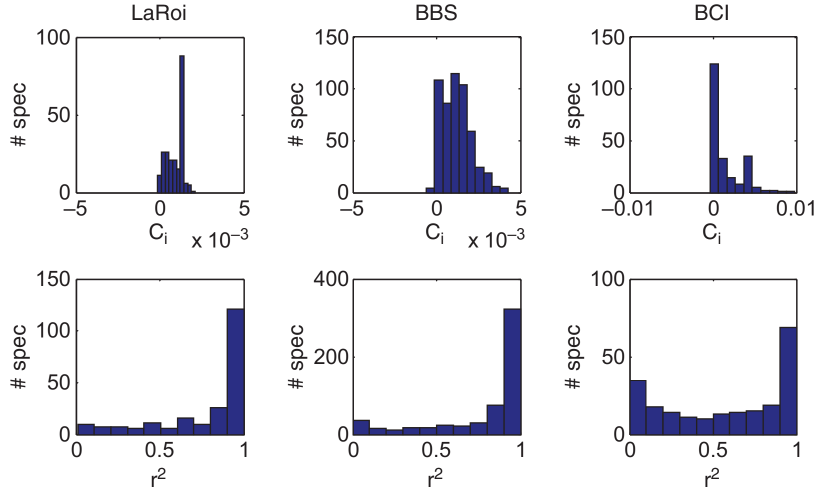

Figure 3. Results of exponential fits to individual species joint-probability occurrence decay. Top row shows distribution of estimated coefficents, c_i. Bottom row shows a histogram of r^2 values for these fits. Left column is for LaRoi data, middle column is for the Breeding Bird Survey, and the right column is for the Barro Colorado Island data.

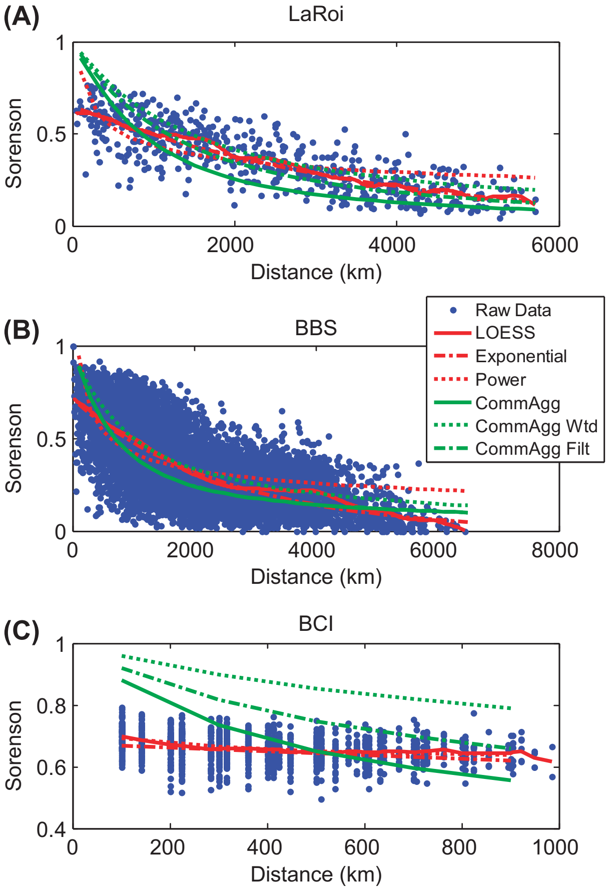

Figure 4. Empirical distance decay relationships, with each blue dot representing a plot pair. Red solid line shows LOESS fit. Red dash-dotted red line shows an exponential fit. Red dotted line shows a power law fit. The green lines show the community aggregated curves. The solid green line equally considers all species (i.e. Eq. 6). The dotted green line weights species by their occupancy (i.e. Eq. 7). The dash-dotted line includes all species equally but eliminates species found in 2 or fewer sites. (A) LaRoi boreal plant data. (B) North American Breeding Bird Survey (note only 10 000 random pairs were used out of the over 2 000 000 possible). (C) Barro Colorado Island data.

distance (Table 2). Based on AIC ranks, each of the three functional forms were found to provide a best-fit to at least some of the ecological datasets under both non-linear regression to mean and quantile regression to tau = 0.95. However, in all four human-system datasets the power-law model was best fit to the data, followed by the exponential model, with the linear model providing the poorest fit. For ecological systems exponential decay was best fit 14 times to the mean, and 13 times to tau = 0.95 (Table 3). Power-law forms were best fit in 8 and 6 cases, respectively, while linear was the best fit in 4 and 7 cases. While exponential equations never provided the poorest fits, in almost half of the datasets linear fits performed the most poorly (13 and 10, respectively), while power-law fits performed worst in at least 50% of datasets (13 and 16, respectively). Fisher-exact tests on these contingency tables indicate a highly significant ($p = 0.00002$ and $p = 0.000014$) deviation of cell frequencies from a uniform null model.

Discussion

These analyses clearly demonstrate that the distance decay of community similarity reflects the aggregate of individual species joint-probability decay functions across the species pool. As shown in both large-scale detailed datasets (BBS, LaRoi), when the grain size and/or extent are large enough to generate exponential individual joint-probability decay, the community decay curve is also best fit by this form. This outcome is replicated in the meta-analysis, where large scale samples crossing into multiple species pools also exhibited exponential community distance decay. Examples include: simulated communities along a strong environmental gradient; vascular plant flora of the Galapagos archipelago; vascular plant and bryophyte assemblages across boreal North America; vascular plants of North American and Asian temperate forests; North American Atlantic coastal plain land snails; BBS data; and the adult emergence of both butterflies/skippers and robberflies along a seasonal gradient.

Table 1. Summary of results for three datasets.

	True		Community aggregate		Weighted community aggregate	
	C	AIC	C	AIC	C	AIC
LaRoi						
Linear	−0.0001	−2578.8	−0.00012	−125.4	−0.0001	−142.4
Exponential	**−0.00027**	**−2590.4**	**−0.00056**	**−183.5**	**−0.00032**	**−185.1**
Power	−0.286	−2355.1	−0.482	−147.0	−0.353	−149.4
BBS						
Linear	−0.00011	−38294	−0.00007	−156.0	−0.00008	−167.5
Exponential	**−0.00039**	**−39287**	−0.00047	−202.3	**−0.00034**	**−215.1**
Power	−0.370	−37635	**−0.484**	**−211.5**	−0.409	−199.0
BCI						
Linear	−0.00006	−7646	−0.00039	−31.0	−0.00021	−43.2
Exponential	−0.00009	−7647	−0.00059	−34.0	**−0.00024**	**−45.4**
Power	**−0.0367**	**−7677**	**−0.202**	**−39.6**	−0.085	−40.9

Table 2. Source, system, sample scale, and regression information for the analyzed datasets. The upper AIC values and ranks represent statistics generated from non-linear regression to mean, while the lower values represent statistics generated from quantile non-linear regression for tau = 0.95.

								AIC value/rank order		
Source	Location	Habitat	Taxa group	Max Extent	Grain	No. samples	Notes	Linear	Exponential	Power
COMPAS	Simulated					50	Constant turnover	−3665.7/2 4730.4/2	−3956.1/1 3837.2/1	−1478.3/3 5430.9/3
COMPAS	Simulated					50	Lognormal turnover	−1317.6/2 7018.5/2	−1976.0/1 6937.4/1	−721.0/3 7372.3/3
Preston 1962	Galapagos Islands	Volcanic archipelago	Vascular plants	286.2 km	1.1–4640 km²	18		−222.7/2 51.0/1	−224.6/1 51.6/2	−206.7/3 61.5/3
LaRoi 1967	North America	Upland taiga	Vascular plants	5687.4 km	9 ha	34		−1212.6/3 1770.0/2	−1244.1/1 1729.3/1	−1027.2/2 2116.4/3
LaRoi and Stringer 1976	North America	Upland taiga	Bryophytes	5687.4 km	9 ha	34		−1205.1/2 1810.7/2	−1221.7/1 1804.4/1	−1122.2/3 1919.9/3
Nekola 1994	Northeastern Iowa	Fen	Specialist vascular plants	254.0 km	0.1–50.1 ha	10		−91.1/1 −91.7/1	−91.0/2 −90.7/2	−89.7/3 −87.4/3
Allen and Sanders 1996	Atlantic abyssal plain	Total fauna	Protobranch bivalves	777.5 km	ca 0.1 ha	21	< 3000 m depth only	−286.8/1 498.3/1	−274.4/2 501.9/2	−208.7/3 522.6/3
Bird 1998	Belize	Tropical forest	Canopy trees	205.5 km	1 ha	30		−798.2/3 1290.1/3	−810.0/2 1282.6/2	−947.6/1 1068.2/1
Nekola 1999	Buck Creek valley, Iowa	Algific talus slope	Vascular plants	3.1 km	0.125–1 ha	7		−83.1/1 −109.2/1	−82.9/2 −109.1/2	−77.6/3 −107.5/3
Condit et al. 2000	Barro Colorado Island	Tropical forest	Trees > 10 cm dbh	1 km	1 ha	50		−4167.7/3 −13446/3	−4168.8/2 −13448/2	−4199.0/1 −13496/1
Condit et al. 2002	Panama	Tropical forest	Canopy trees	110.6 km	1 ha	100		−9045.8/3 38969.4/3	−11850/1 37667.5/1	−11125/2 37820.6/2
Condit et al. 2002	Peru	Tropical forest	Canopy trees	102.2 km	1 ha	15		−275.4/3 −105.6/3	−276.1/2 −107.8/2	−305.8/1 −136.2/1
Barker 2005	New Zealand	Total fauna	Land snails	1590.9 km		28		−460.6/2 1197.3/1	−463.0/1 1205.8/2	−416.5/3 1371.6/3
Qian et al. 2005	E North America	Total flora	Vascular plants	1895.3 km	67000–249 000 km²	25	47 chosen comparisons	−64.6/2 −107.2/1	−67.0/1 −106.6/2	−64.3/3 −38.3/3
Qian et al. 2005	E Asia	Total flora	Vascular plants	1870.6 km	67000–249 000 km²	18	40 chosen comparisons	−61.4/3 −93.0/2	−76.2/1 −116.9/1	−70.9/2 −10.2/3
Schlicht et al. 2007	Iowa	County faunas	Butterflies and skippers	502.1 km	1042–2524 km²	60	Limited to well sampled (40 + taxa) counties	−3973.9/3 9840.0/3	−3975.8/2 9839.1/2	−3982.2/1 9838.4/1
Ernest et al. 2009	Portal, Arizona	Desert scrub and grassland	Winter annual plants	16 yr	Season summary for 250 m²	17	Plot no. 22 from 1989–2005	10.4/3 264.7/3	10.3/2 265.3/1	9.7/1 265.4/2
Ernest et al. 2009	Portal, Arizona	Desert scrub and grassland	Rodents	25 yr	Season summary for 250 m²	26	Plot no. 22 from 1976–2005	−301.9/3 1227.5/3	−310.9/2 1219.0/2	−326.0/1 1197.8/1

(Continued)

Table 2. (Continued).

Source	Location	Habitat	Taxa group	Max Extent	Grain	No. samples	Notes	AIC value/rank order Linear	AIC value/rank order Exponential	AIC value/rank order Power
Nekola 2010	US Atlantic Coast	Acid habitats	Land snails	2013 km	10 000 m^2	15		−147.1/2 70.9/2	−148.5/1 69.9/1	−146.5/3 72.0/3
Nekola 2010	E North America	Rock outcrop	Land snails	3031.7	10 000 m^2	48		−1269.0/2 6446.9/1	−1297.1/1 6462.6/2	−1225.6/3 6553.0/3
Nekola 2010	SW North America	Montane forest	Land snails	841.1 km	10 000 m^2	14		−104.9/1 26.4/2	−102.9/2 26.3/1	−95.7/3 41.0/3
McGlinn and Palmer 2011	Oklahoma	Tallgrass prairie	Vascular plants	15.6 km	100 m^2	151	Comparisons with plot no. 5 only	−358.0/3 7.8/3	−359.8/2 5.6/2	−367.5/1 −11.0/1
McGlinn and Palmer 2011	Oklahoma	Tallgrass prairie	Vascular plants	9 yr	Season summary for 100 m^2	10	Plot no. 5 from 1997–2006	−149.5/3 −156.7/2	−151.0/2 −157.2/1	−155.6/1 −152.2/3
Sauer et al. 2011	North America	Total fauna 2002–2007	Breeding birds	6139.8 km	~16 ha	~3700	1000 draws from all pairwise comparisons	−968.9/2 −8687.5/2	−1084.8/1 −8698.1/1	−878.4/3 −8405.5/3
H. Lease pers. comm.	Sevielleta LTER	Desert scrub	Robber flies	193 d	1 d	26	2006 season	−173.9/3 1289.9/3	−231.7/1 1269.6/1	−227.5/2 1275.2/2
F. Olsen pers. comm.	Rock Island Preserve, Iowa	Tallgrass prairie	Butterflies and skippers	174 d	2–4 h	38	1990 season	−713.1/3 3301.1/3	−741.9/1 3244.2/1	−718.3/2 3277.2/2
Nekola and Brown 2007	Concert setlists	Cowboy Junkies		6856 d	1 show	33	1987 to 2006	−894.8/3 −4559.7/3	−921.3/2 −4657.3/2	−1047.1/1 −4910.7/1
<www.ihoz.com/PhishStats.html>	Concert setlists	Phish		6070 d	1 show	18	1983–2000	−485.5/3 −46.5/3	−511.5/2 −51.0/2	−525.5/1 −69.9/1
Nekola and Brown 2007	Commercially available varieties	Garden Seed Inventory		23 yr	1 Garden Seed Inventory	7	1981 to 2004	−40.4/3 −183.4/3	−50.4/2 −199.4/2	−54.4/1 −231.6/1
Nekola and Brown 2007	Ingredient lists	Global cusines		16500 km	1 ethnic region	10		−126.1/3 −453.2/3	−128.5/2 −454.7/2	−136.6/1 −456.3/1

Table 3. Contingency table of AIC rank vs functional form of the distance decay relationship. The smallest AIC value among the three functional forms was assigned a rank of '1', the second smallest a rank of '2', with the largest being assigned a rank of '3'. The first number in a cell represents the number of datasets achieving that given rank based on AIC values calculated from non-linear regression to mean, while the second represents the number achieving that rank based on quantile non-linear regression for tau = 0.95.

	Mathematical distance decay form		
AIC rank	Linear	Exponential	Power law
1	4/7	14/13	8/6
2	9/9	12/13	5/4
3	13/10	0/0	13/16

Fisher exact test for identical cell frequencies: $p = 0.00001966$ for non-linear regression to mean; $p = 0.00001374$ for quantile non-linear regression.

However when community data is sampled at small grains or within a mostly uniform species pool at limited extents (BCI), exponential decay is a poorer describer of joint-probability decay with community distance decay exhibiting a power-law like form. This result was also replicated in the meta-analysis. Examples include: vascular plants within 100 m^2 quadrats along a 15.6 km extent in the Tallgrass Prairie Preserve in northeastern Oklahoma; canopy trees within 1 ha tropical forest stands along a 1 km extent at BCI, a 100 km extent in lowland Peru, and a 200 km extent in Belize; seasonal summaries for rodents within a 250 m^2 sample over a 25 yr extent in Portal, Arizona. While Iowa county butterfly faunas would appear a violation, with power-law decay being favored even though ~25% of the fauna reaching its range limit within the state boundary, it is also important to realize that range-limit species also tend to be rare. Since rare species do not exhibit a distance decay signal (Nekola and White 1999), they will not contribute greatly to the overall shape of the decay function. As a result, the observed power law shape is largely due to the ~75% of the fauna which is cosmopolitan.

Power-law community distance decay has also previously been shown to describe the variation of vascular plant composition at <10 km extents within Colorado subalpine meadows (Harte et al. 1999) and for soil microbes over ~1000 km extents in Australia (Green et al. 2004). It is important to note in this latter example that because of their exemplary long-distance dispersal abilities (Green and Bohannan 2006) local microbe communities are likely drawn from a much more extensive and uniform species pool than would be the case for most macroscopic organism groups.

The predominance of power-law community distance decay in human-systems is also readily explained using this framework. Because of the immense human capacity to move ideas and goods across large spatial scales, and to store and retrieve data across long time periods, absolute range limits for commercial goods or ideas are likely not crossed at either planetary spatial extents or decadal time spans. For instance, global trade over the last 600 yr has allowed essentially all domesticated crops to be available world wide. As a result, many new world domesticates are now common aspects in old world cuisines – e.g. tomatoes in Italian, chiles in Indian/Ethiopian/Chinese/Thai, while old-world domesticates now feature prominently in new world cuisines – e.g. wheat, cinnamon, anise, chickens and pigs in Mexico. The existence of public and private seed banks has also made it possible for 'lost' commercial varieties to be made available after absences of a few decades. And, it is also highly unlikely that either the Cowboy Junkies or Phish would be unable to play any song in their repertoire given more than a few days' rehearsal. As a result, agents/events within the analyzed human systems tend to be drawn from a uniform pool, with absences being largely the result of occurrence holes or stochastic sampling effects. Such situations should – and do – lead to power-law community distance decay.

While we are unable to analytically prove that exponential community distance decay should be expected in situations where individual species joint-probability curves are also largely exponential, consideration of c_i values for LaRoi and BBS in conjunction with Eq. 8 (the Taylor series expansion), helps explain this correspondence. Recall that convergence to $\exp(-Cd)$ is dependent upon how fast $(\Delta_i d)^n/n!$ converges to zero as n increases. Our empirical data (Fig. 3) indicate that the distribution of Δ_i (or equivalently, c_i) is strongly truncated on both tails, making the values of c_i strongly centered around the mean. As a result c_i (or more specifically $\Delta_i = c_i - \bar{c}_i$) is never larger than a small multiple of $\bar{c}_i$ (e.g. 2–3 times). Second we note that $\bar{c}_i$ is order-of-magnitude close to but slightly larger than $1/d$ such that $c_i d$ is slightly greater than 1 (i.e. approximately in the interval [1,10] for most of the values of d in the decay curve graphs). Since, by tail truncation, Δ_i is never larger than $2\bar{c}_i$ or $3\bar{c}_i$, then $\Delta_i d$ also must fall in the range of roughly 1–10. Additionally note that $(\Delta_i d)^n/n!$ converges on zero quite quickly when $\Delta_i d$ is in the range [1,10]. Also note $\Delta_i d$ is less than 1 when d is close to zero, which also forces a fast convergence on zero. As a result, the Taylor series expansion necessitates a community distance decay function close to $\exp(-Cd)$ when species joint-probability occurrence is exponential and the distribution of c_i values is strongly truncated and order of magnitude close to $1/d$. While providing a numerically based understanding for the preponderance of observed exponential-like community distance decay, this analysis can not be construed as a general proof, as the end result is strongly dependent upon the form of the joint-probability decay curve and c_i distribution properties.

These analyses also document two additional important additional insights regarding the nature of ecological communities. First, it is striking how similar the parameterized and predicted coefficients are between the true and weighted aggregate community distance decay function for large-scale data (Fig. 4; Table 1). This correspondence provides strong evidence of individualistic species sorting (Gleason 1926). Second, the different expected forms for distance decay within (power law) vs between (exponential) communities allows for an empirical test of the observational scales under which communities exist. For instance, in Panamanian tropical forest, strong power-law decay apparent at distances of 1 km or less indicate that samples are being drawn from within the same community. However, the exponential decay observed at distances of 5–100 km indicates that at this larger scale different communities are being surveyed.

Since its popularization within ecological research over a decade ago, there has been a mismatch between theoretical models and empirical results of distance decay analysis. We hope the approach described within this paper helps resolve this conundrum. Specifically, sampling scales associated with small grain, limited extents, and absent/limited environmental gradients are expected to have power-law community distance decay, while sampling scales associated with large grain and strong environmental gradients are expected to have exponential community distance decay.

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References

Allen, J. A. and Sanders, H. L. 1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: the epilogue. – Prog. Oceanogr. 38: 95–153.

Barker, G. M. 2005. The character of the New Zealand land snail fauna and communities: some evolutionary and ecological perspectives. – Rec. West. Aust. Mus. Suppl. 63: 52–102.

Barker, G. M. and Mayhill, P. C. 1999. Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru Ecological District, northeastern New Zealand. – J. Biogeogr. 26: 215–238.

Bell, G. 2003. The interpretation of biological surveys. – Proc. R. Soc. B 270: 2531–2542.

Bird, N. M. 1998. Sustaining the yield: improved timber harvesting practices in Belize, 1992–1998. – Natural Resources Inst., Univ. of Greenwich, NRI Catalog Services, CAB International, Wallingford, UK.

Blanchette, C. A. et al. 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. – J. Biogeogr. 35: 1593–1607.

Chave, J. and Leigh, E. G. Jr 2002. A spatially explicit neutral model of β-diversity in tropical forests. – Theor. Popul. Biol. 62: 153–168.

Condit, R. et al. 2000. Spatial patterns in the distribution of tropical tree species. – Science 288: 1414–1418.

Condit, R. et al. 2002. Beta-diversity in tropical forests. – Science 295: 666–669.

Curtis, J. T. 1955. A prairie continuum in Wisconsin. – Ecology 36: 558–566.

Ernest, S. K. M. et al. 2009. Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. – Ecology 90: 1708.

Gilbert, B. and Lechowicz, M. J. 2004. Neutrality, niches, and dispersal in a temperate forest understory. – Proc. Natl Acad. Sci. USA 101: 7651–7656.

Gleason, H. A. 1926. The individualistic concept of plant association. – Bull. Torrey Bot. Club 53: 7–26.

Green, J. L. and Bohannan, B. J. M. 2006. Spatial scaling of microbial biodiversity. – Trends Ecol. Evol. 21: 501–507.

Green, J. L. and Plotkin, J. B. 2007. A statistical theory for sampling species abundances. – Ecol. Lett. 10: 1037–1045.

Green, J. L. et al. 2004. Spatial scaling of microbial eukaryote diversity. – Nature 432: 747–750.

Harte, J. 2011. Maximum entropy and ecology. – Oxford Univ. Press.

Harte, J. and Kinzig, A. P. 1997. On the implications of species–area relationships for endemism, spatial turnover, and food web patterns. – Oikos 80: 417–427.

Harte, J. et al. 1999. Estimating species–area relationships from plot to landscape scale using species-turnover data. – Oikos 86: 45–54.

He, F. and Legendre, P. 2002. Species diversity patterns derived from species–area models. – Ecology 83: 1185–1198.

Houchmandzadeh, B. 2008. Neutral clustering in a simple experimental ecological community. – Phys. Rev. Lett. 101: 078103.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in population biology no. 32. – Princeton Univ. Press.

Hurlbert, A. H. and White, E. P. 2007. Ecological correlates of geographical range occupancy in North American birds. – Global Ecol. Biogeogr. 16: 764–773.

Jobe, R. T. 2007. Estimating landscape-scale species richness: reconciling frequency- and turnover-based approaches. – Ecology 89: 174–182.

Karlin, S. and Taylor, H. M. 1975. A first course in stochastic processes, 2nd ed. – Academic Press.

LaRoi, G. H. 1967. Ecological studies in the boreal spruce-fir forests of the North American taiga. I. Analysis of the vascular flora. – Ecol. Monogr. 37: 229–253.

LaRoi, G. H. and Stringer, M. H. 1976. Ecological studies in the boreal spruce-fir forests of the North American taiga. II. Analysis of the bryophyte flora. – Can. J. Bot. 54: 619–643.

Lindgren, B. W. 1976. Statistical theory. – Macmillan Publishing.

McGill, B. J. 2010. Towards a unification of unified theories of biodiversity. – Ecol. Lett. 13: 627–642.

McGill, B. J. 2011. Linking biodiversity patterns by autocorrelated random sampling. – Am. J. Bot. 98: 481–502.

McGlinn, D. J. and Palmer, M. W. 2011. Quantifying the influence of environmental texture on the rate of species turnover: evidence from two habitats. – Plant Ecol. 212: 495–506.

McKnight, M. W. et al. 2007. Putting beta-diversity on the map: broad scale congruence and coincidence in the extremes. – PLoS Biol. 5: 2424–2432.

Minchin, P. R. 1987. Simulation of multidimensional community patterns: towards a comprehensive model. – Plant Ecol. 71: 145–156.

Morlon, H. et al. 2008. A general framework for distance-decay of similarity in ecological communities. – Ecol. Lett. 11: 904–917.

Nekola, J. C. 1994. Environment and vascular flora of northeastern Iowa fen communities. – Rhodora 96: 121–169.

Nekola, J. C. 1999. Paleorefugia and neorefugia: the influence of colonization history on community pattern and process. – Ecology 80: 2459–2473.

Nekola, J. C. 2010. Acidophilic terrestrial gastropod communities of North America. – J. Molluscan Stud. 76: 144–156.

Nekola, J. C. and White, P. S. 1999. Distance decay of similarity in biogeography and ecology. – J. Biogeogr. 26: 867–878.

Nekola, J. C. and Brown, J. H. 2007. The wealth of species: ecological communities, complex systems, and the legacy of Frank Preston. – Ecol. Lett. 10: 188–196.

Palmer, M. W. 2005. Distance decay in an old-growth neotropical forest. – J. Veg. Sci. 16: 161–166.

Perez-del-Olmo, A. et al. 2009. Not everything is everywhere: the distance decay of similarity in a marine host–parasite system. – J. Biogeogr. 36: 200–209.

Plotkin, J. B. and Muller-Landau, H. C. 2002. Sampling the species composition of a landscape. – Ecology 83: 3344–3356.

Preston, F. W. 1962. The canonical distribution of commonness and rarity. – Ecology 43: 185–215, 410–432.

Qian, H. et al. 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. – Ecol. Lett. 8: 15–22.

Qian, H. et al. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. – Global Ecol. Biogeogr. 18: 111–122.

Rapoport, E. H. 1982. Areography: geographical strategies of species. – Pergamon Press.

Rocchini, D. and Cade, B. S. 2008. Quantile regression applied to spectral distance decay. – Geosci. Remote Sens. Lett. 5: 640–643.

Root, T. 1989. Atlas of wintering North American birds. – Univ. of Chicago Press.

Sauer, J. R. et al. 2011. The North American Breeding Bird Survey, results and analysis 1966–2009. Version 3.23.2011. – USGS Patuxent Wildlife Research Center, Laurel, MD.

Schlicht, D. W. et al. 2007. The butterflies of Iowa. – Univ. of Iowa Press.

Soininen, J. et al. 2007. The distance decay of similarity in ecological communities. – Ecography 30: 3–12.

Smith, J. 1990. The frugal gourmet on our immigrant ancestors. – Harper-Collins.

Steinitz, O. et al. 2005. Predicting regional patterns of similarity in species composition for conservation planning. – Conserv. Biol. 19: 1978–1988.

Svenning, J.-C. et al. 2004. Ecological determinism in plant community structure across a tropical forest landscape. – Ecology 85: 2526–2538.

Tobler, W. R. 1970. A computer movie simulating urban growth in the Detroit region. – Econ. Geogr. 46: 234–240.

Tuomisto, H. et al. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. – Science 299: 241–244.

Voss, E. G. 1985. Michigan flora. – Cranbrook Inst. of Science, Bloomfield Hills, MI, Bulletin 59.

Whittaker, R. H. 1975. Communities and ecosystems. – MacMillan Publishing.

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IDEA AND PERSPECTIVE

The wealth of species: ecological communities, complex systems and the legacy of Frank Preston

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Abstract

General statistical patterns in community ecology have attracted considerable recent debate. Difficulties in discriminating among mathematical models and the ecological mechanisms underlying them are likely related to a phenomenon first described by Frank Preston. He noted that the frequency distribution of abundances among species was uncannily similar to the Boltzmann distribution of kinetic energies among gas molecules and the Pareto distribution of incomes among wage earners. We provide additional examples to show that four different 'distributions of wealth' (species abundance distributions, species–area and species–time relations, and distance decay of compositional similarity) are not unique to ecology, but have analogues in other physical, geological, economic and cultural systems. Because these appear to be general statistical patterns characteristic of many complex dynamical systems they are likely not generated by uniquely ecological mechanistic processes.

Keywords

Community ecology, competitive sorting, complexity science, distance decay, ecological theory, neutral models, species–abundance distribution, species–area relationship, species–time relationship, statistical mechanics.

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Frank Preston (1950) published a little paper on 'Gas Laws and Wealth Laws' in *The Scientific Monthly*. In it he commented on the remarkable similarities between the Boltzmann frequency distribution of molecular kinetic energies in gasses, the Pareto frequency distribution of personal incomes in countries, and the frequency distribution of species abundances in ecological communities. After noting how such distributions might arise, he went on to remark – in comments which would now be politically incorrect in reference to personal incomes – about whether it is 'wise to try to change the laws of nature'.

Interest in community 'distributions of wealth' (DOWs), in particular the species–abundance distribution (SAD), species–area relationship (SAR), species–time relationship (STR), and distance decay of compositional similarity (DD), have preoccupied community ecologists ever since Preston's seminal papers (Preston 1948, 1962a,b, 1980; see also Williams 1964; MacArthur 1972; May 1975; Nee *et al.* 1991; Rosenzweig 1995; Nekola & White 1999; Gaston & Blackburn 2000; Hubbell 2001). As new, larger, and more comprehensive data sets have become available, the discipline of community ecology has been enlivened by debate over which of several different conceptual frameworks or formal mathematical models might be necessary or sufficient to explain these patterns.

These debates have primarily had two foci. First, authors have argued about the relative roles of 'competitive' (deterministic ecological differences between species) vs. 'neutral' (stochastic processes of birth, death and dispersal) mechanisms in community assembly. This issue has been difficult to resolve as formal models invoking complete neutrality generate very similar outcomes to models that assume unique species-level abiotic requirements or strong biotic interactions (e.g. Bell 2000; Chave *et al.* 2002; Mouquet & Loreau 2003; Chave 2004; Tilman 2004; Gaston & Chown 2005).

The second focus has been about which particular mathematical distribution (and corresponding ecological mechanism) best describes empirical DOWs. This debate has been constrained by the fact that mathematical distributions having different mechanistic interpretations can be very difficult to empirically distinguish. For instance, it has proved extremely difficult to determine whether a particular SAD data set is best fit by a power law, truncated log-normal, or zero sum multinomial (ZSM) distribution (e.g. McGill 2003a; Volkov *et al.* 2003; Chave 2004; Etienne & Olff 2005), and similarly whether a power law or exponential distribution best fits a given SAR/STR relationship (Loehle 1990; White *et al.* 2006). May (1975) and Connor & McCoy (1979) made these points decades ago for the SAD and SAR.

We regard as healthy the renewed interest in community ecology, and especially the focus on large-scale, multispecies macroecological pattern and process which are often not amenable to testing by manipulative experiments. But we also wonder whether the current framing of questions and tenor of debates are productive. Perhaps, as Preston suggested, DOWs are not the unique provenance of ecology, but rather are common properties of many seemingly disparate systems. If so, it may be best to seek explanations for these patterns that are as general as the systems that exhibit them.

To address this issue, we have extended Preston's examples to a broader selection of data sets spanning a wide range of physical and human economic, social and artistic systems. ***Physical systems:*** (i) Yearly precipitation averages for each of 1027 North American sites (see Nekola 2005). These data are based on 1-km resolution global precipitation maps created by the WORLDCLIM Project (http://www.worldclim.org); (ii) Mineral species richness from county to global scales, as reported by the MINDAT data base (http://www.mindat.org). Data represent the total number of minerals for the entire terrestrial globe, for 10 countries (Australia, Canada, Chile, China, India, Mexico, Namibia, Turkey, the UK and the USA), all the USA states (including the District of Columbia), all Canadian provinces/territories, and two selected counties per state. Areas for each unit were based on data provided with ArcMap 9.1 (ESRI, Redlands, California, USA). ***Economic systems:*** 2004 Stock volumes for all publicly traded corporations in the USA, based on data reported by Bloomberg (http://pages.stern.nyu.edu/~adamodar/New_Home_Page/data.html). ***Social systems:*** (i) Citation frequencies for all papers catalogued by the *Institute for Scientific Information* from 1981 to 1997 (http://physics.bu.edu/~redner/projects/citation/isi.html); (ii) the list of all commercially sold garden vegetable varieties in the USA and Canada from 1981 to 2004 as reported by the Garden Seed Inventory of the Seed Savers Exchange; (iii) the list of all ingredients reported in recipes for 10 global cuisines (Ethiopia, Hungary, India, Iran, Ireland, Korea, Mexico, Norway, Puerto Rico and Thailand) from Smith (1990). ***Artistic systems:*** (i) The number of unique words and total word length for the 1863 texts documented in Project Gutenberg as of 2000 (http://www.mine-control.com/zack/guttenberg/); (ii) concert setlists for 33 approximately evenly spaced Cowboy Junkies performances from 1987 to 2006 (http://setlist.com).

Using standard ecological protocols (e.g. 'octaves' or $\log_2$ bin widths for SADs and Jaccard's similarity in the calculation of compositional similarity between all pairwise combinations of observations for DD analyses), we treated each as if they were ecological data sets. All DOW analogues were calculated from the Cowboy Junkies example, as only this data set provided abundance data across multiple observations. For the remaining, analyses were limited to the DOW equivalents that could be assessed from the given data: SAD analogues for precipitation class frequencies, stock volumes and scientific citations; SAR analogues for mineral species richness and Project Gutenberg texts; STR analogues for North American garden seed offerings; and DD analogues for global cuisine and vegetable seed offerings.

These analyses corroborate Preston's observation that typical DOW patterns are by no means unique to ecological systems. North American precipitation classes, 2004 stock volumes, scientific citation frequency and song frequencies from Cowboy Junkies setlists (Fig. 1) are all similar to truncated log-normal or ZSM distributions with rare events being more frequent than abundant ones. Using code developed by McGill (2003a) the ZSM can be shown to well fit both the precipitation ($\theta = 55.173$, $m = 0.179$) and Cowboy Junkies setlist ($\theta = 89.446$, $m = 0.240$) data. Power law SAR and STR-like relationships are also widespread (Fig. 2), being observed not only for the accumulation of mineral species across space, but also for unique words as a function of book size and for unique vegetable varieties and Cowboy Junkies song performances as a function of time. The fitted relationships explained 46–99% of observed variance. Finally, nonlinear DD relationships are also common (Fig. 3), being evident in cuisine ingredient lists, the garden seed industry, and Cowboy Junkies setlists. For these examples, power law decay models fit best, accounting for 38–88% of observed variance.

The convergence between ecological and non-ecological community patterns is not limited to these examples. In his final *Ecology* paper, Preston (1981) documented rarity-enriched ZSM-like SAD analogues for the service life of restaurant drink tumblers, the static fatigue of glass and other materials, and first marriage age for Danish, UK and the USA women. Power law STR analogues have also been noted in comprehensive examination scores for degree candidates in the University of Oslo, Department of Biology and for Norsk Hydro stock prices on the Norwegian market (Ugland *et al.* 2005). And, given the convergence between the body-size distribution of beetles in Borneo tree canopies and cars in York and Heathrow Airport parking lots (Gaston *et al.* 1993), it appears such similarities may not be limited to DOWs.

These examples caution that the general mechanisms generating many familiar DOW patterns are not unique to ecology. Certainly, the processes of birth, death,

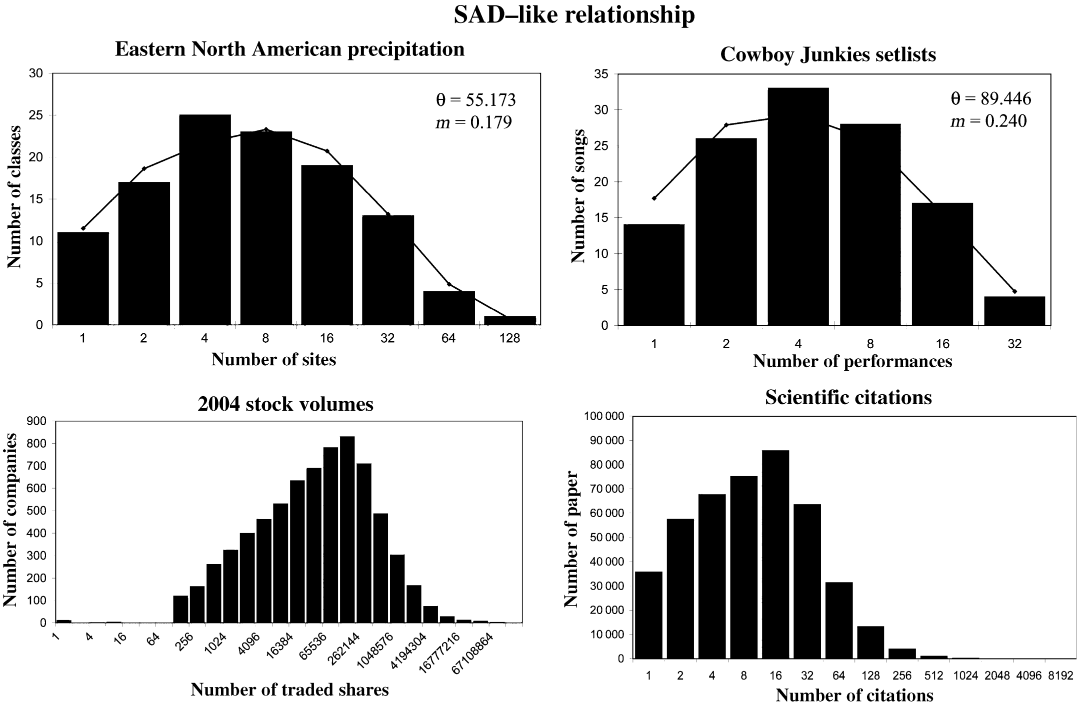

Figure 1 Species–abundance distribution analogues for non-ecological systems, including North American precipitation classes, stock volumes for all publicly traded US corporations, song performances for Cowboy Junkies setlists, and citation frequencies for scientific papers. All distributions have been binned into $\log_2$ 'octaves'. For precipitation classes and Cowboy Junkies performance frequencies, the best-fit zero sum multinomial distribution has also been calculated using code provided by McGill (2003a). These best-fit curves are presented as the graphed lines in both of these panels.

immigration and speciation invoked by Hubbell (2001), or the competitive tradeoffs invoked by Tilman (2004) or Chave *et al.* (2002) could not have generated the ZSM-like SADs for precipitation classes, paper citations, stock volumes, drink tumbler longevity, and marriage ages, or power law SARs/STRs for unique mineral, word, and garden seed occurrences, or comprehensive examination scores. Conversely, it seems unlikely that Cowboy Junkies performances mimic community ecology process, even though they display rarity-enriched SAD, power law STD and nonlinear DD patterns.

Preston (1950) concluded that the remarkable convergence between the Boltzmann, Pareto and SAD might be the result of 'statistical mechanics'. Even though he could not identify the common underlying mechanisms, he urged scientists to 'understand [this] law, and the causes that bring it about'. We question whether the recent revival of interest in ecological DOWs has advanced this goal. These congruent patterns seem to beg for some kind of explanation that is both more universal and also less explicitly mechanistic than the kinds typically sought and offered by community ecologists.

Over the last few decades investigations in the new interdisciplinary field of complexity science have begun to address such issues. Complexity science developed as natural and social scientists sought to identify and explain common features exhibited by complex dynamical systems in such seemingly disparate fields as quantum physics, computer science, economics, sociology, political science, linguistics, astronomy, geology and meteorology. While a single definition for a 'complex system' remains elusive, a number of common features have been identified (Brown 1994a,b; West 2006a,b):

(1) They are composed of many components of many different kinds.
(2) These components interact with each other and the extrinsic environment in many different ways and on multiple spatial and temporal scales.
(3) These interactions give rise to complex structures and complicated nonlinear dynamics.
(4) These structures and dynamics are neither completely stochastic nor entirely deterministic, but instead represent a combination of randomness and order.
(5) They contain both positive and negative feedback mechanisms, causing either amplification or damping of temporal and spatial variation, depending on conditions.

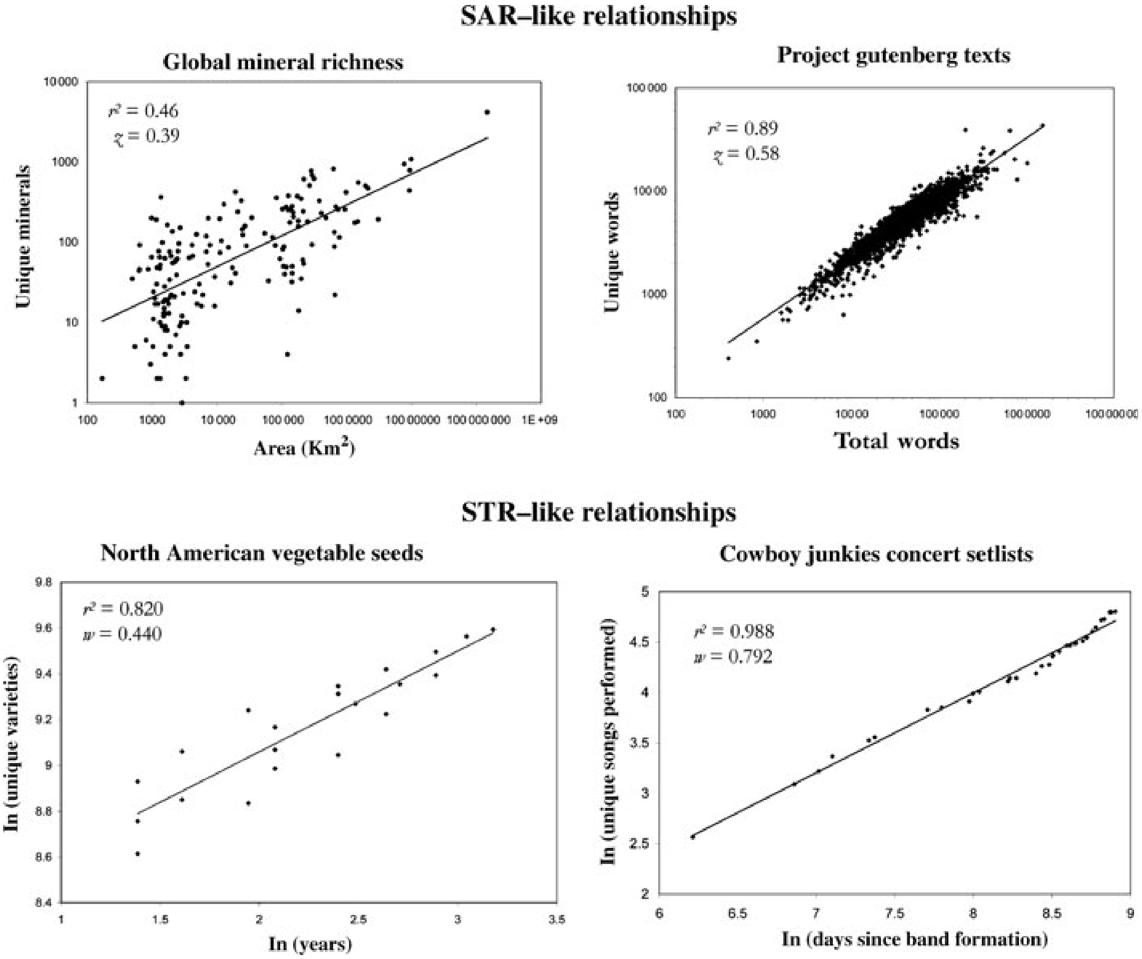

Figure 2 Species–area relationship and species–time relationship analogues for non-ecological systems, including the accumulation of unique mineral varieties by sample area, unique words by total document words, and unique vegetable varieties and Cowboy Junkies songs by time. All data are graphed on log-transformed axes. Best-fit linear regression lines have been plotted for each relationship.

(6) They are open systems which require exchanges of energy, materials, and/or information from extrinsic sources to maintain highly organized states far from thermodynamic equilibrium.
(7) They are historically contingent, so that their present configurations reflect the influence of initial conditions and subsequent perturbations.
(8) They are often nested within other complex systems, giving rise to hierarchical organizations that can be approximated by fractal geometry and dynamic scaling laws.

Ecological communities clearly demonstrate these features. Even the simplest contain thousands to billions of individuals of tens to thousands of different species, ranging from unicellular procaryotes, protists, and fungi to multicellular plants and animals. These individuals and species interact with each other and their extrinsic abiotic environment across multiple spatial and temporal scales. These relationships are often inherently nonlinear, ranging from Michaelis–Menten curves for nutrient uptake to exponential or logistic population growth to the normal, skewed or bimodal distribution of species along environmental gradients. Feedbacks are prevalent, as demonstrated by effects of keystone species on ecosystem function or fuel buildup on fire return frequencies. Ecological communities require the continual transformation of energy, material and information to maintain their highly organized, far-from-equilibrium thermodynamic states. Many ecological processes are historically contingent, with contemporaneous patterns reflecting legacies of past events in both shallow (e.g. the sequence of habitat colonization) and deep (e.g. plate tectonics and evolution) time. And finally, ecological communities are composed of nested hierarchies of complex components, ranging from organic

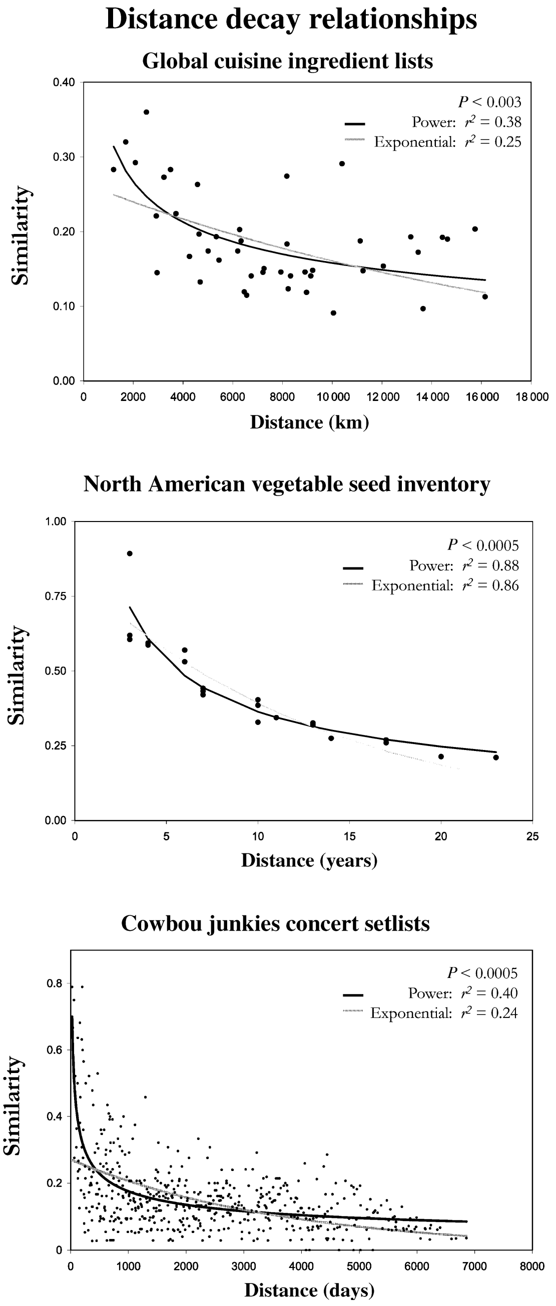

Figure 3 Distance decay analogues for non-ecological systems, including the change of compositional similarity of global cuisine ingredient lists over space, and garden seed offerings and Cowboy Junkies song performances over time. Best-fit exponential and power law decay lines have been plotted for each relationship.

molecules and cells through populations, species, guilds and trophic levels.

Because of these shared structural and dynamical properties, ecological communities and other kinds of complex systems tend to develop similar patterns of whole-system structure and dynamics. An example of this is the occurrence of many small and few large magnitude events, which can be observed in the cumulative frequency distributions of word use, scientific paper citations, Internet web hits, copies of books sold, telephone calls received on a single day, earthquake magnitudes, lunar crater diameters, solar flare intensity, deaths in wars, wealth of rich people, surname frequencies, and city populations (Newman 2005). These patterns can often be nearly equally well fit by power law or log-normal probability distribution functions (West & Shlesinger 1989). The finding of DOW analogues (rarity-enriched SADs, roughly power law SAR and STR, and nonlinear DD) across multiple non-ecological systems thus suggests that these patterns represent shared statistical properties of a large class of complex systems. To discover the 'law' sought by Preston to explain these striking convergences may therefore require an understanding of the general principles that govern the structure and dynamics of all these systems.

The uncanny similarity of ecological DOWs to those exhibited by other complex systems has been largely ignored by community ecologists, who for the most part have sought explanation strictly from biological processes (but see Limpert *et al.* 2001; McGill 2003b; Halloy & Whigham 2004; Ugland *et al.* 2005). A few authors have pointed out phenomenological similarities between ecological and other complex systems and suggested that these may hold clues to common causes (e.g. Preston 1950, 1981; May 1975, 1981; Bak *et al.* 1987; Brown 1994b; Brown *et al.* 2000, 2002; Allen & Holling 2002; Solé & Bascompte 2006), but others have suggested that such similarities are spurious (Root 1989). Until such convergences are taken seriously and efforts are made to identify their root causes, community ecology risks becoming a myopic enterprise.

There are, in fact, a number of general processes that might influence wealth accumulation across a wide variety of systems. First, and perhaps most importantly, log-normal and mathematically related power law probability distributions are easily generated by the multiplicative rather than additive interaction of variables. Such processes have been shown to commonly apply to many physical (Meijer *et al.* 1981), biological (May 1975; McGill 2003b) and human systems (Montroll & Shlesinger 1982). Even the log-normal distribution of publication rates for researchers within scientific institutions is governed by such multiplicative processes (Shockley 1957). Similar distributions may also be generated by the interaction of multiple agents governed by nonlinear processes (Bak *et al.* 1987; West & Shlesinger 1989). Because of these processes, rarity-enriched SAD analogues may be a universal expectation for many complex systems (McGill 2003b). Second, many physical, biological and human systems exist within environments that exhibit power law or fractal-like spatial and temporal variation

(Mandelbrot 1982; Milne 1991; Ritchie & Olff 1999; Brown *et al.* 2002). Not only can these environmental templates be generated via simple hierarchical random models (Sizling & Storch in press), but can also in turn give rise to typical DOW patterns such as the power law SAR and nonlinear DD (Sizling & Storch 2004; Harte *et al.* 2005). Third, proximity effects, which occur when the influence of an event on an agent is dependent upon the distance in space and/or time between agent and event, occur in many physical, biological and human systems. Such relationships may be found across phenomena as diverse as electromagnetic radiation and gravitation to natural disturbances, dispersal and diffusion to migration, trade and wars. Proximity effects not only can directly give rise to DD relationships (Nekola & White 1999), but also can be an important source of multiplicative relationships over space or time. It is also possible to identify direct analogues in the processes governing different systems. For instance, both ecological and human systems exhibit hierarchical arrangements of agents, including individuals within populations and soldiers within armies and specialized classes of workers within insect societies and manufacturing firms. The structures and dynamics of both ecological and human systems also reflect a complicated dynamic balance among diverse cohesive and divisive forces, such as mutualism, reciprocity, and cooperation on the one hand and self-interest, competition, and predatory or parasitic exploitation on the other. The joint effects of such factors conspire to ensure that 'wealth' is distributed highly unequally among agents and nonlinearly over space or time.

What lessons can be learned from viewing ecological communities as complex systems and ecological DOWs as shared statistical properties of such systems? First, the mechanistic explanation for many of ecology's most venerable statistical patterns lie at a level of abstraction extending far beyond the realm of ecological process. The paradox that rarity-enriched SADs, power law SAR/STR, and nonlinear DD are generated by models assuming either complete neutrality or resource competition is therefore explained by realizing both models generate dynamical complexity. In competition models complexity arises as multiple agents, each with individualistic resource utilization and dispersal functions, interact in an elaborate network with multiple other agents often over multiple temporal and spatial scales. Such interactions can be made even more complicated and realistic by inclusion of some degree of stochasticity in resource requirements and dispersal processes (Tilman 2004). In neutral models complexity arises as multiple agents, each with a unique community and metacommunity frequency, undergo a lottery for recruitment of vacated spaces. These interactions are further complicated as new species are supplied to the system across multiple scales via dispersal and speciation. As a result it may prove impossible to infer underlying mechanisms from DOW mathematical forms, both in general and for specific cases. However, this should not suggest that efforts to adduce ecological community assembly mechanisms must be abandoned. For instance, while a power law relationship describes the relationship between mean and variance for heartbeat frequency or interstride interval, the slope of this function supplies information about the relative importance of deterministic vs. stochastic drivers (West & Latka 2005; West 2006b). Similar mechanistic inferences can be made in ecological systems. In the case of the SAR, it has long been recognized that differences in slope over local-to-global scales or between islands and mainlands convey information about the mechanisms that generate and maintain diversity (Rosenzweig 1995). Similarly, DD rates provide information about niche characteristics and dispersal capacities in relation to the environmental template of spatial and temporal variations. So, for example, isolated spruce-fir forests of the Appalachians demonstrate an almost threefold greater DD rate when compared with continuous northern Taiga, and large-fruited, more dispersal-limited plant species have almost twice the DD rate when compared with smaller-seeded taxa (Nekola & White 1999).

Second, we question the utility of investing great effort to determine whether competition or neutrality might be responsible for observed DOWs when there is no logical reason to expect these mechanisms to be mutually exclusive – or, for that matter, to represent the only possible alternatives. Such patterns are almost certainly generated by combinations of stochastic and deterministic processes, local and regional processes, current and historical events, biotic interactions and abiotic factors, direct and indirect interactions, and cohesive and divisive forces. Similarly, diverse combinations of factors likely generate analogous properties in some physical and many human social and economic systems.

Third, it is long overdue that community ecologists keep abreast of developments in the field of complexity science. We are not suggesting that complexity science has all the solutions to the big important questions of community ecology. Indeed, complexity science is struggling to address similar problems and can currently offer few definitive answers. However, we are suggesting that ecological, physical and social scientists have much to learn from each other. Ideas, models and data from community ecology have the potential to make important contributions to complexity science, just as theoretical and empirical advances in complexity science have the potential to enlighten community ecology. This focus on interdisciplinarity is not a revolutionary concept. Community ecology has a long tradition of borrowing ideas and techniques from many other fields including economics (e.g. law of supply and demand, MacArthur & Wilson 1967; game theory, Smith 1982; Gini coefficients, Weiner & Solbrig 1984; supply side ecology, Roughgarden *et al.* 1987), geography (DD, Nekola & White 1999; gravity models, Bossenbroek *et al.* 2001); the behavioural sciences (e.g. multidimensional scaling ordination, Minchin 1987), and physics (e.g. diffusion models, Skellam 1951; chaos, May 1976; percolation theory, O'Neill *et al.* 1992).

Finally, complexity science suggests that certain aspects of community ecology may never be highly predictable. While qualitative forecasts may be possible, the precise quantitative prediction of individual events may pose insurmountable challenges. For example, while it might be possible to predict qualitatively how community-wide SADs and SARs will be altered by invasions of multiple exotic species, it will be much more difficult to exactly predict resultant species abundances and spatial distributions. Indeed, such an effort may be as quixotic as attempting to predict the exact location of an electron in a shell or date and magnitude of the next earthquake in the San Francisco Bay area or price of General Motors stock in 2050. As in weather forecasting, some level of short-term predictability will often be possible from understanding current drivers, recent trajectories, and spatial/temporal autocorrelations. However, predictions based on these dynamics will necessarily become increasingly imprecise as the forecast period increases.

Rather than emphasizing prediction, community ecologists perhaps should spend more effort on understanding the mechanisms and events that have conspired to generate current and past patterns. Even when it may be practically impossible to predict the exact future trajectory of a system, by looking backward it may be possible to deduce quite accurately when and how specific mechanisms came into play. In complex human systems mechanisms are deduced by historians who analyse *post hoc* the particular combination of initial conditions and drivers that generated pattern. Similarly, community ecologists could enhance their understanding of the spatial and temporal patterns of biodiversity by becoming better natural historians, using *post hoc* analysis to decipher how past events have left lasting influences. By retrospectively studying systems, community ecologists may thus be able to establish what factors lead to the dominance of a particular taxon or to the occurrence of a particular hantavirus outbreak or simply whether Schrödinger's Cat survived.

For community ecology to continue making exciting advances, it must recognize that the distribution of abundance among species has much in common with distributions of 'wealth' in many other non-ecological systems. The fact that the distribution of species abundance is very similar to the distribution of drinking glass longevities or Cowboy Junkies song performances is thus both empowering and humbling in equal parts. While such similarities suggest a possible unification between ecological communities and other complex systems, they also suggest that many of ecology's cherished fundamental patterns may reflect general phenomena that have more in common with statistical physics than species biology. The apparent universality of the rarity-enriched SAD, power law SAR/STR, and nonlinear DD suggests that community ecologists should pay attention to these more fundamental levels of inquiry and explanation. Complexity researchers of all types, including community ecologists, would be well advised to follow Frank Preston's path and to focus on the common factors that underlie these seemingly ubiquitous distributions of wealth.

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REFERENCES

Allen, C.R. & Holling, C.S. (2002). Cross-scale structure and scale breaks in ecosystems and other complex systems. *Ecosystems*, 5, 315–318.

Bak, P., Tang, C. & Wiesenfeld, K. (1987). Self-organized criticality: an explanation of 1/f noise. *Phys. Rev. Lett.*, 59, 381–384.

Bell, G. (2000). The distribution of abundance in neutral communities. *Am. Nat.*, 155, 606–617.

Bossenbroek, J.M., Kraft, C.E. & Nekola, J.C. (2001). Prediction of long-distance dispersal using gravity models: Zebra Mussel invasion of inland lakes. *Ecol. Appl.*, 11, 1178–1788.

Brown, J.H. (1994a). Organisms and species as complex adaptive systems: linking the biology of populations with the physics of ecosystems. In: *Linking Species and Ecosystems* (eds Jones, C.G. & Lawton, J.H.). Chapman and Hall, London, pp. 16–24.

Brown, J.H. (1994b). Complex ecological systems. In: *Complexity: Metaphors, Models, and Reality* (eds Cowan, G.A., Pines, D. & Melzer, D.). Santa Fe Institute Studies in the Science of Complexity, Proceedings Volume XVIII. Addison-Wesley, Reading, pp. 419–449.

Brown, J.H., West, G.B. & Enquist, B.J. (2000). Scaling in Biology: Patterns and processes, causes and consequences. In: *Scaling in Biology* (eds Brown, J.H. & West, G.B.). Oxford University Press, Oxford, pp. 1–24.

Brown, J.H., Gupta, V.K., Li, B.L., Milne, B.T., Restrepo, C. & West, G.B. (2002). The fractal nature of nature: power laws, ecological complexity, and biodiversity. *Proc. R. Soc. Lond. B, Biol. Sci.*, 357, 619–626.

Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.

Chave, J., Muller-Landau, H.C. & Levin, S.A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.*, 159, 1–23.

Connor, E.F. & McCoy, E.D. (1979). The statistics and biology of the species–area relationship. *Am. Nat.*, 113, 791–833.

Etienne, R.S. & Olff, H. (2005). Confronting different models of community structure to species–abundance data: a Bayesian model comparison. *Ecol. Lett.*, 8, 493–504.

Gaston, K.J. & Blackburn, T.M. (2000). *Pattern and Process in Macroecology*. Blackwell Science, Oxford.

Gaston, K.J. & Chown, S.L. (2005). Neutrality and the niche. *Funct. Ecol.*, 19, 1–6.

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1993). Comparing animals and automobiles: a vehicle for understanding body size and abundance relationships in species assemblages? *Oikos*, 66, 172–178.

Halloy, S. R. P. & Whigham, P.A. (2004). The lognormal as universal descriptor of unconstrained complex systems: a unifying theory for complexity. In: *Proceedings of the 7th Asia-Pacific Complex Systems Conference*. Cairns Convention Centre, Cairns, Qld, Australia, pp. 309–320.

Harte, J., Conlisk, E., Ostling, A., Green, J.L., Smith, A.B. (2005). A theory of spatial structure in ecological communities at multiple spatial scales. *Ecol. Monogr.*, 75, 179–197.

Hubbell, S.P. (2001). The unified neutral theory of biodiversity and biogeography. *Monographs in Population Biology #32*. Princeton University Press, Princeton, NJ.

Limpert, E., Stahel, W.A. & Abbt, M. (2001). Log-normal distributions across the sciences: keys and clues. *Bioscience*, 51, 341–352.

Loehle, C. (1990). Proper statistical treatment of species–area data. *Oikos*, 57, 143–146.

MacArthur, R.H. (1972). *Geographical Ecology*. Harper and Row, New York, NY.

MacArthur, R.H. & Wilson, E.O. (1967). Theory of island biogeography. *Monographs in Population Biology #1*. Princeton University Press, Princeton, NJ.

Mandelbrot, B.B. (1982). *The Fractal Geometry of Nature*. W.H. Freeman & Co., New York, NY.

May, R.M. (1975). Patterns of species abundance and diversity. In: *Ecology and Evolution of Communities* (eds Cody, M.L. & Diamond, J.). Belknap Press of Harvard University Press, Cambridge, MA, pp. 81–120.

May, R.M. (1976). Simple mathematical models with very complicated dynamics. *Nature*, 261, 459–467.

May, R.M. (1981). Patterns in multi-species communities. In: *Theoretical Ecology* (ed. May, R.M.). Blackwell Scientific, Oxford, pp. 197–227.

McGill, B.J. (2003a). A test of the unified neutral theory of biodiversity. *Nature*, 422, 881–885.

McGill, B.J. (2003b). Strong and weak tests of macroecological theory. *Oikos*, 102, 679–685.

Meijer, P.H.E., Mountain, R.D. & Soulen, R.J. Jr (1981). *Sixth International Conference on Noise in Physical Systems*. National Bureau of Standards Special Publication #614, Washington, DC.

Milne, B.T. (1991). Lessons from applying fractal models to landscape patterns. In: *Quantitative Methods in Landscape Ecology* (eds Turner, M.G. & Gardner, R.H.). Springer-Verlag, New York, NY, pp. 199–235.

Minchin, P.R. (1987). An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, 69, 89–108.

Montroll, E.W. & Shlesinger, M.F. (1982). On 1/f noise and other distributions with long tails. *Proc. Natl Acad. Sci. USA*, 79, 3380–3383.

Mouquet, N. & Loreau, M. (2003). Community patterns in source-sink metacommunities. *Am. Nat.*, 162, 544–557.

Nee, S., Harvey, P.H. & May, R.M. (1991). Lifting the veil on abundance patterns. *Proc. R. Soc. Lond. B, Biol. Sci.*, 243, 161–163.

Nekola, J.C. (2005). Latitudinal richness, evenness, and shell size gradients in eastern North American land snail communities. *Rec. West. Aust. Mus. Suppl.*, 68, 39–51.

Nekola, J.C. & White, P.S. (1999). Distance decay of similarity in biogeography and ecology. *J. Biogeogr.*, 26, 867–878.

Newman, M.E.J. (2005). Power laws, Pareto distributions, and Zipf's law. *Contemp. Phys.*, 46, 323–351.

O'Neill, R.V., Gardner, R.H. & Turner, M.G. (1992). A hierarchical neutral model for landscape analysis. *Landscape Ecol.*, 7, 55–61.

Preston, F.W. (1948). The commonness, and rarity, of species. *Ecology*, 29, 254–283.

Preston, F.W. (1950). Gas laws and wealth laws. *Sci. Mon.*, 71, 309–311.

Preston, F.W. (1962a). The canonical distribution of commonness and rarity – I. *Ecology*, 43, 185–215.

Preston, F.W. (1962b). The canonical distribution of commonness and rarity – II. *Ecology*, 43, 410–432.

Preston, F.W. (1980). Noncanonical distributions of commonness and rarity. *Ecology*, 6, 88–97.

Preston, F.W. (1981). Pseudo-lognormal distributions. *Ecology*, 62, 355–364.

Ritchie, M.E. & Olff, H. (1999). Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, 400, 557–560.

Root, R.B. (1989). Resolution of respect Frank W. Preston 1896–1989. *Bull. Ecol. Soc. Am.* 70, 244–247.

Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Roughgarden, J., Gaines, S.D. & Pacala, S.W. (1987). Supply-side ecology: the role of physical transport processes. *Symp. Br. Ecol. Soc.*, 27, 491–518.

Shockley, W. (1957). On the statistics of individual variations of productivity in research laboratories. *Proc. Inst. Radio Eng.*, 45, 279–290.

Sizling, A.L. & Storch, D. (2004). Power-law species-area relationships and self-similar species distributions within finite areas. *Ecol. Lett.*, 7, 60–68.

Sizling, A.L. & Storch, D. (in press). Geometry of species distributions: random clustering and scale invariance. In: *Scaling Biodiversity* (eds Storch, D., Marquet, P.A. & Brown, J.H.), Cambridge University Press, Cambridge.

Skellam, J.G. (1951). Random dispersal in theoretical populations. *Biometrika*, 38, 196–218.

Smith, J.M. (1982). *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Smith, J. (1990). *The Frugal Gourmet on our Immigrant Ancestors*. Harper-Collins, New York, NY.

Solé, R.V. & Bascompte, J. (2006). *Self-organization in complex ecosystems. Monographs in Population Biology #42*. Princeton University Press, Princeton, NJ.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl Acad. Sci. USA*, 101, 10854–10861.

Ugland, K.I., Gray, J.S. & Lambshead, J.D. (2005). Species accumulation curves analysed by a class of null models discovered by Arrhenius. *Oikos*, 108, 263–274.

Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.

Weiner, J. & Solbrig, O.T. (1984). The meaning and measurement of size hierarchies in plant populations. *Oecologia*, 61, 334–336.

West, B.J. (2006a). Thoughts on modeling complexity. *Complexity*, 11, 33–43.

West, B.J. (2006b). Complexity, scaling and fractals in biological signals. In: *Wiley Encyclopedia of Biomedical Engineering* (ed. Akay M.). Wiley-Interscience, New York, NY.

West, B.J. & Latka, M. (2005). Fractional Langevin model of gait variability. *J. Neuroeng. Rehabil.*, 2, 24.

West, B.J. & Shlesinger, M.F. (1989). On the ubiquity of 1/f noise. *Int. J. Mod. Phys. B*, 3, 795–819.

White, E.P., Adler, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., Kaufman, D.M. *et al.* (2006). A comparison of the species–time relationship across ecosystems and taxonomic groups. *Oikos*, 112, 185–195.

Williams, C.B. (1964). *Patterns in the Balance of Nature and Related Problems in Quantitative Biology*. Academic Press, London.

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PREDICTION OF LONG-DISTANCE DISPERSAL USING GRAVITY MODELS: ZEBRA MUSSEL INVASION OF INLAND LAKES

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Abstract. Gravity models are commonly used by geographers to predict migration and interaction between populations and regions. Even though rarely used by ecologists, gravity models allow estimation of long-distance dispersal between discrete points in heterogeneous landscapes. We developed a production-constrained gravity model to forecast zebra mussel (*Dreissena polymorpha*) dispersal into inland lakes of Illinois, Indiana, Michigan, and Wisconsin (USA) based on the site and location of lakes and the number and location of boats within 364 counties. A deterministic form of this model was used to estimate best-fit parameters for distance coefficient, Great Lakes boat-ramp attractiveness, and colonization cutoff threshold. A stochastic model thus developed from these parameters allows for random changes in colonization likelihood. The results of our model are highly correlated with the actual pattern of colonized lakes in southern Michigan and southeastern Wisconsin at the end of 1997. Areas of central Wisconsin and western Michigan, where zebra mussel colonies have not been documented, were also predicted to be colonized, suggesting that future invasions may be imminent in these locations. These analyses suggest that gravity models may be useful in predicting long-distance dispersal when dispersal abilities of species and the attractiveness of potential habitats are known.

Key words: colonization; exotic species invasion; gravity model; gravity models vs. diffusion models; invasion of aquatic habitats; lakes, upper Midwest (USA); landscape ecology; long-distance dispersal, modeling; migration; modeling dispersal patterns; spatial interaction; zebra mussels.

INTRODUCTION

Understanding long-distance dispersal is essential to predicting the spatial and temporal patterns of colonization within heterogeneous landscapes. Patterns of species colonization have primarily been predicted through diffusion models (Shigesada and Kawasaki 1997). While early diffusion models assumed a homogeneous landscape with dispersal resulting from short-range random movements (Skellam 1951), more recently, stratified diffusion models have been implemented to also incorporate long-distance dispersal events (Hengeveld 1989, Shigesada and Kawasaki 1997) that permit organisms to "jump" over or across habitats (Lewis 1997).

Even with these advancements, diffusion models have difficulty in predicting long-range dispersal events and, because of this, organism movement as well. For example, Andow et al. (1990) suggested that macroscale processes, such as air currents or human transport, govern the dispersal of the cereal leaf beetle (*Oulema melanopus*). Surveys of rare, long-distance boater movements provided a better indicator of zebra mussel (*Dreissena polymorpha*) dispersal than diffusion models (Buchan and Padilla 1999). Thus, in spite of their rarity, long-distance dispersal events appear to drive migration patterns for many species (Dean 1998).

Gravity models allow for the prediction of long-distance dispersal events by considering not only the nature of source populations, but also the spatial configuration and nature of potential colonization sites. Because of this, gravity models have the potential to more accurately forecast species movement through heterogeneous landscapes than do diffusion models, which do not explicitly consider the spatial pattern of distant sites. Geographers have used gravity models to predict human dispersal patterns by estimating the flow of people per unit time based on the distance to and attractiveness of destination points (Thomas and Hugget 1980, Sklar and Costanza 1991). Schneider et al. (1998) used a gravity model to assess the relative risk of zebra mussel invasions to the inland lakes and reservoirs of Illinois (USA).

The colonization of inland lakes in the Upper Midwest (USA) by zebra mussels presents an ideal system for testing the use of gravity models for prediction of long-distance dispersal. The spread of zebra mussels across the North American landscape has been closely monitored since their initial North American discovery in 1988 (Hebert et al. 1989). Range expansion quickly occurred throughout commercially navigable waters (Griffiths et al. 1991), but overland dispersal into inland lakes has been slower (Kraft and Johnson 2000). The

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first U.S. inland lake colonization occurred in 1991 in northeast Indiana, and by December 1997 only 56 inland lakes were colonized in Michigan (37 lakes), Indiana (12 lakes), Wisconsin (6 lakes), and Illinois (1 lake) (Kraft and Johnson 2000).

Although many other potential mechanisms exist (Carlton 1993), the overland transport of recreational boats is widely believed to be the primary vector for zebra mussel dispersal into inland lakes (Carlton 1993, Johnson and Carlton 1996, Johnson and Padilla 1996, Schneider et al. 1998, Buchan and Padilla 1999). Recent attempts have been made to compare patterns of boater activities to inland lake invasions of zebra mussels in Wisconsin lakes. Based upon a small number of known lake invasions, the rate of Wisconsin inland-lake zebra mussel invasion appeared to be related to the frequency of recreational boating (Padilla et al. 1996). Additionally, surveys of long-distance boat movements provide better forecasts of zebra mussel dispersal than do diffusion models (Buchan and Padilla 1999). Boater movements have also been incorporated in a risk assessment of the potential zebra mussel invasion of Illinois inland lakes (Schneider et al. 1998). Assessment of these predictions is not currently possible, as only a single Illinois lake has been colonized.

In this study we describe the implementation of a production-constrained gravity model to forecast the overland dispersal of zebra mussels into inland lakes within a four-state region (Illinois, Indiana, Michigan, and Wisconsin). We then describe the use of this model to address: (1) the role of recreational boating in the spread of zebra mussels; (2) regions most prone to future colonization events; and (3) the utility of gravity models for predicting long-distance dispersal.

METHODS

General characteristics of gravity models

Gravity models, in general, develop a matrix that calculates the flow of individuals that move from a series of origins to a series of destinations based on the distance and attractiveness of the destinations (Thomas and Hugget 1980). For example, variables such as population size, unemployment rate, or crime rate can be used to rate the attractiveness of a given city. Gravity models are functionally different from diffusion models in that diffusion models estimate movement rates by an organism, whereas gravity models estimate the force of attraction between an origin and a destination, with movement rates being a function of this force. Thus, a diffusion model is more appropriate if a movement rate can be estimated, whereas a gravity model is more appropriate when distance to and attractiveness of destinations are known or are of interest.

Different types of gravity models exist based upon prior information; a production-constrained gravity model is used when information about the population of the site of origin is known, but not the number of people who travel to a particular destination, while a production–attraction-constrained gravity model is used when information is known about both the source and destination populations. Schneider et al. (1998) were able to use a production–attraction-constrained gravity model to estimate zebra mussel dispersal in Illinois because estimates were available for the number of boaters at both origins and destinations for movement.

We have developed a production-constrained gravity model to simulate zebra mussel dispersal over a larger region for which data regarding the number of registered boats per county were available, but data were not generally available regarding the number of boats traveling to given lakes.

Deterministic model

The colonization of an inland lake by zebra mussels is the result of a three-step process. First, boats travel to a colonized lake or boat ramp and pick up juvenile or adult zebra mussels. Second, these infested boats travel to an uncolonized lake on a subsequent outing, inadvertently releasing zebra mussels into this water body. Third, these transported individuals recruit a new colony based upon the physical nature of the lake (water chemistry, depth) and stochastic demographic events (Johnson and Padilla 1996). As a result, our model will estimate the potential for colonization based upon three factors: (1) the probability of a boat traveling to a zebra mussel source, (2) the probability of the same boat making a subsequent outing to an uncolonized lake, and (3) the probability of zebra mussels becoming established once released in that uncolonized lake.

The first step of the model calculates the number of boats from each county that travel to a zebra mussel source and thus have the potential to transport zebra mussels to an uncolonized lake on a subsequent outing. The number of boats, T, that travel from county i to a lake or boat ramp, j, is estimated as

$$T_{ij} = A_i O_i W_j c_{ij}^{-\alpha} \tag{1}$$

where, A_i is a scalar, O_i is the number of boats in county i, W_j is the attractiveness of location j, c_{ij} is the distance from county i to location j, and α is the distance coefficient. A_i ensures that all the boats from county i reach some lake. Without A_i a production-constrained gravity model calculates the proportion of boats that move from county i to each lake. Such scalars are referred to as "balancing factors" in the spatial interaction literature (Fotheringham and O'Kelly 1989). A_i is estimated via

$$A_i = 1 \Big/ \sum_{j=1}^{N} W_j c_{ij}^{-\alpha} \tag{2}$$

where N represents the total number of lakes and boat ramps and j represents each lake in the study region.

The number of potentially infested boats for each county is expressed as P_i and calculated by

$$P_i = \sum_{s=1}^{n} T_{is} \tag{3}$$

where T_{is} is the subset of T_{ij} which consists of those boaters who travel from county i to a source of zebra mussels, s. T_{is} is summed for each county over the total number of zebra mussel sources, n.

In the second step of our model, the "infested" boats, P_i, make a second excursion during which they transport zebra mussels to other lakes. T_{iu} represents the number of these boats that travel from county i to an uncolonized lake u:

$$T_{iu} = A_i P_i W_u c_{iu}^{-\alpha}. \tag{4}$$

The total number of infested boats that arrive at a given uncolonized lake, Q_u, is calculated by summing over all counties, M:

$$Q_u = \sum_{i=1}^{M} T_{iu}. \tag{5}$$

Thus, Q_u is the relative number of infested boats that visit lake u in one iteration (year) of the model.

The third step of the model determines whether overland-dispersal events lead to the establishment of zebra mussel colonies. Establishment of new colonies is based on two factors: (1) physical characteristics of the lake and (2) stochastic demographic events.

The single transfer of a few zebra mussel adults or juveniles to an environmentally appropriate lake will not guarantee development of a new colony. Because of environmental and demographic factors, multiple zebra mussel deliveries by infested boats are likely necessary before successful colonization occurs. This statement is supported by the observation that the delivery estimates of adult zebra mussels to inland waters exceed the number of invasions (Johnson et al. 2001). The relative number of infested boats required to guarantee establishment of a new colony, f, was determined through a best-fit parameterization of the data (see *Best-fit parameterization*, below). In subsequent trials, lakes with values of Q_u (number of infested boats visiting a lake per year) greater than this colonization threshold, f, were designated as "colonized" and became new zebra mussel sources for subsequent model iterations, while lakes with values of Q_u below this limit remained uncolonized. To generate a deterministic distribution of zebra mussel-colonized lakes, the deterministic model was run for seven iterations (years) using the best-fit parameters (see *Best-fit parameterization*, below).

Stochastic model

Given the stochastic nature of the transport and deposition of zebra mussels, the establishment of new colonies will not be static. Analysis of the deterministic model showed that for many lakes, the value of Q_u was just slightly above or below the colonization threshold (f). For the deterministic model, lakes with values of Q_u slightly below the colonization threshold (f) were never designated as colonized; consequently a stochastic process was incorporated into the model. Even though multiple deliveries of zebra mussels are most likely necessary for colonization to occur, theoretically it is possible for a single boat to cause a lake to become colonized. Therefore, we estimated the relative probability that a single boat would cause a lake to become colonized, p_f. For this stochastic model, the probability of an uncolonized lake becoming colonized, x_u, was estimated as

$$x_u = Q_u p_f. \tag{6}$$

For each model iteration the probability of colonization of a given lake is based on the number of infested boats that arrive at each lake. At the end of each model iteration, each lake is assigned a probability of colonization, x_u, and then subjected to a Bernoulli trial, by which each lake is either designated as colonized (a score of 1 from the Bernoulli trial) or remains uncolonized, based on the probability x_u. Newly colonized lakes then become sources for the subsequent iterations (years).

To estimate p_f, probabilities ranging from 0.0000118 to 0.000235 (equivalent to a 1 to 20% chance of colonization when 850 boaters arrive at a lake) were incorporated into the stochastic model. Each probability was used in 100 trials of the model to determine which probability resulted in an average of 47 colonized lakes after seven iterations of the model. The selected probability, p_f, was then used in the 2000 trials of the stochastic model.

To generate a probabilistic distribution of zebra mussel-colonized lakes, 2000 trials of the stochastic model were conducted over a simulated period of seven years (seven iterations). From these, the probability of colonization for each lake was determined by dividing the number of times each lake was predicted to become colonized by the number of trails (2000). The number of colonized lakes for each county was determined by summing the individual colonization probabilities of each lake within that county.

Data sets

The region over which the model was tested includes all of Michigan and Wisconsin and those Illinois, Indiana, and Ohio counties within 300 km of the western Great Lakes shoreline (Fig. 1). Empirical data incorporated in the model consisted of the number of registered recreational boats per county, O_i; the location and area of lakes, W_j; the location of public-access boat ramps along the Great Lakes, Mississippi River, and Illinois River, the observed pattern of zebra mussel-colonized lakes; and limnological data for inland lakes.

FIG. 1. Region of study (Michigan and Wisconsin, and portions of Illinois, Indiana, and Ohio [USA]). The shaded counties contain lakes included in the gravity model. All the registered boaters in the shaded counties were considered in the model, while only 10% of the registered boaters in the non-shaded counties were incorporated. The black polygons are the lakes >25 ha in surface area within the study region. "A" represents the point through which all travels between Area 3 and Area 2 were routed; "B" represents the point through which all travels between Area 3 and Area 1 were routed (see Table 1 caption).

Recreational-boat registration records were obtained for 368 counties: all counties within the study region, as well as Minnesota, Iowa, and Ohio counties within 50 km of the region's boundary (Bossenbroek 1999). Only 10% of the boats beyond the primary study region were included, as 90% of boater movements are less than 50 km (Buchan and Padilla 1999). As such, we assumed that 90% of boater movements for these counties either took place in that county, or outside of our study region.

The surface area and location of inland lakes were based on data sets acquired from the Wisconsin Department of Natural Resources (Wisconsin DNR, Bureau of Fisheries Management and Habitat Protection, *unpublished data*), Michigan State University (MSU, Center for Remote Sensing and Geographic Information Science, *unpublished data*), and EPA River Reach files (U.S. Environmental Protection Agency, Office of Water 1999), while the locations of water bodies too large to be considered single entities (the Great Lakes, Mississippi River, and Illinois River) were designated by the location of 399 public access boat ramps. In order to limit the number of potential-destination lakes to a tractable amount, we only included those lakes that have a surface area >25 ha (3600 lakes). The largest lake in the region was Lake Winnebago in Wisconsin (53 504 ha).

The attractiveness of a given lake, W_j, is assumed to be positively correlated with lake area, with large lakes being more attractive than small ones (Reed-Anderson et al. 2000). As such, the value of W_j for a given inland lake is equal to that lake's surface area in hectares. For rivers, the surface area was estimated by multiplying the length of a river within the study region by the average width and then dividing by the number of boat ramps on each river. (The estimated W_j values for the Illinois and Mississippi River ramps are 269 ha and 6835 ha, respectively). The value of W_j for Great Lakes boat ramps was determined through best-fit parameterization (see Best-fit parameterization, below).

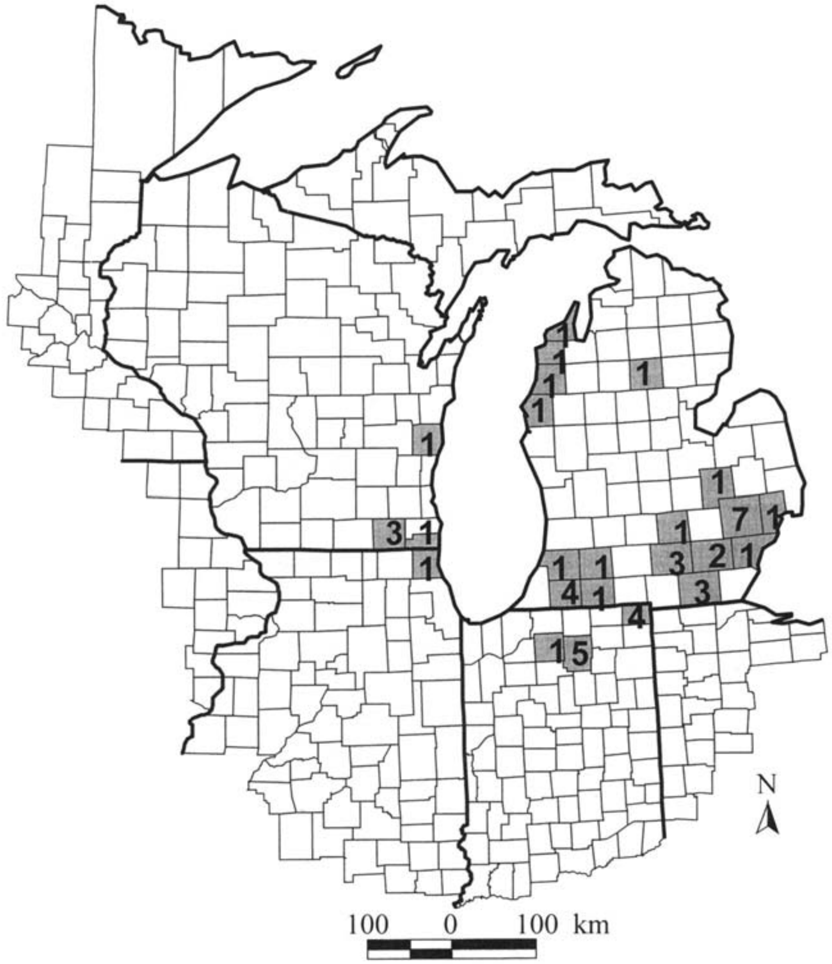

FIG. 2. The observed distribution of zebra-mussel-colonized lakes in the Western Great Lakes States as of December 1997. This distribution only includes lakes thought to have been colonized as a result of overland transport. The numbers indicate the number of colonized lakes within that county. Data are from Kraft and Johnson (2000).

The distribution of zebra mussel-colonized lakes within the study region was based on known colonization patterns as of December 1997 (Fig. 2; Kraft and Johnson 2000). Only the 47 lakes considered to be colonized via overland dispersal were used, eliminating the 9 lakes that are thought to have been secondarily colonized by such means as stream flow or water pumped from a colonized lake into an uncolonized lake (L. E. Johnson, *personal communication*). The Great Lakes, Mississippi River, and Illinois River boat ramps were considered the initial zebra mussel sources. Lakes colonized during an iteration of the model were considered sources during subsequent iterations.

The appropriateness of a given lake's physical characteristics for establishment of zebra mussel colonies was based on Ramcharan et al. (1992), in which lakes with low pH and calcium levels were not colonized. They estimated the suitability of a given lake through the equation:

$$B = 1.246 \text{ pH} + 0.045[\text{Ca}] - 11.696. \qquad (7)$$

Lakes with B values exceeding -0.638 were considered suitable for zebra mussel colonization. Based on this model, those lakes in our study with B values below this threshold were designated as unsuitable for colonization. Additionally, lakes with a maximum depth <4 m were considered uninhabitable (Strayer 1991), and were excluded from analysis.

To estimate B, pH and Ca levels were obtained for 50% and 30%, respectively, of the lakes within the study region via the EPA STORET data bank (U.S. Environmental Protection Agency, Office of Water 1999). For the study region, lake pH and calcium levels are closely tied to bedrock formation, and general regional patterns among lakes are apparent (Omernik and Powers 1983, Omernik et al. 1988). Because of this spatial autocorrelation, pH and calcium values for lakes not included in this database were estimated through punctual kriging (Burgess and Webster 1980) of the nearest 20 recorded lakes, using the GS+ software package (Gamma Design Software 1992). Based on this

TABLE 1. Measures for calculating distance between each county and each lake within the study region.

Distance to be calculated		
From area:	To area:	Distance calculation
1	2,4	County *i* to Lake *j*
1	3	County *i* to Pt. B + Pt. B to Lake *j*
2	1,4	County *i* to Lake *j*
2	3	County *i* to Pt. A + Pt. A to Lake *j*
3	1	County *i* to Pt. B + Pt. B to Lake *j*
3	2	County *i* to Pt. A + Pt. A to Lake *j*
3	4	County *i* to Lake *j*
4	1,2,3	County *i* to Lake *j*

Notes: The study region was divided into four areas. Area 1 = the portion of Wisconsin south of the southern tip of Green Bay and northwest Illinois; Area 2 = northern Wisconsin and the upper peninsula of Michigan; Area 3 = the lower peninsula of Michigan, northeast Indiana, and northwest Ohio; and Area 4 = the portion of Illinois not in Area 2 and the portion of Indiana not in Area 3. Point A is located at the Straits of Mackinac (northern end of Lake Michigan), and point B is located at the south end of Lake Michigan.

analysis, 1843 lakes in the region were considered to be environmentally inappropriate for zebra mussels. Most of these lakes were concentrated in northern Wisconsin, where igneous bedrock and alluvium predominates. Although these lakes were excluded for establishment of zebra mussel populations, they were still considered as destinations for boater movements.

Distances from each lake and boat ramp to each county were calculated from lake centroids to the center of lake polygons within each county. The center of lake polygons within a county was used instead of the county centroid because it was assumed that recreational boat owners are more likely to live close to lakes. For those counties with no lakes, the county centroid was used.

Although simple Euclidean distance estimates were used in most cases, these estimates were not appropriate when the lake/boat ramp and county in question were located on opposite sides of Lake Michigan, which is a barrier to straight-line travel. To address this problem, the study region was divided into four areas. For boats traveling from a county to a lake within the same area, or between areas on the same side of Lake Michigan, Euclidean distance estimates were used. For boats traveling between areas on opposite sides of Lake Michigan, distances were calculated by routing trips around Lake Michigan. The paths used to calculate these trips are shown in Table 1.

Best-fit parameterization

Three model parameters were estimated using least-sum-of-squares (LSS) parameterization: distance coefficient (α); colonization threshold (f); and attractiveness of Great Lakes boat ramps (W). Best-fit values were determined through LSS comparison of model predictions with the observed distribution of zebra mussels at the county level. Comparisons were made at this scale because the county is the minimum resolution of boat registration data. In the parameterization routine, α was varied from 1.0 to 7.0 in increments of 0.1, f ranged from 400 to 1500 in increments of 50, and W ranged from 5000 to 70 000 ha in increments of 5000 ha. Parameter estimation was conducted deterministically without inclusion of stochastic variables.

Sensitivity analysis and model robustness

To analyze the sensitivity of parameter estimation with respect to the number of lakes predicted to be colonized, the deterministic model was run while varying the values of the three estimated parameters from −20% to +20% of their best-fit estimate across seven model iterations. Since 47 lakes were included in the fitted data set, and the best-fit parameterization predicted 44 colonized lakes, we defined the least sensitive region to parameter adjustments as that range of predicted colonized lakes from 44 to 47 lakes.

Two additional tests were used to evaluate model robustness. First, the distance of the predicted colonized lakes to Great Lakes boat ramps and to county centroids was compared with observed distributions to assess the ability of the model to simulate regional and within-county distribution patterns. Second, correlation coefficients were calculated for the predicted and observed number of colonized lakes per county and compared to a random selection of 47 suitable lakes over 1000 trials

RESULTS

The best-fit results of the deterministic model designated 44 lakes as colonized with a least sum of squares (LSS) of 85. The best-fit parameterizations for this model were: distance coefficient of 1.9, colonization threshold of 850 boats, and attractiveness value of 55 000 ha for Great Lakes boat ramps. For the stochastic model, it was determined that an infested boat has a probability of 0.0000411 to establish a zebra mussel colony; this translates into a 3.5% chance of a zebra mussel colony becoming established when visited by 850 infested boats.

Sensitivity analysis (Fig. 3) showed that the model produced 44 to 47 colonized lakes over a wide range of parameter values. Changes in the distance coefficient produced the largest changes in estimated number of infected lakes, while ramp attractiveness and colonization threshold produced the least.

The results of the two tests for model robustness showed that the model was successful in duplicating the actual patterns of zebra mussel colonization. First, on a regional scale the number of colonized lakes at various distances from Great Lakes boat ramps was calculated and compared between each model (deterministic and stochastic) and the observed data (Table 2), and no significant differences were found (P = 0.8014 for the deterministic and P = 0.9974 for the

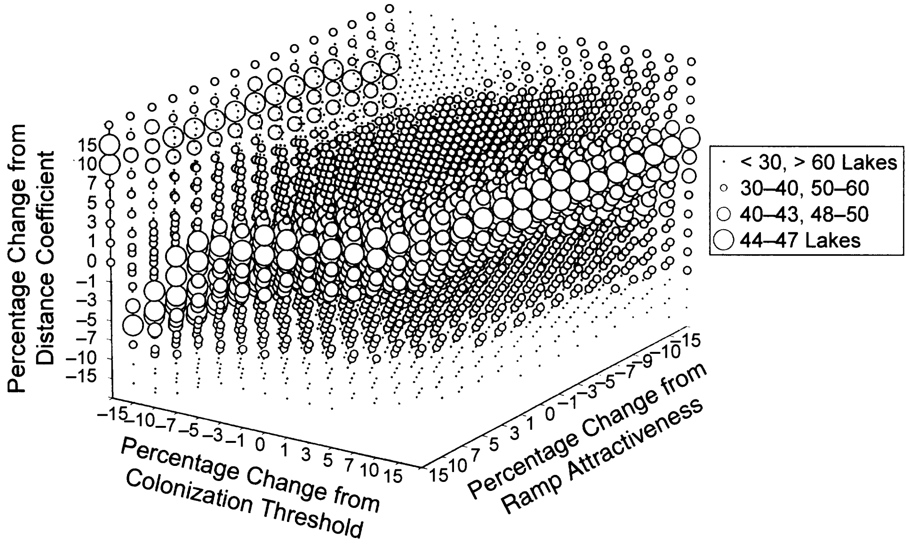

FIG. 3. Results of the sensitivity analysis. Each circle represents the number of lakes designated as colonized for combinations of values for the three test parameters: distance coefficient, colonization threshold, and attractiveness of a Great Lakes boat ramp. The size of the circles represents the number of infected lakes produced by each test parameter. The axis numbers are the percentage change of the best-fit values of the three parameters.

stochastic model). At a local scale, the number of colonized lakes within given distances of county centroids was also compared (Table 3). These results showed that patterns predicted by the models do not differ significantly from the observed data at either regional or local scales. Second, the number of colonized lakes predicted per county is highly correlated with the actual number of colonized lakes (r^2 = 0.639 and 0.681 for the deterministic and stochastic models, respectively). These correlation coefficients are outside the 95% confidence intervals generated from correlation of observed vs. random numbers of colonized lakes per county based on 1000 simulations (Fig. 4).

Deterministic model

The deterministic model was successful in matching the pattern of colonization within three areas of the study region (Fig. 5A): southeast Wisconsin, southwest Michigan, and the western suburbs of Detroit. In southeast Wisconsin, the observed distribution of zebra mussels consisted of five colonized lakes in three counties of Wisconsin and northern Illinois. The model predicted three colonized lakes in the same counties, including Lake Geneva, which is colonized, with a fourth lake only 5 km outside one of the counties. Four counties in southwest Michigan have colonized lakes, while the model predicted colonized lakes in three of these counties. In the Detroit region, the most colonized county in 1997 was Oakland County, which had seven colonized lakes, and five more colonized lakes were found in neighboring counties. The model predicted that seven colonized lakes would occur in Oakland County, with three additional lakes found in surrounding counties. (Of the lakes known to be colonized in Oakland and surrounding counties, the model predicted Elizabeth Lake, Lake Maceday, Union Lake, Belleville Lake, and Stony Creek Lake to be colonized.)

The model was less successful in predicting the observed distribution of zebra mussels in central Wisconsin, southeast Michigan, and northern Indiana. The model predicted six lakes to become colonized from Dane County to Shawano County in eastern Wisconsin, where no colonized lakes had been observed. In south-

TABLE 2. A comparison of the number of observed and predicted zebra-mussel-colonized lakes within different distances to a Great Lakes boat ramp.

Distance to ramps	No. of lakes colonized Observed	 Deterministic model†	 Stochastic model‡
<50 km	21	23	19
<100 km	40	35	38
<150 km	47	41	44

† χ^2 = 0.4429, df = 2, P = 0.8014.
‡ χ^2 = 0.0053, df = 2, P = 0.9974.

TABLE 3. A comparison of the number of observed and predicted zebra-mussel-colonized lakes within the specified distance of county centroids.

Distance to centroid	No. of lakes colonized Observed	 Deterministic model†	 Stochastic model‡
<20 km	42	42	43
<10 km	14	27	21
<5 km	6	19	11
<2 km	2	3	2

† χ^2 = 6.5783, df = 3, P = 0.0866.
‡ χ^2 = 1.6751, df = 3, P = 0.6425.

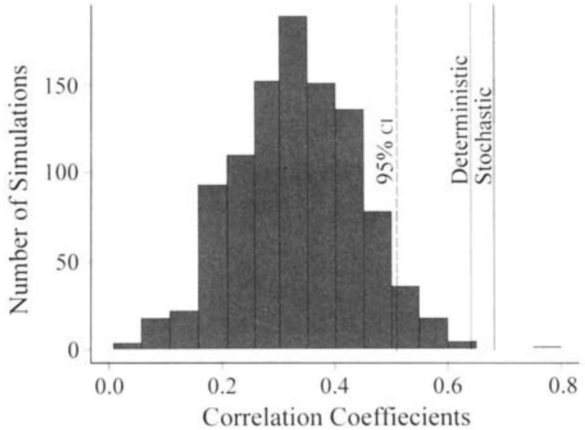

FIG. 4. Histogram of the correlation coefficients comparing the observed number of colonized lakes per county with 1000 simulations of randomly sampled lakes. The vertical lines represent the value of the correlation coefficients for the deterministic and stochastic model results compared with the observed distribution of zebra-mussel-colonized lakes. The correlation coefficient was calculated based on the number of colonized lakes per county. Both the deterministic and stochastic model correlations exceed the 95th percentile for the random distribution.

east Michigan, nine colonized lakes were found in four counties, whereas the model only predicted two colonized lakes in that region. The model also predicted four colonized lakes in northern Indiana, where 10 were observed.

Stochastic model

Similarities between observed and stochastically modeled distributions were evident in southern Michigan and southeast Wisconsin (Fig. 5B). In these regions, for all counties that had >1 colonized lake, the model predicted at least 0.61 colonized lakes, and the model showed similar clusters of colonized counties as were evident in the observed distribution.

Differences between the predicted and observed pattern of colonized-lake distribution were again evident in central Wisconsin, where counties that had no record of colonization were predicted to have colonized lakes. As with the deterministic model, the stochastic model predicted that colonized lakes would occur in four counties in west-central Michigan, but no lakes were known to be colonized in that region as of December 1997.

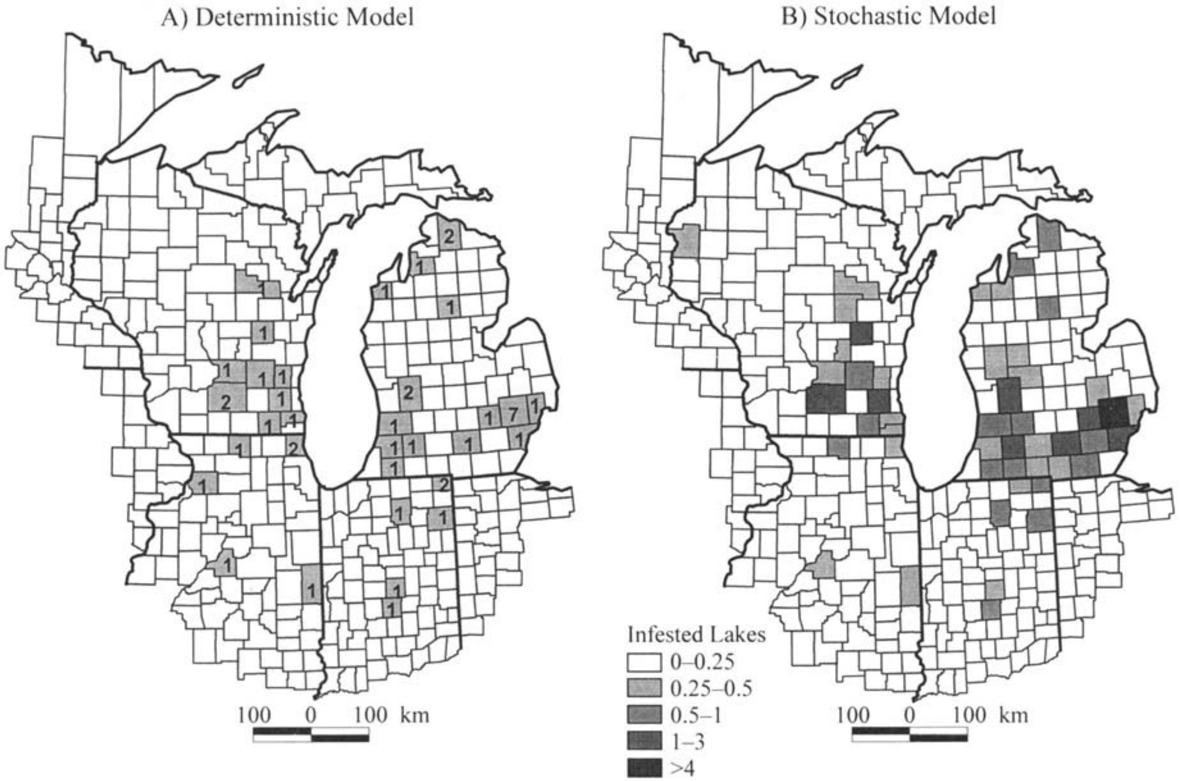

FIG. 5. The predicted distribution of zebra-mussel-colonized lakes for the (A) deterministic and (B) stochastic models. The deterministic model results were based on the best-fit parameters, and the numbers indicate the number of colonized lakes within that county. The stochastic model used the same parameters, but colonization of a particular lake was based on a colonization probability. The stochastic model was run for 2000 iterations. The number of colonized lakes for each county was determined by summing the number of lakes predicted to become colonized through all iterations and dividing by the number of trials (2000).

DISCUSSION

Advances over previous models

Initial predictions of zebra mussel colonization patterns in North America were limited to forecasts of the potential geographic range at continental (Strayer 1991) or provincial (Neary and Leach 1992) scales, based upon general trends in climate, bedrock, water chemistry, and proximity to roads. Subsequent efforts have attempted to predict invasion susceptibility of lakes within more limited geographic regions (Padilla et al. 1996, Schneider et al. 1998, Buchan and Padilla 1999). The production-constrained gravity model presented in this paper builds upon these previous efforts by predicting colonization probabilities based only upon the number of registered recreational boats per county and the size, location, and water chemistry of lakes and location of boat ramps as input data. These input data are much more readily available than are data for models based upon boater surveys (Padilla et al. 1996, Schneider et al. 1998, Buchan and Padilla 1999). Boater surveys are not available for most of the study region, are expensive to generate, and are rarely repeated. For example, the boater data used by Padilla et al. (1996) and Buchan and Padilla (1999) resulted from an intense, year-long, social survey, which involved contacting 58 000 licensed Wisconsin boaters (Penaloza 1991). The boater data used by Schneider et al. (1998) was gathered from a landscape with a limited number of inland lakes (55) and zebra mussel sources (~60 sources, which included boat ramps on Lake Michigan and the Illinois, Ohio, and Mississippi rivers). Similar data are unavailable from most neighboring states with numerous lakes, even for a single year.

Avenues for future investigation

During model development, we were restricted by available data to fitting a model to 47 colonized lakes out of 1700+ suitable lakes. As such, not enough data were available to parameterize the model using a subset of these 47 colonized lakes, and then test the validity of the model on the remaining subset. Even though we were not able to validate our model using traditional methods, achieving a 0.67 correlation between the model forecast and fitted data suggests that the model is useful. It is important to point out that we did not simply choose one particular model while ignoring alternative ones. During parameter estimation, we essentially rejected numerous "poorer fitting" models. Our method of model selection follows the philosophy described by Hilborn and Mangel (1997), in that we selected a best-fit model from numerous alternative models with alternative parameter values. Future efforts to validate this model will only become possible when more lakes become colonized within the study region. It is interesting to note that all of the reported additional colonized lakes that have occurred since 1997 occurred in counties our model identifies as having high colonization potentials, and that the uncolonized lake deemed most likely to become colonized (Lake Winnebago) became recognized as colonized in 1999.

We also recognize that other factors not incorporated in our model likely influence zebra mussel transport, including local boater behavior, boat type, and lake access (Penaloza 1991, Reed-Anderson et al. 2000). Some of the discrepancies between observed countywide colonization patterns and model results suggest that such additional factors might enhance or detract from the likelihood of colonization at this spatial scale. For example, the over-prediction of colonized lakes in west-central Michigan and central Wisconsin could result from reduced attractiveness of Great Lakes boat ramps to boaters living in this region. By contrast, the under-prediction of colonized lakes in northeastern Indiana could result from increased lake attractiveness in this area.

Efforts to forecast the likelihood of colonization for specific lakes will need to take these additional factors into account. We believe our model is resilient to these factors because colonization rates are predicted only at a countywide scale. However, because colonization predictions for specific lakes will be important to resource managers, incorporating such additional information regarding boater behavior into a gravity-modeling approach will be an important future advancement.

Implications

Our ability to model the invasion of zebra mussels into the inland lakes of the upper Midwest provides insight into a number of important ecological issues regarding zebra mussel ecology, exotic species invasion, and the modeling of dispersal.

First, this analysis helps to resolve the debate over which vectors are likely responsible for the dispersal of zebra mussels to North American inland lakes. The mechanisms invoked in our model to reproduce observed patterns of inland zebra mussel invasions support assertions by Johnson and Carlton (1996) that recreational boat use is a more important vector of spread than are other vectors, such as waterfowl. Our analysis also helps to clarify the scale at which long-distance dispersal operates for this organism. Although 106-km distances were previously identified to represent long-distance movements for zebra mussels (Buchan and Padilla 1999), 43 of the 47 observed colonized lakes are located within this distance of a zebra mussel source. Using the definition of "long-distance" dispersal from Shigesada and Kawasaki (1997), we conclude that movement over any amount of land (no matter how short) will constitute a "long-distance" dispersal event for zebra mussels. Our model demonstrates that, at least over countywide scales (<45 km), the regional effects of such relatively short "long-distance" dispersal events are predictable.

Second, our modeling effort helps identify why the North American zebra mussel invasion has not and will not occur as a moving-wave front. Within our study region, regional aggregations of colonized-lakes are evident in observed colonized-lake distributions (Kraft and Johnson 2000) as well as in our model forecasts. It appears that the expansion of inland-lake zebra mussel range has occurred through the development of isolated centers of distribution, which have lead to further aggregations of colonized lakes. This pattern is similar to that reported for many other invasive species, in which new colonies are formed beyond the boundaries of previous colonies due to long-distance dispersal across barriers (Shigesada and Kawasaki 1997). Plant invasions often demonstrate this type of spatial colonization pattern, in which satellite populations occur away from a center of introduction (Baker 1986). Such colonization patterns have not been previously described for invasive aquatic species colonizing a heterogeneous landscape of hydrologically isolated lakes, although they have been observed for wetland butterflies (Nève et al. 1996).

Last, this model demonstrates that a gravity model better predicts the overland spread of zebra mussels as compared to the diffusion model evaluated and rejected by Buchan and Padilla (1999). In general, the characteristics of gravity models provide potential advantages over diffusion models in forecasting organism movement under certain conditions. For instance, gravity models operate when potential destinations, such as inland lakes or islands, represent isolated habitats in heterogeneous landscapes where the structure and spatial pattern of potential habitat is known. Since diffusion models assume that all of a landscape is accessible, they may not be effective in situations where parts of the landscape are uninhabitable. Like stratified diffusion models (Hengeveld 1989), gravity models enable dispersing organisms to "leap-frog" suitable habitat. However, unlike stratified diffusion models, gravity models also permit organisms to jump over unsuitable habitats and dispersal barriers. For this reason, stratified diffusion models are not likely to be as useful in forecasting the dispersal of aquatic organisms to lakes within a terrestrial landscape.

Since humans are the principal overland vector for zebra mussel dispersal, the use of a model developed to forecast human movement appears clearly justified for this invasive organism. A larger question is whether gravity models have utility beyond human-dispersed taxa. We believe that gravity models are appropriate in any situation where movement between areas is negatively correlated with intersite distance and positively correlated with site "attractiveness." We suggest that such conditions apply to other taxa and landscapes. Across a wide array of systems, the biological interaction between areas can be shown to co-vary negatively with increasing intersite distance (Okubo and Levin 1989, Nekola and White 1999). Many organisms have been shown to exhibit nonrandom movement patterns, particularly when moving a long distance (Zollnar and Lima 1999). If these organisms are responding to environmental cues from potential habitat, such as the preferential uphill movement of checkerspot butterflies (*Euphydryas editha*; Turchin 1998) or female chrysomelid beetles (*Trirhabda virgata*) responding to lush host patches (Herzig and Root 1996), gravity models can be used to incorporate an attractiveness value to destination sites. The concept of attraction may also be expanded to include organisms that do not exhibit behaviors associated with neural processes, such as plants. For instance, it could be argued that passively dispersing propagules are more "attracted" to larger habitats simply because they represent larger catchment zones. It is thus possible that the two underlying conditions of gravity models exist for other examples of natural and anthropogenically mediated dispersal.

Dispersal processes occur at different scales (Levin 1992), and diffusion is obviously at work at local scales (e.g., the spread of zebra mussels throughout a lake). However, at larger landscape or regional scales, long-distance dispersal results from different mechanisms. We have demonstrated that the pattern and structure of suitable habitat is essential for modeling long-distance dispersal by zebra mussels. If an organism's dispersal is affected by distance and the attractiveness of specific destinations, gravity models may represent another important class of dispersal models that, along with diffusion models, can be used to predict the spread of native and non-native species through heterogeneous landscapes.

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LITERATURE CITED

Andow, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. Landscape Ecology **4**:177–188.

Baker, H. G. 1986. Patterns of plant invasion in North America. Pages 44–57 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, Berlin, Germany.

Bossenbroek, J. M. 1999. Modeling the dispersal of *Dreissena polymorpha* (zebra mussel) into the inland lakes of the western Great Lakes region using a gravity model. Thesis. University of Wisconsin, Green Bay, Wisconsin, USA.

Buchan, L. A. J., and D. K. Padilla. 1999. Estimating the probability of long-distance overland dispersal of invading aquatic species. Ecological Applications **9**:254–265.

Burgess, T. M., and R. Webster. 1980. Optimal interpolation and isarithmic mapping of soil properties. I. The semivariogram and punctual kriging. Journal of Soil Science **31**: 315–331.

Carlton, J. T. 1993. Dispersal mechanisms of the zebra mussel. Pages 677–697 *in* D. Schloesser and T. Nalepa, editors. Zebra mussels: biology, impacts and control. Lewis, Ann Arbor, Michigan, USA.

Dean, W. R. 1998. Space invaders: modeling the distribution, impacts and control of alien organisms. Trends in Ecology & Evolution **13**:256–258.

Fotheringham, A. S., and M. E. O'Kelly. 1989. Spatial interaction models: formulations and applications. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gamma Design Software. 1992. GS+ statistical package. Gamma Design Software, Plainwell, Michigan, USA.

Griffiths, R. W., D. W. Schloesser, J. H. Leach, and W. P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Canadian Journal of Fisheries and Aquatic Sciences **48**: 1381–1388.

Hebert, P. D. N., B. W. Muncaster, and G. L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Canadian Journal of Fisheries and Aquatic Science **48**:1381–1388.

Hengeveld, R. 1989. Dynamics of biological invasions. Chapman & Hall, London, UK.

Herzig, A. L., and R. B. Root. 1996. Colonization of host patches following long-distance dispersal by a goldenrod beetle, *Trirhabda virgata*. Ecological Entomology **21**:344–351.

Hilborn, R., and M. Mangel, 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey, USA.

Johnson, L. E., and J. T. Carlton. 1996. Post-establishment spread in large-scale invasions: dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*). Ecology **77**: 1686–1690.

Johnson, L. E., and D. K. Padilla. 1996. Geographic spread of exotic species: ecological lessons and opportunities from the invasion of the zebra mussel *Dreissena polymorpha*. Biological Conservation **78**:22–33.

Johnson, L. E., A. Ricciardi, and J. T. Carlton. 2001. Overland dispersal of aquatic invasive species: a risk assessment of mechanisms associated with transient recreational boating. Ecological Applications **11**, *in press*.

Kraft, C. E., and L. E. Johnson. 2000. Regional differences in rates and patterns of North American inland lake invasions by zebra mussels (*Dreissena polymorpha*). Canadian Journal of Fisheries and Aquatic Sciences **57**:993–1001.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1967.

Lewis, M. A. 1997. Variability, patchiness, and jump dispersal in the spread of an invading population. Pages 46–69 *in* D. Tilman and P. Kareiva, editors. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, New Jersey, USA.

Neary, B. P., and J. H. Leach. 1992. Mapping the potential spread of the zebra mussel (*Dreissena polymorpha*) in Ontario. Canadian Journal of Fisheries and Aquatic Sciences **49**:406–415.

Nekola, J. C., and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography **26**:867–878.

Nève, G., B. Barascud, R. Hughes, J. Aubert, N. Descimon, P. Lebrun, and M. Baguette. 1996. Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). Journal of Applied Ecology **33**:14–22.

Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecology **70**:329–338.

Omernik, J. M., D. P. Larsen, C. M. Rohm, and S. E. Clarke. 1988. Summer total phosphorus in lakes: a map of Minnesota, Wisconsin, and Michigan, USA. Environmental Management **12**:815–825.

Omernik, J. M., and C. F. Powers. 1983. Total alkalinity of surface waters—a national map. Annals of the Association of American Geographers **73**:133–136.

Padilla, D. K., M. A. Chotkowski, and L. A. J. Buchan. 1996. Predicting the spread of zebra mussels (*Dreissena polymorpha*) to inland waters using boater movement patterns. Global Ecology and Biogeography Letters **5**:353–359.

Penaloza, L. J. 1991. Boating pressure on Wisconsin's lakes and rivers. Results of the 1989–1990 Wisconsin recreational boater survey, phase I. Technical Bulletin 174. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

Ramcharan, C. W., D. K. Padilla, and S. I. Dodson. 1992. Models to predict the potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Canadian Journal of Fisheries and Aquatic Sciences **49**:2611–2629.

Reed-Anderson, T., E. M. Bennett, B. S. Jorgensen, G. Lauster, D. B. Lewis, D. Nowacek, J. L. Riera, B. L. Sanderson, and R. Stedman. In press. The distribution of recreational boating across lakes: Do landscape variables affect recreational use? Freshwater Biology. **43**:439–448.

Schneider, D. W., C. D. Ellis, and K. S. Cummings. 1998. A transportation model assessment of the risk to native mussel communities from zebra mussel spread. Conservation Biology **12**:788–800.

Shigesada, N., and K. Kawasaki. 1997. Biological invasions: theory and practice. Oxford University Press, Oxford, UK.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika **38**:196–218.

Sklar, F. H., and R. Costanza. 1991. The development of dynamic spatial models for landscape ecology: a review and prognosis. Pages 239–288 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity. Springer-Verlag, New York, New York, USA.

Strayer, D. L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. Canadian Journal of Fisheries and Aquatic Sciences **48**:1389–1395.

Thomas, R. W., and R. J. Hugget. 1980. Modeling in geography. Barnes & Noble Books, Totowa, New Jersey, USA.

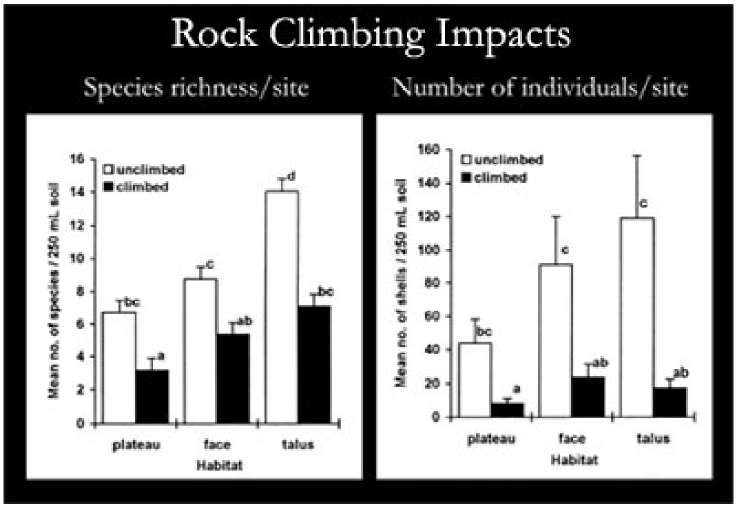
Turchin, P. 1998. Quantitative analysis of movement. Sinauer Associates, Sunderland, Massachusetts, USA.

U.S. Environmental Protection Agency, Office of Water. 1999. Environmental and program information systems compendium. U.S. Environmental Protection Agency, Washington, D.C., USA.

Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology **80**:1019–1030.

Section VI: Conservation Biology

Because of the precarious status of biodiversity across the globe, it is important for ecologists to apply their pure research findings to the development of optimal conservation strategies. As suggested by Susan Bratton, the current state of conservation biology is not unlike that of the medical profession in 1700's Vienna, when patients faced a lower chance of survival after treatment than if they had let the disease run its course. Because of the complex nature of ecological systems, we should not search for universally applicable and beneficial reserve design or management strategies or seek exact quantitative predictions regarding particular environmental perturbations. Rather, each reserve will face unique series of threats and will require artist-like managers who develop unique management protocols for each site. Much of my conservation biology research has been focused on documenting the unintended negative impacts posed by fire management policies on biodiversity, especially in fragmented landscapes with low potential for recolonization. Total biodiversity maintenance in these situations requires reduced use of fire across both space and time, with sensitive application of large vertebrate grazing and use of more labor intensive techniques such as hand-removal of woody vegetation. I have also published on the importance of distance and colonization history in reserve design, have documented the negative impact of recreational rock climbing and soil disturbance on land snail diversity, and have investigated the impact of powerline corridors on biodiversity.



Representative Publications
[number of citations as of October 27, 2017]

Nekola, J.C. 2012. The impact of utility corridors on terrestrial gastropod biodiversity. *Biodiversity and Conservation*. 21:781–795. **[9]**

McMillan, M., **J.C. Nekola** & D.W. Larson. 2003. Impact of recreational rock climbing on land snail communities of the Niagara Escarpment, southern Ontario, Canada. *Conservation Biology*. 17:616-621. **[41]**

Nekola, J.C. 2002. Effects of fire management on the richness and abundance of central North American grassland land snail faunas. *Animal Biodiversity and Conservation.* 25:53-66. **[46]**

Nekola, J.C. & P.S. White. 2002. Conservation, the two pillars of ecological explanation, and the paradigm of distance. *Natural Areas Journal.* 22:305-310. **[23]**

White, P.S. & **J.C. Nekola.** 1992. Biological diversity in an ecological context. Pages 10-29 *in:* Barker, J.R. and D.T. Tingey (eds), *Air pollution and biodiversity.* Van Nostrand Reinhold, New York. **[6]**

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ORIGINAL PAPER

The impact of a utility corridor on terrestrial gastropod biodiversity

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Abstract Utility corridors are often thought to be disruptive to biodiversity because they cause habitat fragmentation that may lead to increases in predation, parasitism, disease transmittance and vagrant species while decreasing migration rates, gene flow and genetic diversity for interior species. Species with poor dispersal abilities, sedentary lifestyles, and specialized habitats have been thought to be potentially the most vulnerable to these effects. Terrestrial gastropods thus serve as a valuable system in which to investigate these impacts because they are among the poorest active dispersers in the animal kingdom. To document the impact of corridor formation on land snail biodiversity, a 75-year old powerline right-of-way in the eastern Upper Peninsula of Michigan was chosen for analysis. While terrestrial gastropod richness and abundance was significantly reduced for corridor as compared to adjacent control subsamples, with a 2/3 turnover in species composition, the corridor fauna is similar to nearby native grassland sites in terms of species composition, abundance distribution, and numbers and abundance of species of conservation concern. The fauna of control subsamples immediately adjacent to the corridor remained similar to other undisturbed sites in the region, with multiple species of conservation concern persisting at distances of only 30 m from the corridor. Thus, the net impact of corridor generation has been arguably positive: while the surrounding forest fauna has not been degraded, within the corridor the reduction of forest species has been compensated for by establishment of even rarer grassland species.

Keywords Land snail · Right-of-way · Landscape · Community ecology · Community structure · Soil architecture

Introduction

Utility corridors have often been thought to be disruptive to biodiversity (Forman 1986; Andrews 1990) because they fragment habitats, leading to increased predation, parasitism and disease transmittance rates (Simberloff and Cox 1987; Yahner et al. 1989; Bennett

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1991), decreased migration abilities and lowering of gene flow and within-population genetic diversity (Fahig and Mirriam 1985; Goosem and Marsh 1997; Gerlach and Mustov 2000), and expansion of vagrant species at the expense of interior species (Arnold et al. 1987). Species with poor dispersal abilities, sedentary habits, and specialized habitat preferences have been thought to be the most vulnerable to these effects (Shaffer and Samson 1985; Andrews 1990).

Terrestrial gastropods would therefore appear particularly sensitive to utility corridor formation. The North American fauna, particularly at mid-to-high latitudes, is dominated by species with shells <5 mm in maximum dimension that represent approximately 50–80% of regional species richness and 80–95% of individuals (Nekola 2005). Such species have very poor active dispersal abilities: individuals move perhaps only 1–10 m over a lifetime (Schilthuizen and Lombaerts 1994; Hausdorf and Hennig 2003). Even active movement of larger species (maximum shell dimension >20 mm) has been effectively inhibited by barriers of no more than 3–8 m (Baur 1988; Baur and Baur 1990; Schilthuizen and Lombaerts 1994). Also, terrestrial gastropods exhibit a high degree of habitat specialization, with order-of-magnitude changes in richness and abundance over as little as 1 m (Nekola and Smith 1999).

Even though utility corridors may have serious negative impacts on terrestrial gastropod biodiversity and community structure, no prior research has specifically addressed this issue. This study therefore investigates changes in community structure and composition between paired corridor and matrix habitats along a 75-year old utility corridor passing through the Hiawatha National Forest in the eastern Upper Peninsula of Michigan. Comparisons were also made with other undisturbed habitats in the surrounding landscape.

Materials and methods

Study system

ESE-6904/6905 is a 42 km powerline operated by the American Transmission Company in Chippewa and Mackinac counties in the eastern Upper Peninsula of Michigan. The line connects St. Ignace in the south to the Pine River Substation near Rudyard in the north. The corridor was initially constructed in the 1930s and is 30–60 m in width. The line currently runs at 69,000 volts with approximately 395 double-circuit wood pole structures. In Mackinac County a considerable proportion of the corridor passes though the St. Ignace Ranger District of the Hiawatha National Forest, where it has been maintained by mowing and mechanical woody plant removal.

In total, 58 land snail species have been previously identified from the eastern Upper Peninsula (Hubricht 1985; Nekola 2004). Of these, 13 are listed as of conservation concern by the Michigan Natural Features Inventory (2011): *Catinella exile*—Threatened; *Euconulus alderi*—Threatened; *Planogyra asteriscus*—Special Concern; *Pupilla muscorum*—Special Concern; *Vallonia gracilicosta*—Endangered; *Vertigo bollesiana*—Threatened; *Vertigo cristata*—Special Concern; *Vertigo elatior*—Special Concern; *Vertigo hubrichti*—Endangered; *Vertigo morsei*—Endangered; *Vertigo nylanderi*—Endangered; *Vertigo paradoxa*—Special Concern and *Vertigo pygmaea*—Special Concern. Six species (*Cochlicopa lubrica*, *Oxychilus draparnaudi*, *Pupilla muscorum*, *Vallonia costata*, *Vallonia pulchella*, *Vertigo pygmaea*) appear to be Eurasian exotics based on their preference for anthropogenic habitats, known North American history and/or population genetics (Pilsbry 1948; Nekola and Coles 2010).

Sampling design

Eighteen sample sites were identified along the ESE-6904/6905 route as it passes through the Hiawatha National Forest in eastern Mackinac County, Michigan. Sample sites were spread across the entire corridor route, were separated by at least 0.5 km, and represented all natural habitats crossed by the corridor. These included marl ponds, fens, sedge meadows, upland and lowland Northern White Cedar stands, sandy pine forest, mixed deciduous forest, and rocky slopes. Sample sites were located in conjunction with pole numbers 505, 520, 567, 600, 605, 623, 652, 680, 696, 705, 717, 726, 728, 755, 772, 790, 811 and 813 (Fig. 1). At most sites three subsamples were collected: one within the existing corridor, and two controls located within intact vegetation 30 m to both the west and east of the corridor. No private lands were surveyed. For this reason only the corridor and west margin subsamples were collected at Pole 811 and only the corridor subsample was collected at Pole 600. Also, because of abundance of Poison Ivy and lack of leaf litter accumulation within the corridor, only the western margin at Pole 813 was sampled.

Comparisons were also made with 32 additional sites in the surrounding landscape, including 11 wooded bedrock outcrops, 5 upland forests, 7 lowland forests, 8 lowland grasslands and a single upland grassland. These capture the full compositional range of regional land snail assemblages (Nekola 2003, 2004, 2005; Fig. 1).

Field methods

The land snail assemblage of each 100 m^2 subsample was documented from September 25–30, 2009 through hand collection of larger shells and litter sampling for smaller taxa following protocols of Cameron and Pokryszko (2005) and Oggier et al. (1998).

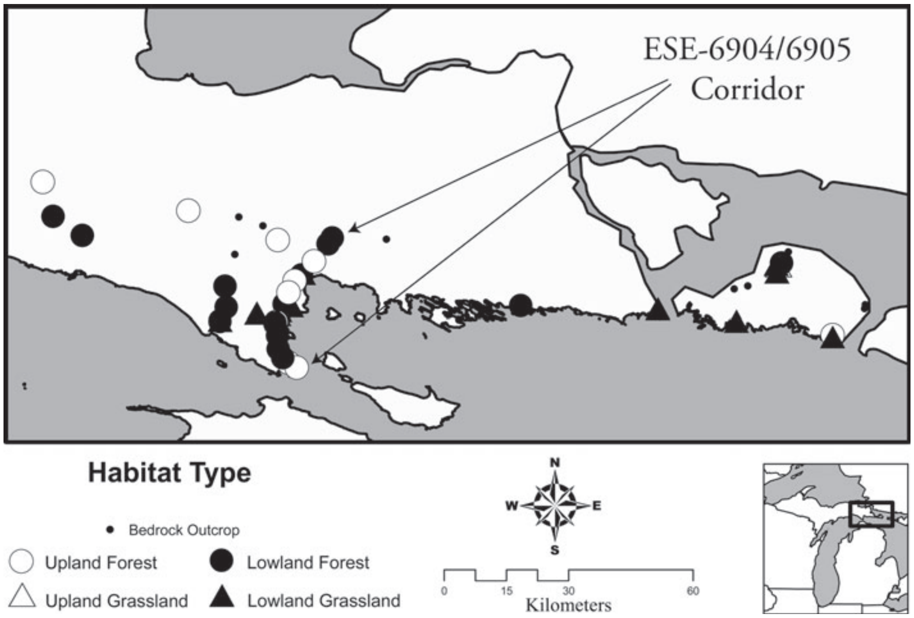

Fig. 1 Map of the eastern Upper Peninsula of Michigan showing location of the 18 sample sites analyzed along the ESE-6904/6905 corridor along with locations of the 32 additional comparison sites

Approximately 30 min were spent collecting each subsample. Soil litter collections followed protocols of Nekola and Coles (2010), and emphasized microsites known to support high micro-snail densities (e.g., Emberton et al. 1996). Approximately 200 ml of litter were collected per subsample. This generally captured ten times as many individuals as species, which is advocated by Cameron and Pokryszko (2005) for accurate land snail community documentation. The latitude-longitude position of each pole location was determined using a Garmin 12XL hand-held GPS unit.

Sampling of comparison sites elsewhere in the eastern Upper Peninsula was conducted from July 1997–October 2009 in a similar fashion (see Nekola 2003, 2004, 2005) although at an order of magnitude larger spatial sampling grain. Any systematic bias would thus result in underestimating the relative richness of ESE-6904/6905 subsamples through random undersampling of the rarest species. However, this will not obscure community composition gradients (Jobe 2007).

Laboratory procedures

As outlined by Nekola and Coles (2010), dried litter samples were passed through a standard sieve series and handpicked against a neutral-brown background. All shells and shell fragments were removed. All shells were assigned to species (or subspecies) using the author's reference collection, with the total numbers of shells per species per site being recorded. The number of unassignable immature individuals and fragmentary shells was recorded. Nomenclature is based principally on Hubricht (1985) with updates by Turgeon et al. (1998), Nekola (2004) and Nekola and Coles (2010).

Data summary and statistical analysis

Species richness and abundance

For each species, the total number of subsamples in which it was recorded and the total number of encountered individuals was calculated. Using the non-parametric Kruskal–Wallis Rank Sum Test, these values were compared among the west of corridor, corridor, and east of corridor subsamples, and were graphically illustrated using boxplots. To better visualize the upper and lower bounds, boxplots were constructed using a natural-log scale. However, raw values were used for statistical testing. Variation in community structure among the three subsample positions was illustrated by dominance–diversity curves generated from median proportional abundance values calculated within each of the three subsample locations. Median values were used because they are more robust descriptors of central tendency, being less influenced by outliers as compared to mean values. Variation in richness and abundance of three soil architecture preference classes (duff specialist, generalist, turf specialist) among the three subsample positions was also statistically tested using the Kruskal–Wallis Rank Sum Test and illustrated with boxplots. As before, abundance distributions were visualized using natural-log scaled box-plots, but tested using raw data. The soil architecture nomenclature and preferences of Nekola (2003) were used, with 'duff specialists' being species that favor soils with loose organic horizons and 'turf specialists' being those that favor organic horizons that are tightly bound with living plant roots. The only exception was *Striatura exigua*, which is here considered a 'generalist' rather than a 'turf' species (Nekola 2003) based on additional eastern North American data (Nekola 2010). Differences in richness and abundance for species of conservation concern and alien species among the three subsample positions was also quantified using the Kruskal–Wallis Rank Sum Test.

Community composition

The impact of the corridor on community composition was analyzed through global non-metric multidimensional scaling (NMDS) using DECODA (Minchin 1990). NMDS makes no assumptions regarding the underlying nature of species distributions along compositional gradients, and is thus the most robust form of ordination for detection of ecological patterns (Minchin 1987). All 49 ESE-6904/6905 subsamples in addition to the 32 additional regional comparison sites were included in this analysis. To ordinate sites a matrix of dissimilarity coefficients was calculated based on species abundance data using the Czekanowski index (Faith et al. 1987). Data were untransformed to avoid mathematical artifacts (Nekola et al. 2008). NMDS in one through four dimensions was then performed with 200 iterations, a stress ratio stopping value of 0.9999, and a small stress stopping value of 0.01. Output was scaled in half-change units, so that points in the resulting diagram separated by a distance of 1.0 will correspond, on average, to a 50% turnover in species composition.

Because a given NMDS run may locate a local, rather than the global, stress minimum, solution stability was assessed via 50 NMDS runs using different random initial starting points (Minchin 1987). Solutions in each of the four dimensions were compared using a Procrustes transformation to identify those that were statistically similar. The number of unique solutions and number of individual runs that fell into each was then calculated. The global optimum solution was identified as the smallest stress solution that was achieved in a plurality of starts.

To assess the impact of corridor construction on community composition, a vector was generated using a given control subsample as the origin and the adjacent corridor subsample as the endpoint. Each of these vectors was plotted on the ordination diagram and its length and angle from vertical calculated. This allowed a median vector of compositional change to be determined across the entire dataset. The significance of these changes in ordination space was estimated using the non-parametric paired Wilcoxon Rank Sum Test.

Fisher Exact contingency table tests were used to identify those species that were statistically more abundant within the corridor or control subsamples as compared to a null hypothesis of uniform distribution. Analysis was limited to paired subsamples (i.e. 600C and 813W were eliminated). Species with fewer than ten total occurrences were not analyzed due to the likelihood of Type-II errors. Because this test was repeated for each species, a Bonferroni correction was used to modify the significance threshold. The results of this analysis were then compared to the results of the duff vs. turf soil preference tests of Nekola (2003) by use of a 3 × 3 contingency table. This table was compared to uniform expectations using a Fishers exact test.

Results

In total, 44 species were observed from the 49 subsamples collected along the ESE-6904/6905 corridor (Table 1). Of these, five (*Gastrocopta pentodon*, *Oxychylus draparnaudi*, *Vertigo bollesiana*, *Vertigo ovata* and *Vertigo pygmaea*) are reported here for the first time from Mackinac county (Hubricht 1985; Nekola 2004), raising the total county fauna to 54 species. Nine of the thirteen species of conservation concern known from the region

Table 1 Number of occupied subsamples and individuals for all encountered terrestrial gastropod species

Species name	Soil architecture preference	Number of subsamples/individuals		
		West of corridor	Powerline corridor	East of corridor
Anguispira alternata	D	2/3	1/1	1/2
Carychium exiguum	T	9/293	12/543	7/292
Carychium exile	D	6/99	3/19	7/88
**Cochlicopa lubrica*	D	4/93	3/18	1/1
Columella simplex	D	14/127	10/49	16/167
Deroceras spp.	G	4/5	7/12	6/9
Discus catskillensis	D	9/167	4/5	12/109
Euchemotrema fraternum	D	0/0	1/2	1/1
Euconulus alderi	T	6/26	8/57	5/19
Euconulus fulvus	D	8/31	2/10	9/75
Euconulus polygyratus	D	3/16	2/9	2/4
Gastrocopta pentodon	D	1/1	1/33	0/0
Gastrocopta tappaniana	T	2/25	7/101	3/24
Glyphyalinia indentata	D	1/1	1/1	1/1
Helicodiscus parallelus	G	0/0	1/2	0/0
Helicodiscus shimeki	D	3/11	1/2	9/54
Nesovitrea binneyana	D	8/102	0/0	9/144
Nesovitrea electrina	T	4/28	10/158	4/43
**Oxychylus draparnaudi*	G	0/0	1/3	0/0
Oxyloma retusa	T	1/1	4/6	0/0
Paravitrea multidentata	D	1/8	0/0	0/0
Planogyra asteriscus	G	8/814	2/7	8/603
Punctum minutissimum	D	16/1,653	7/141	16/1,371
Punctum n.sp.	T	6/84	8/410	6/70
**Pupilla muscorum*	G	1/9	1/8	0/0
Striatura exigua	G	13/248	9/195	15/351
Striatura ferrea	G	9/176	3/52	12/102
Striatura milium	G	12/332	6/65	14/334
Strobilops labyrinthica	D	15/1,279	14/275	16/993
Succinea ovalis	D	0/0	3/4	0/0
**Vallonia costata*	G	2/55	1/5	0/0
**Vallonia pulchella*	T	0/0	2/4	0/0
Vertigo bollesiana	D	6/15	0/0	6/14
Vertigo cristata	D	7/33	2/20	5/19
Vertigo elatior	T	5/42	11/118	7/17
Vertigo gouldii	D	2/3	0/0	2/7
Vertigo morsei	T	1/9	4/48	0/0
Vertigo nylanderi	T	2/24	0/0	2/8
Vertigo ovata	T	0/0	3/3	1/1
**Vertigo pygmaea*	G	1/4	2/2	0/0
Vitrina limpida	G	2/8	2/7	0/0
Zonitoides arboreus	D	6/14	3/5	5/9

Table 1 continued

Species name	Soil architecture preference	Number of subsamples/individuals		
		West of corridor	Powerline corridor	East of corridor
Zonitoides nitidus	T	1/4	0/0	0/0
Zoogenetes harpa	D	2/4	1/4	1/2
Total terrestrial gastropods		16/5,847	17/2,404	16/4,934

Species underlined are species of conservation concern in Michigan (Michigan Natural Features Inventory 2011). Species preceded by an asterisk are Eurasian aliens. Soil architecture preference is based on Nekola (2003) with minor revisions as per text; *D* Duff specialist, *T* turf specialist, *G* generalist

(*Euconulus alderi, Planogyra asteriscus, Pupilla muscorum, Vertigo bollesiana*, *Vertigo cristata*, *Vertigo elatior*, *Vertigo morsei*, *Vertigo nylanderi*, and *Vertigo pygmaea*) were observed. In total, 14, 242 individuals were collected, of which 13,185 were identifiable to species. Thirty-one of the subsamples included at least 200 individuals. The 32 eastern Upper Peninsula comparison sites ranged in richness from 3 to 25 species and in abundance from 19 to 1,480, with a total of 12,831 individuals being identified to species.

Impact on species richness and abundance

Based on paired observations, both species richness and abundance were lower within the corridor than in adjacent control subsamples (Fig. 2): median richness fell by approximately ¼ (from 14 to 10; $P = 0.015$) and abundance by approximately ¾ (from 400 to 100; $P < 0.00003$). However, dominance-diversity curves demonstrated that median proportional abundance was very similar for up to approximately the 7th most abundant species (Fig. 3), after which median abundance fell off more rapidly for the corridor subsamples.

Comparison of richness and abundance across species with differing soil architecture preferences (Fig. 4) demonstrates that control subsamples were dominated by duff

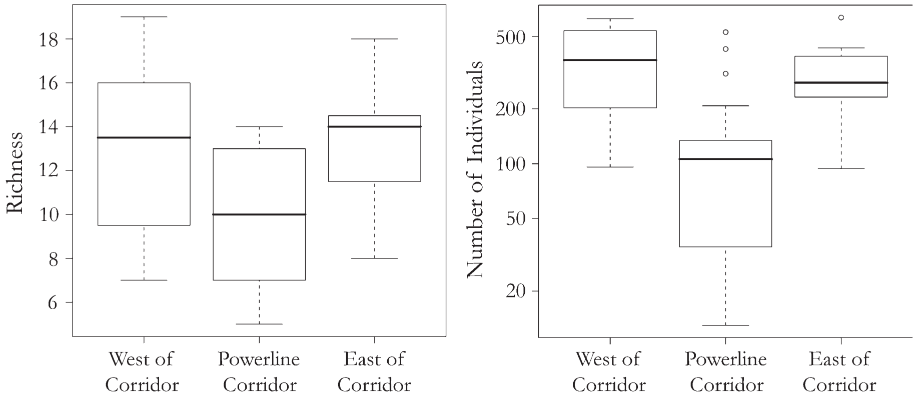

Fig. 2 *Boxplots* showing variation in terrestrial gastropod richness and abundance among the three subsample positions along the ESE-6904/6905 corridor. Abundance data are presented along a log-scaled axis. The *central line* represents the median of the sample, the margins of each *box* represent the interquartile distances, and the *fences* represent 1.5 times the interquartile distances. Outliers falling outside of the *fences* are shown with *circles*

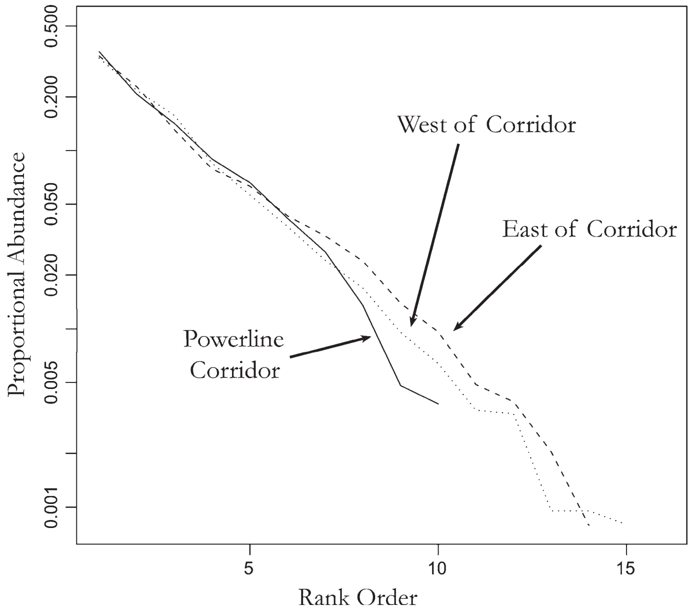

Fig. 3 Dominance-diversity curves demonstrating proportional abundance versus rank order of terrestrial gastropod species for the three subample positions along the ESE-6904/6905 corridor

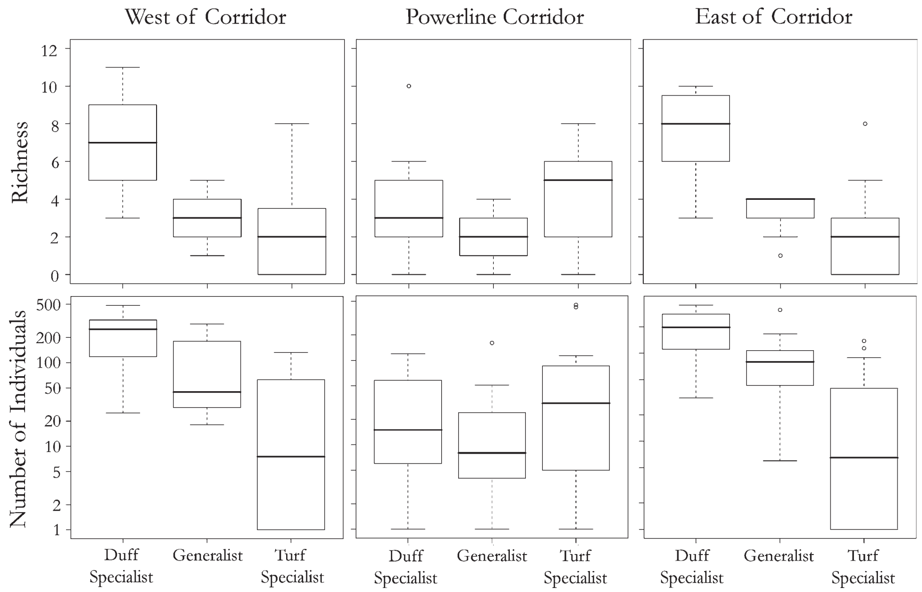

Fig. 4 *Boxplots* showing variation in duff specialist, generalist, and turf specialist terrestrial gastropod species richness and abundance among the three subsample categories along the ESE-6904/6905 corridor. Abundance data are presented along a log-scaled axis. The *central line* represents the median of the sample, the margins of each *box* represent the interquartile distances, and the *fences* represent 1.5 times the interquartile distances. Outliers falling outside of the *fences* are shown with *circles*

specialists (~57% of taxa and ~80% of individuals), followed by generalists (~27% and ~18%) and turf specialists (~16% and ~2%; Fig. 4). However, corridor subsamples were dominated by turf specialists (~50% and ~63%) followed by duff specialists (~30% and ~23%), and generalists (~20% and ~14%). While these differences were statistically significant for duff and turf specialists ($P = 0.016$ and $P = 0.0020$, respectively, for richness, and $P = 0.0095$ and $P = 0.0037$ for individuals), generalist species did not differ significantly ($P = 0.1054$ for richness and $P = 0.0948$ for individuals).

No significant differences were noted in richness ($P = 0.7842$) or abundance ($P = 0.7350$) of species of conservation concern or in exotic species richness ($P = 0.2095$) or abundance ($P = 0.2124$) among corridor and adjacent control subsamples.

Impact on community composition

NMDS along two dimensions was chosen as the most robust solution, given that all five minimum stress configurations fell into a single group. The 1-, 3-, and 4-dimensional solutions were not considered as they either possessed larger stress values or had no single modal solution. The chosen ordination documents a dramatic alteration of terrestrial gastropod community composition within the corridor (Fig. 5). While control subsample assemblages remain similar to other regional lowland conifer forest, upland forest, and lowland grassland assemblages, corridor faunas tend to be displaced down and/or left in the diagram, being similar to the faunas of native lowland grassland sites (e.g., sedge meadows, fens). Displacement vectors from a given control subsample to its paired corridor subsample ranged from 0.18 to 3.4, or 9% to 170% change in composition. Across all pairs, the median distance was 1.27 (indicating roughly a 2/3 turnover in composition) at −110° from the top of the diagram. This displacement was highly significant ($P < 0.00002$) along both axes.

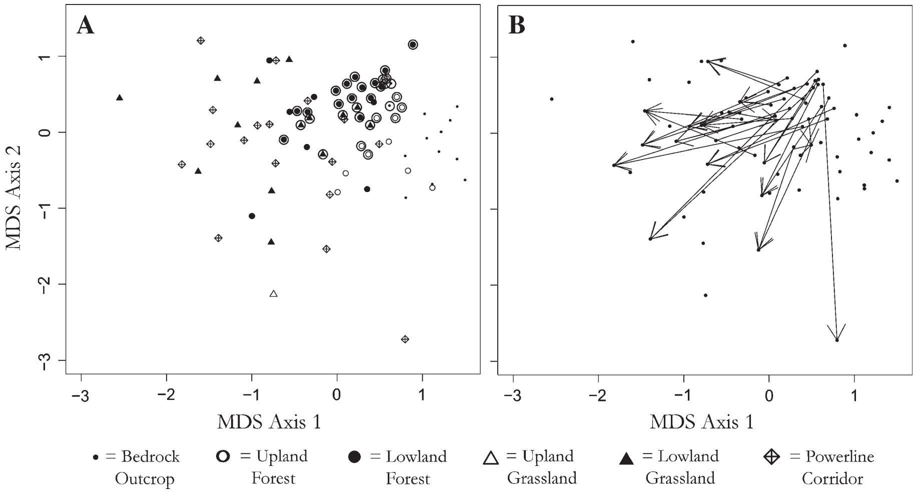

Fig. 5 NMDS ordination of terrestrial gastropod faunas from the 49 ESE-6904/6905 subsamples and 32 comparison sites. *Axes* are scaled in half-change units. **a** Optimum two-dimensional NMDS solution. Powerline corridor subsamples are represented by *hatched diamonds*; control subsamples are indicated by a *circle* surrounding the appropriate *habitat icon*; *uncircled habitat icons* represent comparison sites. **b** Vectors demonstrating the change in composition between control (origin) and adjacent corridor (endpoint) samples

Following removal of unpaired subsamples, fifteen species were eliminated from further analysis because they were represented by ten or fewer individuals. Fisher exact tests of the remaining 29 species (Table 2) demonstrated that eight either significantly favored (Bonferroni corrected P-threshold $= 0.0017$) or tended to favor ($0.05 > P > 0.0017$) corridor subsamples, 14 significantly favored the adjacent control subsamples, while the remaining six were generalists ($0.05 < P$). While three species of conservation concern favored control subsamples (*Planogyra asteriscus*, *Vertigo bollesiana*, *Vertigo nylanderi*) an additional three favored corridor subsamples (*Euconulus alderi*, *Vertigo elatior*, *Vertigo morsei*) with two more being generalists (*Pupilla muscorum*, *Vertigo cristata*). Although *Vertigo pygmaea* was not statistically analyzed because not enough individuals were encountered, 2/3 of its occurrences were within the corridor.

Comparison of these responses to known soil architecture preferences (Nekola 2003) indicates that the two factors are significantly linked ($P = 0.0154$; Table 3): species that favored corridor subsamples tended to favor turf soils, while species favoring control subsamples tended to favor duff soils.

Discussion

The sampling protocols used in this study were found to be more than adequate to accurately characterize the land snail fauna and its response to powerline corridor formation. First, roughly 80% of the known county and 75% of the eastern Upper Peninsula fauna was encountered despite the fact that the corridor does not intersect the carbonate cliff sites that serve as one of the most important regional reservoirs for land snail biodiversity (Nekola 1999). This sampling design also resulted in documenting well the regional species of conservation concern. Only four such species were not encountered: *Vallonia gracilicosta*, *Vertigo hubrichti* and *Vertigo paradoxa* were not observed because their stable carbonate cliff habitat was not intersected by the ESE-6904/6905 corridor; and *Catinella exile* was also not recorded even though it has been observed in low numbers on the marl fen at Summerby Swamp to the northwest of the corridor. While seemingly appropriate habitat for this species exists within the ESE-6904/6905 corridor and adjacent habitats, its absence was not surprising as it is also absent from the immediately adjacent Martineau Creek fen (Nekola 1998). Additionally, both the entire dataset as well as ¾ of the individual subsamples meet the criteria of Cameron and Pokryszko (2005) for accurate portrayal of land snail community patterns.

These data show that creation of a treeless powerline corridor has led to profound changes in the terrestrial gastropod community. Both the richness and abundance of land snails within the corridor have fallen in comparison to adjacent habitats, with composition turning over by roughly 2/3 as turf (i.e., grassland) specialists replace duff (i.e., forest) specialists.

This change, however, has not led to a reduction in total land snail biodiversity. First, faunas of control subsamples remain compositionally similar to those of other undisturbed sites in the region, with multiple species of conservation concern persisting only 30 m from the corridor edge. Second, species abundance distributions were generally unaffected, with proportional abundance being similar for corridor and control subsamples up to the seventh-most abundant species. Although abundance levels trailed off more rapidly for corridor subsamples from the eighth-most-abundant species on, this general pattern is characteristic for native grassland faunas throughout the region (Nekola 2002, 2010). As a result, the more rapid fall off of abundance is probably not due to the corridor, per se, but

Table 2 Impact of powerline corridor on species abundance

Name	Corridor samples		Control samples		*P* value
	Obs.	Exp.	Obs.	Exp.	
A. Species with too few observations (10 or less) to characterize preference					
Anguispira alternata; *Euchemotrema fraternum*; *Glyphyalinia indentata*; *Helicodiscus parallelus*; *Oxychilus draparnaudi*; *Oxyloma retusa*; *Paravitrea multidentata*; *Succinea ovalis*; *Vallonia costata*; *Vallonia pulchella*; *Vertigo gouldii*; *Vertigo ovata*; *Vertigo pygmaea*; *Vitrina limpida*; *Zoogenetes harpa*					
B. Generalist species					
Name	Corridor Obs.	Subamples Exp.	Control Obs.	Subamples Exp.	*P* value
Deroceras sp.	12	9	14	17	0.572488900
Euconulus polygyratus	9	10	20	19	1.000000000
Punctum n.sp.	85	81	154	158	0.773239300
Pupilla muscorum	8	6	9	11	0.728282100
Vertigo cristata	20	25	52	47	0.472278900
Zonitoides arboreus	5	10	23	18	0.226957500
C. Species that favor ($P < 0.0017$) or tend to favor ($0.05 > P > 0.0017$) corridor subsamples					
Carychium exiguum	465	357	585	693	0.000001676
Cochlicopa lubrica	18	8	6	16	0.008414732
Euconulus alderi	48	32	45	61	0.026030660
Gastrocopta pentodon	33	12	1	22	0.000000047
Gastrocopta tappaniana	95	49	49	95	0.000000090
Nesovitrea electrina	151	76	71	146	0.000000000
Vertigo elatior	118	60	59	117	0.000000001
Vertigo morsei	48	19	9	38	0.000000047
D. Species that favor ($P < 0.0017$) or tend to favor ($0.05 > P > 0.0017$) control subsamples					
Carychium exile	19	70	187	136	0.000000001
Columella simplex	49	116	293	226	0.000000002
Discus catskillensis	5	96	276	185	0.000000000
Euconulus fulvus	10	39	106	77	0.000004013
Helicodiscus shimeki	2	23	65	44	0.000002788
Nesovitrea binneyana	0	84	246	162	0.000000000
Planogyra asteriscus	7	485	1,417	939	0.000000000
Punctum minutissumum	141	1,028	2,879	1,992	0.000000000
Striatura exigua	195	270	599	524	0.000043710
Striatura ferrea	52	112	278	218	0.000000083
Striatura milium	65	249	666	482	0.000000000
Strobilops labyrinthica	275	867	2,271	1,679	0.000000000
Vertigo bollesiana	0	10	29	19	0.000767735
Vertigo nylanderi	0	11	32	21	0.000347028

Species considered of conservation concern by the Michigan Natural Features Inventory are underlined

rather indirectly to the conversion to grassland habitats/faunas. Third, ordination demonstrates that within 75 years the corridor fauna has evolved into assemblages very similar to other native lowland grassland sites in the region, in particular sedge meadows and fens.

Table 3 Species response to subsamples placement versus duff/turf soil architecture preference, with numbers in each cell representing number of species

	Soil architecture preference		
	Duff species	Generalist species	Turf species
Corridor preference			
Control subsamples	9	4	1
Generalist	3	1	1
Corridor subsamples	2	0	6

Fisher's exact test: $P = 0.0154$

The ultimate impact of corridor formation has been for the expansion of lowland grassland land snail faunas into the previously largely forested matrix. Fourteen species (~30% of total) were found to favor control subsamples, while eight (~20%) favored the corridor itself. These changes are similar to those previously noted with forest clearing (Nekola 2003). Because species of conservation concern in this region are roughly equally partitioned between forests and open habitats, the decrease in population occurrence/size of forest-favoring rare species (*Planogyra asteriscus*, *Vertigo bollesiana*, *Vertigo nylanderi*) in the corridor has been compensated by the increase of grassland-favoring rare species (*Euconulus alderi*, *Vertigo elatior*, *Vertigo morsei*), with *Vertigo morsei* representing one of the rarest land snail species in the Great Lakes region (Nekola 2004). As a result, no significant change in either the total richness or abundance of species of conservation concern was noted between corridor and adjacent forest habitats. However, the increase in coverage and population sizes of grassland species that would otherwise be rare or absent from the corridor has enriched total biodiversity. This result holds even when the two alien species listed by the Michigan Natural Features Inventory (*Pupilla muscorum, Vertigo pygmaea*) are removed from analysis.

Even though terrestrial gastropods appear to be ideal candidates for documenting detrimental biodiversity impacts from corridor formation, these data demonstrate that system-wide diversity has not been lowered by corridor formation. Rather, the net impact appears positive, as the corridor has allowed for an expansion of grassland/turf specialists, including one of the rarest species in the landscape, while at the same time not seriously impacting the faunas of adjacent habitats.

How have small grassland snails with poor active dispersal abilities been able to occupy the new grassland habitats created by corridor formation within the relatively short ecological time frame that the ESE-6904/6905 corridor has been in existence? The explanation is probably that small land snails, such as those that dominate the Upper Peninsula fauna, possess great passive dispersal capabilities. For example, DNA sequence data demonstrate that members of the genus *Balea* have been repeatedly carried across 9,000 km of open eastern Atlantic Ocean by migrating birds (Gittenberger et al. 2006). Similarly, in North America many members of the *Vertigo gouldii* group have ranges exceeding 5,000 km in extent even though they inhabit areas covered by continental ice as recently as 10 ka (Nekola et al. 2009). Passive dispersal of some small land snail species is also facilitated by their ability to reproduce uniparentally (Pokryszko 1987), allowing only single individuals to found populations. As a result, small land snails tend to possess much larger ranges and to more completely saturate their available habitats than larger taxa (McClain and Nekola 2008; Nekola 2009).

The most likely vectors for passive land snail dispersal in the ESE-6904/6905 corridor are birds and small mammals. For both of these groups, utility corridors represent travel paths for grassland species through forested landscapes (Kroodsma 1982; Gates 1991). This will allow for movement of grassland/turf specialist land snails through corridors as well. Additionally, narrow corridors such as that for ESE-6904/6905 have been found to not restrict movements of small mammals in eastern North American forests (Schreiber and Graves 1977; Gates 1991), and gliding mammals (Asari et al. 2010), small mammals, reptiles, and amphibians (Carthew et al. 2009) in Australia. Consequently, the ESE-6904/6905 corridor probably does not serve as a barrier to passive movements of minute forest snails. It should thus not be surprising that the richness, abundance, and community structure of land snail assemblages on either side of the corridor were found to be very similar.

These results mirror numerous studies that have shown that utility corridors serve as refuges for grassland species within forested landscapes. This effect has been repeatedly shown for birds (Kroodsma 1982; King et al. 2009; Meehan and Haas 1997) and mammals (Gates 1991) in eastern North America and for a variety of small vertebrates in Australia (Goosem and Marsh 1997; Clarke et al. 2006; Clarke and White 2008a, b). As was found in the current study, these grassland species may be quite uncommon elsewhere within the landscape (Clarke and White 2008b). Similar patterns exist for vascular plants in the southeastern USA, where powerline corridors serve as refuges in an otherwise forested matrix for a number of critically endangered grassland/savanna species (Sorrie and Weakley 2001).

Thus, as long as a given utility corridor (1) does not substantially impact the overall population of a given forest-specialist species, (2) exists within a forest-dominated landscape that also includes native grassland habitats and (3) is maintained through manual vegetation cutting, it may actually benefit terrestrial gastropod biodiversity by maintaining refuges for both common and rare grassland species while not leading to the extirpation of sensitive forest species. For the current alignment of ESE-6904/6905 this equates to roughly 3–6 ha of grassland habitat per kilometer of corridor. However, it should not be assumed that these positive benefits will also accrue in landscapes lacking native grassland habitats, or for corridors maintained through herbicide application (Nowak et al. 1993). Although quantitative sampling for land snails was not conducted in areas subjected to this type of management, it appeared that terrestrial gastropod richness and abundance was much lower in herbicide-managed sections of the corridor just outside of the National Forest boundary.

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References

Andrews A (1990) Fragmentation of habitat by roads and utility corridors: a review. Aust Zool 26:130–141

Arnold GW, Algar D, Hobbs RJ, Atkins L (1987) A survey of vegetation and its relationship to vertebrate fauna present in winter on road verges in the Kellerberrin District, Western Australia. Technical Report 18, Department of Conservation and Land Management, Western Australia

Asari Y, Johnson CN, Parsons M, Larson J (2010) Gap-crossing in fragmented habitats by mahogany gliders (*Petaurus gracilis*). Do they cross roads and powerline corridors? Aust Mammol 32:10–15

Baur B (1988) Microgeographical variation in shell size of the land snail *Chondrina clienta*. Biol J Linn Soc 35:247–259

Baur A, Baur B (1990) Are roads barriers to dispersal in the land snail *Arianta arbustorum*? Can J Zool 68:613–617

Bennett AF (1991) Roads, roadsides, and wildlife conservation: a review. In: Saunders DA, Hobbs RJ (eds) Conservation 2: the role of corridors. Surrey Beatty & Sons, Chipping Norton

Cameron RAD, Pokryszko BM (2005) Estimating the species richness and composition of land mollusc communities. J Conchol 38:529–547

Carthew SM, Horner B, Jones KMW (2009) Do utility corridors affect movements of small terrestrial fauna? Wildl Res 36:488–495

Clarke DJ, White JG (2008a) Towards ecological management of Australian powerline corridor vegetation. Landsc Urban Plan 86:257–266

Clarke DJ, White JG (2008b) Recolonization of powerline corridor vegetation by small mammals: timing and influence of vegetation management. Landsc Urban Plann 87:108–116

Clarke DJ, Pearce KA, White JG (2006) Powerline corridors: degraded ecosystems or wildlife havens? Wildl Res 33:615–626

Emberton KC, Pearce TA, Randalana R (1996) Quantitatively sampling land-snail species richness in Madagascan rainforests. Malacologia 38:203–212

Fahig L, Mirriam G (1985) Habitat patch connectivity and population survival. Ecology 66:1762–1768

Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57–68

Forman RTT (1986) Landscape ecology. Wiley, New York

Gates JE (1991) Powerline corridors, edge effects, and wildlife in forested landscapes of the central Appalachians. In: Rodiek JE, Bolen EG (eds) Wildlife and habitats in managed landscapes: an overview. Island Press, Washington

Gerlach G, Mustov K (2000) Fragmentation of landscape as a cause for genetic subdivision in bank voles. Conserv Biol 14:1066–1074

Gittenberger E, Groenenberg DSJ, Kokshoorn B, Preece RC (2006) Molecular trails from hitch-hiking snails. Nature 439:409

Goosem M, Marsh H (1997) Fragmentation of a small mammal community by a powerline corridor through tropical rainforest. Wildl Res 24:613–629

Hausdorf B, Hennig C (2003) Nestedness of north-west European land snail ranges as a consequence of differential immigration from Pleistocene glacial refuges. Oecologia 35:102–109

Hubricht L (1985) The distributions of the native land mollusks of the eastern United States. Fieldiana New Ser 24:1–191

Jobe RT (2007) Estimating landscape-scale species richness: reconciling frequency- and turnover-based approaches. Ecology 89:174–182

King DI, Chandler RB, Collins JM, Petersen WR, Lautzenheiser TE (2009) Effects of width, edge and habitat on the abundance and nesting success of scrub-shrub birds in powerline corridors. Biol Conserv 142:2672–2680

Kroodsma RL (1982) Edge effect on breeding forest birds along a power-line corridor. J Appl Ecol 19:361–370

McClain C, Nekola JC (2008) The role of local-scale on terrestrial and deep-sea Gastropod body size distributions across multiple scales. Evol Ecol Res 10:129–146

Meehan AL, Haas CA (1997) Use of a powerline corridor by breeding and wintering birds in Giles County, Virginia. Va J Sci 48:259–264

Michigan Natural Features Inventory (2011) Michigan's Special Animals. http://web4.msue.msu.edu/mnfi/data/specialanimals.cfm. Accessed 7 Mar 2011

Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69:89–108

Minchin PR (1990) DECODA software. Australian National University, Canberra

Nekola JC (1998) Terrestrial gastropod inventory of the Niagaran escarpment and Keweenaw volcanic belt in Michigan's Upper Peninsula. Final Report, Michigan Department of Natural Resources Small Grants Program, Lansin

Nekola JC (1999) Terrestrial gastropod richness of carbonate cliff and associated habitats in the Great Lakes region of North America. Malacologia 41:231–252

Nekola JC (2002) Effects of fire management on the richness and abundance of central North American grassland land snail faunas. Animal Biodivers Conserv 25:53–66

Nekola JC (2003) Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. Divers Distrib 9:55–71

Nekola JC (2004) Terrestrial gastropod fauna of northeastern Wisconsin and the southern Upper Peninsula of Michigan. Am Malacol Bull 18:21–44

Nekola JC (2005) Latitudinal richness, evenness, and shell size gradients in eastern North American land snail communities. Rec West Aust Mus Suppl 68:39–51

Nekola JC (2009) Big ranges from small packages: North American vertiginids more widespread than thought. Tentacle 17:26–27

Nekola JC (2010) Acidophilic terrestrial gastropod communities of North America. J Mollus Stud 76:144–156

Nekola JC, Coles BF (2010) Pupillid land snails of eastern North America. Am Malacol Bull 28:29–57

Nekola JC, Smith TA (1999) Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. Malacologia 41:253–269

Nekola JC, Šizling AL, Boyer AG, Storch D (2008) Artifactions in the log-transformation of species abundance distributions. Folia Geobot 43:259–468

Nekola JC, Coles BF, Bergthorsson U (2009) Evolutionary pattern and process in the *Vertigo gouldii* (Mollusca: Pulmonata, Pupillidae) group of minute North American land snails. Mol Phylogenet Evol 53:1010–1024

Nowak CA, Abrahamson LP, Raynal DJ (1993) Powerline corridor vegetation management trends in New York State: has a post-herbicide era begun? J Arboric 19:20–26

Oggier P, Zschokke S, Baur B (1998) A comparison of three methods for assessing the gastropod community in dry grasslands. Pedobiologia 42:348–357

Pilsbry HA (1948) Land Mollusca of North America (North of Mexico). Academy of Natural Sciences of Philadelphia, Monograph #3

Pokryszko BM (1987) On aphally in the Vertiginidae (Gastrocopta: Pulmonata: Orthurethra). J Conchol 32:365–375

Schilthuizen M, Lombaerts M (1994) Population structure and levels of gene flow in the Mediterranean land snail *Albinaria corrugata* (Pulmonata: Clausiliidae). Evolution 48:577–586

Schreiber RK, Graves JH (1977) Powerline corridors as possible barriers to movements of small mammals. Am Midl Nat 97:504–508

Shaffer ML, Samson FB (1985) Population size and extinction: a note on determining critical sizes. Am Nat 125:144–152

Simberloff D, Cox J (1987) Consequences and costs of conservation corridors. Conserv Biol 1:63–71

Sorrie BA, Weakley AS (2001) Coastal plain vascular plant endemics and phytogeographic patterns. Castanea 66:50–82

Turgeon DD, Quinn JF Jr, Bogan AE, Coan EV, Hochberg FG, Lyons WG, Mikkelsen P, Neves RJ, Roper CFE, Rosenberg G, Roth B, Scheltema A, Thompson FG, Vecchione M, Williams JD (1998) Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks, 2nd edn. Bethesda: American Fisheries Society Special Publication 26

Yahner RH, Morrell TE, Rachael JS (1989) Effects and edge contrast on depredation of artificial avian nests. J Wildl Manag 53:1135–1138

Research Note

Effects of Rock Climbing on the Land Snail Community of the Niagara Escarpment in Southern Ontario, Canada

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Abstract: *The cliffs of the Niagara Escarpment provide habitat for extremely diverse communities of land snails that may be at risk as a result of recreational rock climbing. We examined the effects of rock climbing on the density, richness, diversity, and community composition of snails on the Niagara Escarpment in southern Ontario, Canada. We sampled from randomly selected climbed and unclimbed sections of cliffs on the plateau (cliff edge), cliff face, and talus (cliff base). Snail density, richness, and diversity were lower along climbing routes than in unclimbed areas, and community composition differed between climbed and unclimbed samples. These results suggest that rock climbing has significant negative effects on all aspects of the snail community on cliffs; therefore, we recommend the inclusion of gastropods in conservation plans for protected areas containing cliffs.*

Efectos del Alpinismo en la Comunidad de Caracoles Terrestres del Acantilado del Niagara en Ontario Meridional, Canadá

Resumen: *Las barrancas del acantilado del Niagara proveen hábitat para comunidades extremadamente diversas de caracoles terrestres que pueden estar en riesgo debido al alpinismo recreativo. Examinamos los efectos del alpinismo en la densidad, riqueza, diversidad y composición de comunidades de caracoles del acantilado del Niagara en Ontario Meridional, Canadá. Tomamos muestras de las mesetas (bordes de acantilados), la cara del acantilado y el talud (base del acantilado) de secciones de barrancas usadas y no usadas para el alpinismo y seleccionadas al azar. La densidad, la riqueza y la diversidad de caracoles fueron más bajas en las rutas escaladas que en aquellas áreas no escaladas y la composición de la comunidad difirió entre muestras escaladas y no escaladas. Estos resultados sugieren que el alpinismo tiene impactos negativos significativos en todos los aspectos de la comunidad de caracoles en acantilados; por lo tanto, recomendamos la inclusión de gasterópodos en los planes de conservación para áreas protegidas que contengan acantilados.*

Introduction

Since its introduction to eastern North America 50 years ago, recreational rock climbing has continually increased in popularity, with the most dramatic increases occurring over the past 20 years (Valis 1991). Cliff ecosystems contribute greatly to the regional biodiversity of plants and animals (Larson et al. 2000). Research conducted thus far has demonstrated that rock climbing can lead to decreased abundance and richness of vascular and nonvascular plants and lichens (Nuzzo 1995; Herter 1996; Nuzzo 1996; Kelly & Larson 1997; Camp & Knight 1998; Farris 1998; McMillan & Larson 2002), suggesting that the entire biotic community might be affected.

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The potential exists for rock climbing to have a particularly strong influence on land snails because land snail diversity is generally higher on limestone outcrops than in other habitats (Burch 1962; Baur et al. 1995). In fact, maximum global richness levels for terrestrial gastropods are often associated with wooded carbonate cliffs and talus slopes. This has been demonstrated in New South Wales (Stanisic 1997), Scotland (Cameron & Greenwood 1991), Germany (Schmid 1966), Sweden (Waldén 1981), the Appalachian mountains (Getz & Uetz 1994), and the Great Lakes region of North America (Nekola 1999).

The Niagara Escarpment is a series of dolomitic limestone outcrops that extends from the Bruce Peninsula to the Niagara Region in Ontario and through Michigan, Wisconsin, Illinois, and Iowa. These cliffs support the most ancient forest ecosystem east of the Rocky Mountains (Larson & Kelly 1991), with eastern white cedar trees (*Thuja occidentalis*) living in excess of 900 years (Larson et al. 2000). These cliffs also support extremely high levels of snail diversity. Up to 34 species have been observed in soil collected from a surface area of 1000 m^2, up to 23 species in 1 m^2, and up to 21 species in 0.04 m^2 (Nekola 1999; Nekola & Smith 1999). Unfortunately, these cliffs are also exposed to the highest levels of recreational rock climbing in Ontario (Bracken et al. 1991).

The importance of the Niagara Escarpment as a reservoir for biotic biodiversity necessitates the creation of formal conservation policies that protect this community. Here, we document the effects of rock climbing on the density, richness, diversity, and community composition of land snails on dolomitic limestone cliffs in Ontario.

Methods

Study Site

We conducted field work from late August to early October 1998 along a 35-km section of the Niagara Escarpment near Milton, Ontario (Universal Transverse Mercator Zone 17, 4806800–4818000 mN, 587500–591500 mE). The public and privately owned cliffs we sampled are composed of Silurian dolomitic limestone (Niagara Escarpment Commission 1979) surrounded by a green belt of second-growth deciduous forest that runs through larger areas of urban development and agricultural land.

Climbed cliffs were sampled at Buffalo Crag (90 graded routes), Rattlesnake Point (142 graded routes), Mt. Nemo (236 graded routes), and Kelso (54 graded routes) conservation areas. Unclimbed cliffs were sampled at Mt. Nemo and Crawford Lake conservation areas and from an adjacent cliff on the property of Milton Limestone Incorporated. Sections of climbed and unclimbed cliffs were within 15 km of one another.

Sampling Design

We determined the impact of climbing through the comparison of "climbed" and "unclimbed" areas. A region was classified as climbed when climbing manuals described an established climbing route for that area (Bracken et al. 1991; Oates & Bracken 1997). A section of the cliff was classified as unclimbed when no routes were described for the area and when no other obvious signs of climbing were present (e.g., implanted climbing hardware, chalk marks on hand holds).

We sampled from 50 vertical belt transects, each 1 m in width, that extended the height of the cliff. Twenty-five climbed transects were chosen randomly from a pool of 101 climbing routes, and 25 unclimbed transects were chosen randomly from a pool of 106 transects. The pool of climbed transects included all documented climbing routes for the area with a difficulty rating between 5.7 and 5.9 and a star rating in the climbing manual (Bracken et al. 1991). We chose these routes because they represented the best routes for climbers with an intermediate skill level. As such, they likely attract higher and more regular amounts of climbing activity than other routes. We restricted unclimbed transects to sections of the cliff that were ≥ 7 m wide, that appeared physically suitable for climbing, and that two experienced climbers and the first author agreed would be rated between 5.7 and 5.9 if graded. Climbed and unclimbed transects were rejected if they were <10 m in height or contained a roof or overhang of more than 1 m, continuous water seeps, or loose rocks.

Land snails were sampled from three positions within each transect for a total of 150 observations: cliff face (vertical surface), plateau (or cliff edge), and talus (cliff base). These adjacent habitats were sampled in addition to the cliff face because they are also subjected to climbing-related disturbances such as being used as a place from which to belay (hold the ropes for the climber), to anchor climbing ropes, to store packs and other equipment, and for climbers to rest between ascents.

Transects extended from 2 m beyond the cliff face on the plateau to 2 m beyond the cliff base in the subtending talus. We collected 250 mL of soil from each of the three positions within each transect. In plateau and talus habitats, we collected soil from the upper 5 cm of the organic soil horizon within a 1 × 2 m area. Because of the paucity of soil on the cliff face, we collected soil samples from ledges and cracks extending the entire height of the cliff within the 1-m transect (ranging from 11.5 to 30 m). Although the sample extent for the cliff-face samples was greater, the total surface area over which the samples were taken did not exceed 2 m^2. To minimize the effects of sampling on the cliff community, no ledge was deprived of more than half its soil.

Each 1 × 2 m quadrat sampled from the plateau and talus was divided into 50 20 × 20 cm subquadrats, and

Table 1. Frequency (% of quadrats) in which each species of land snail was present for unclimbed (U) and climbed (C) quadrats sampled in 1998 from the Niagara Escarpment in southern Ontario, Canada.

			Freq. (%)						*Freq. (%)*		
Species	*G rank*[a]	*S rank*[b]	*U*	*C*	$\chi^{2c,d}$	*Species*	*G rank*[a]	*S rank*[b]	*U*	*C*	$\chi^{2c,d}$
Anguispira alternata	G5	S5	49.3	24.0	9.30*	*Nesovitrea binneyana*	G?	S4-S5	28.0	2.7	16.64**
Carychium exile	G4?	S3-S4	28.0	9.3	7.42	*Paravitrea multidentata*	G4-G5	S2-S3	6.7	2.7	0.60
Carychium nannodes	G4-G5	S1-S2	6.7	1.3	1.56	*Punctum minutissimum*	/	/	85.3	2.7	50.03****
Cochlicopa lubrica	G4-G5	S5	14.7	0.0	9.81*	*Pupilla muscorum*	/	/	1.3	32.0	23.23****
Cochlicopa lubricella	G4-G5	S4	2.7	1.3	0.00	*Stenotrema fraternum fraternum*	/	/	5.3	0.0	2.31
Columella simplex	/	/	28.0	0.0	22.15***	*Striatura exigua*	G4	S4	17.0	1.3	9.53*
Discus catskillensis	G3-G5	S5	72.0	32.0	22.46****	*Striatura ferrea*	G4-G5	S5	1.3	0.0	0.00
Euconulus fulvus	G4-G5	S4-S5	28.0	0.0	22.15***	*Striatura milium*	G4	S4-S5	40.0	2.7	28.96****
Euconulus polygyratus	G?	S4	6.7	0.0	3.31	*Strobilops labyrinthica*	G5	S5	18.7	10.7	1.33
Gastrocopta contracta	G5	S5	14.7	18.7	0.19	*Succinea ovalis*	G5	S3-S4	20.0	0.0	14.52**
Gastrocopta corticaria	G4-G5	S2	32.0	38.7	0.47	*Triodopsis albolabris*	/	/	2.7	0.0	0.51
Gastrocopta holzingeri	G4-G5	S2-S3	53.3	49.3	0.11	*Triodopsis denotata*	/	/	1.3	0.0	0.00
Gastrocopta pentodon	G5	S5	61.3	17.3	28.61****	*Triodopsis tridentata*	G5	S3-S4	6.7	4.0	0.13
Glyphyalinia indentata	/	/	4.0	1.3	0.26	*Vallonia costata*	G4-G5	S5	0.0	1.3	0.00
Glyphyalina rhoadsi	G5	S3-S4	16.0	4.0	4.74	*Vallonia gracilicosta*	G?	S1-S2	65.3	72.0	0.50
Guppya sterkii	G4-G5	SH	5.3	1.3	0.83	*Vallonia pulchella*	G4-G5	S5	0.0	1.3	0.00
Hawaiia miniscula	G5	S3	0.0	8.0	4.34	*Vertigo bollesiana*	G3	S3	26.7	5.3	11.16*
Helicodiscus parallelus	G5	S5	12.0	6.7	0.71	*Vertigo gouldi*	G4-G5	S3	78.7	33.3	29.46****
Helicodiscus shimeki	G4	S4-S5	2.7	6.7	0.60	*Vertigo paradoxa*	G2-G4	S2-S3	76.0	42.7	15.91**
Mesomphix cupreus	G5	S3	1.3	0.0	0.00	*Zonitoides arboreus*	G5	S5	50.1	26.7	8.12

[a] *Global conservation rank: G1, extremely rare; G2, very rare; G3, rare to uncommon; G4, common; G5, very common; G?, unranked or not listed.*

[b] *Provincial conservation ranking: S1, extremely rare; S2, very rare; S3, rare to uncommon; S4, common; S5, very common; SH, historically present in Ontario but not observed recently (typically not recorded for 20 years) or not listed.*

[c] *Adjusted using Yates' correction for continuity as suggested for cases in which there is a single degree of freedom. The Bonferroni correction for multiple comparisons was used to calculate significance levels (Ministry of Natural Resources 2002).*

[d] *Probability:* * $p < 0.1$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$.

the number of subquadrats containing exposed rock was recorded. A 1 × 2 m quadrat was similarly sampled from the vertical center of each cliff-face transect. We recorded this data prior to soil collection.

We collected soil samples in muslin bags. We placed fresh samples in a drying oven at 80° C for 4–7 days and then stored them at room temperature for several months. We soaked each bag in water from 12–24 hours, after which we removed the soil and washed it through a graduated sieve series (4, 2, 1, and 0.42 mm). We discarded particles that passed through the smallest sieve. We returned the soil to muslin bags and redried them. We then dry-sieved the soil through the graduated sieve series and examined the factions of soil under an 8× dissecting microscope against a neutral brown background. We removed intact shells from the soil with a moist paintbrush and identified them to species (or subspecies) following the nomenclature of Hubricht (1985). We checked our identifications against the Hubricht Collection at the Field Museum of Natural History and the second author's reference collection at the University of Wisconsin, Green Bay. We counted and recorded the number of shells for each species. We also calculated the species richness and heterogeneity (Shannon-Wiener index) of each sample. The reference collection from this study is housed in the Department of Botany at the University of Guelph.

Statistical Analysis

We used a split-plot experimental design (Steel & Torrie 1980; Kuehl 1994) to compare the density, richness, and heterogeneity of the sampled snails. We used climbing intensity (climbed vs. unclimbed) as the whole-plot factor and habitat (plateau, cliff face, and talus) as the split-plot factor.

To minimize the impact of factors other than climbing and habitat on the outcome of the statistical analysis, we included cliff height, percent canopy cover, and compass direction of the cliff face in the model as covariates. The compass direction of the cliff was broken down into a north component and an east component, with the former being equal to the cosine (compass reading * π) and the latter being equal to sine (compass reading * π). We used these conversions because the use of an untransformed compass reading would determine 1° and 359° to be very different from one another, when they are both almost due north.

We analyzed the effects of rock climbing and habitat type on snail density, richness, and heterogeneity through analysis of variance (ANOVA) tables generated by SAS computer software (Anonymous 1995). We used the MIXED procedure due to the combination of covariates within the split-plot design. We analyzed the results for both main and simple effects, the main effects with F statistics and the simple effects with Tukey's procedure (Steel & Torrie 1980).

We employed chi-square tests to determine the impact of climbing and habitat type on the abundance of individual species. We used the Bonferroni correction for multiple comparisons (Kuehl 1994) and Yates's correction for continuity when there was only a single degree of freedom (Steel & Torrie 1980).

Results

We retrieved 14,023 intact shells from the 37.5 L of soil collected. These individuals belonged to 40 different species, which represents almost half the diversity of land snails in Ontario (88 taxa). The species varied in global conservation ranking from G3 (*Vertigo bollesiana*) to G5 and in provincial ranking from S1/S2 (*Carychium nannodes, Vallonia gracilicosta*) to S5 (Table 1).

Most of the species were <5 mm at their widest point and are thus referred to as "minute" snails (Emberton 1995). We found a large amount of broken shell material but did not include this in our analysis.

Shell density was over five times greater in unclimbed samples than in climbed samples (78.26 vs. 14.86 individuals per 250 mL of soil; $p < 0.00001$). Shell density was significantly lower along climbing routes in each of the three habitat positions (Fig. 1). In addition, shell density varied significantly between the three habitat positions ($p < 0.005$). The average density of shells found in

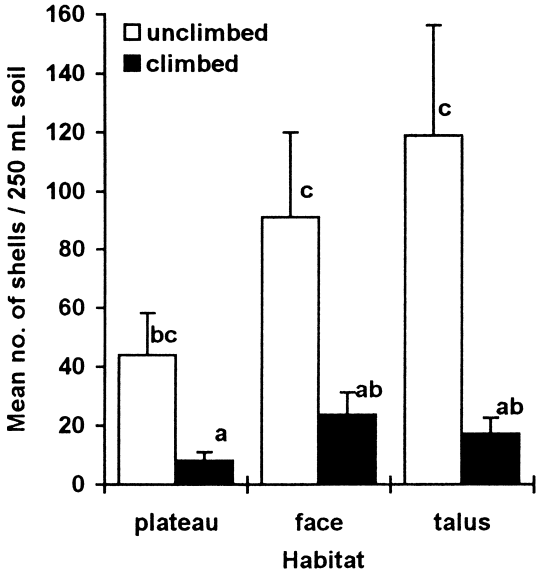

Figure 1. Mean density of land snails per 250 mL soil sample collected from the Niagara Escarpment, Ontario, Canada. Each bar represents the mean from 25 samples. Bars that share a letter code are not significantly different from one another at $\alpha = 0.05$.

cliff face and talus samples (46.63 and 45.41 individuals per 250 mL soil) was more than twice the average density of shells found in plateau samples (19.15 individuals per 250 mL soil; $p < 0.005$).

The species richness of land snails was significantly lower along climbing routes ($p < 0.00001$). Unclimbed areas supported almost two times more species than undisturbed areas (9.84 vs. 5.20 species per 250 mL soil). This significant reduction in richness along climbing routes occurred in all habitat positions (Fig. 2). Similarly, climbed areas showed significantly lower levels of Shannon-Wiener diversity than did unclimbed areas (1.11 vs. 1.53; $p < 0.001$). Species richness was lowest on the plateau (4.94 species per 250 mL soil) and highest on the talus (10.56 species per 250 mL soil; $p < 0.00001$).

Fourteen of the 40 species had significantly greater frequency in unclimbed samples, whereas only one species had a significantly greater frequency in climbed areas (Table 1). The remaining species showed no statistical preference for either climbed or unclimbed areas.

The proportion of subquadrats containing exposed rock was significantly higher in climbed than unclimbed quadrats (79.6% vs. 48.0%; $p < 0.00001$). This trend occurred in each of the three habitat types, but was significant for the plateau (10.6% vs. 66.8%; $p < 0.0001$) and talus (40.2% vs. 73.9%; $p < 0.0001$) habitats only. Unclimbed and climbed quadrats contained similar amounts of exposed rock (93.1% vs. 98.0%; $p = 0.98$).

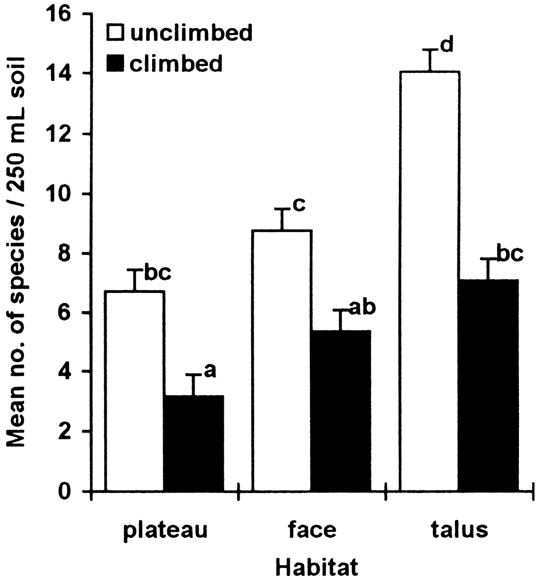

Figure 2. Mean number of land snail species present in 250 mL soil samples collected from the Niagara Escarpment, Ontario, Canada. Each bar represents the mean from 25 samples. Bars that share a letter code are not significantly different from one another at α = 0.05.

Discussion

Our results suggest that rock climbing has strong negative effects on the extremely diverse and abundant community of land snails that normally occurs on undisturbed cliffs of the Niagara Escarpment. Snail density, richness, and diversity were all significantly lower in climbed areas than in undisturbed areas, in spite of the fact that the amount of soil collected was constant. Because the surface area of soil was also lower in climbed areas, it is likely that rock climbing has an even larger impact on land snails than is suggested by our results.

The enormous local abundance of land snails and the unusually high species richness in undisturbed sites suggest that snails may be processing energy and matter at high rates and therefore may be important natural components of cliff-ecosystem food webs. Whatever their role, their recolonization and the subsequent restoration of function are likely to occur very slowly on denuded cliffs in view of the slow rates of dispersal of such snails (Baur & Baur 1994).

Rock climbing also appears to affect the composition of land snail communities. There are several possible mechanisms that might account for this change. First, the ledges and cracks in the vertical rock surface that are the primary habitat for cliff land snails are also the primary means by which climbers ascend the cliff face. The use of these microsites for hand and foot holds causes removal of unconsolidated soil and organic matter, thereby decreasing the amount and quality of available habitat for snails. In some instances, climbers purposefully remove soil to increase the security of the hold and to reduce the chance of slipping. The soil that is left is then subject to direct pressure from the hands and feet of climbers, which probably causes soil compaction and a reduction in organic material, as is found in other disturbed sites. Soil compaction and removal from staging areas in the talus and at tie-off sites on the plateau also decrease the amount of habitat and resources available for these species. Future research is required to determine the effects of climbing on physical soil properties and chemistry.

Due to the detrimental effect of rock climbing on the land snail community we observed in this study, we recommend that management plans for the Niagara Escarpment be modified to include specific policies regarding recreational rock climbing. The most effective management practices for the protection of gastropod species on the Niagara Escarpment would limit the aerial extent of climbing activity. We believe that land snail communities on other cliffs may react similarly to climbing pressure, because other cliffs around the world also support extremely diverse communities of terrestrial gastropods (Schmid 1966; Waldén 1981; Cameron & Greenwood 1991; Getz & Uetz 1994; Stanisic 1997; Nekola 1999). We therefore recommend that gastropods also be included in management policies for other areas containing cliffs. Special attention should be given to areas in which rare species are known to exist.

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Literature Cited

Anonymous. 1995. SAS system for Windows. Version 6.11. SAS Institute, Cary, North Carolina.

Baur, B., and A. Baur. 1994. Dispersal of the land snail *Chondrina avenacea* on vertical rock walls. Malacological Review **27:**53–59.

Baur, B., L. Fröberg, and A. Baur. 1995. Species diversity and grazing damage in a calcicolous lichen community on top of stone walls in Öland, Sweden. Annales Botanici Fennici **32:**239–250.

Bracken, M., J. Barnes, and C. Oates. 1991. The escarpment: a climbers guide. Borealis Press, Toronto.

Burch, J. B. 1962. How to know the eastern land snails. WM.C. Brown, Dubuque, Iowa.

Cameron, R. A. D., and J. J. D. Greenwood. 1991. Some montane and forest molluscan fauna from eastern Scotland: effects of altitude, disturbance, and isolation. Pages 437–442 in Proceedings of the tenth international malacological congress. Unitas Malacologica, Tübingen, Germany.

Camp, R. J., and R. L. Knight. 1998. Effects of rock climbing on cliff plant communities at Joshua Tree National Park, California. Conservation Biology **12:**1302–1306.

Emberton, K. C. 1995. Land-snail community morphologies of the highest-diversity sites of Madagascar, North America, and New Zealand, with recommended alternatives to height-diameter plots. Malacologia **36:**43–66.

Farris, M. A. 1998. The effects of rock climbing on the vegetation of three Minnesota cliff systems. Canadian Journal of Botany **76:** 1981–1990.

Getz, L. L., and G. W. Uetz. 1994. Species diversity of terrestrial snails in the southern Appalachian mountains, U.S.A. Malacological Review **27:**61–74.

Herter, W. 1996. Die Xerothermvegetation des Oberen Donautals—Gefaerhrdung der Vegetation durchMensch und Wild sowie Schutz—und Erhaltungsvorschlaege. Veroeffentlichungen des projekts AAngewandte Oekologie@ PAoe 10. Veroef, Karlsruhe, Germany.

Hubricht, L. 1985. The distributions of the native land mollusks of the eastern United States. Fieldiana **24:**1–191.

Kelly, P. E., and D. W. Larson. 1997. Effects of rock climbing on populations of presettlement eastern white cedar (*Thuja occidentalis*) on cliffs of the Niagara Escarpment, Canada. Conservation Biology **11:**1125–1132.

Kuehl, R. O. 1994. Statistical principles of research design and analysis. Wadsworth Publishing, Belmont, California.

Larson, D. W., and P. E. Kelly. 1991. The extent of old-growth *Thuja occidentalis* on cliffs of the Niagara Escarpment. Canadian Journal of Botany **69:**1628–1636.

Larson, D. W., U. Matthes, and P. E. Kelly. 2000. Cliff ecology: pattern and process in cliff ecosystems. Cambridge University Press, Cambridge, United Kingdom.

McMillan, M. A., and D. W. Larson. 2002. The effects of rock climbing on the vegetation of the Niagara Escarpment in Southern Ontario, Canada. Conservation Biology **16:**389–398.

Ministry of Natural Resources. 2002. Natural heritage information centre list of Ontario mollusks. Ministry of Natural Resources, Peterborough, Ontario, Canada. Available from http://www.mnr.gov.on.ca/MNR/nhic/nhic.html (accessed March 2002).

Nekola, J. C. 1999. Terrestrial gastropod richness of carbonate cliff and associated habitats in the great lakes region of North America. Malacologia **41:**231–252.

Nekola, J. C., and T. M. Smith. 1999. Terrestrial gastropod richness patterns in Wisconsin and carbonate cliff communities. Malacologia **41:**253–269.

Niagara Escarpment Commission. 1979. Geology: the Niagara Escarpment. Niagara Escarpment Commission, Georgetown, Ontario, Canada.

Nuzzo, V. A. 1995. Effects of rock climbing on cliff goldenrod (*Solidago sciaphila* Steele) in Northwest Illinois. American Midland Naturalist **133:**229–241.

Nuzzo, V. A. 1996. Structure of cliff vegetation on exposed cliffs and the effect of rock climbing. Canadian Journal of Botany **74:**607–617.

Oates, C., and M. Bracken. 1997. A sport climbers guide to Ontario limestone. Borealis Press, Toronto.

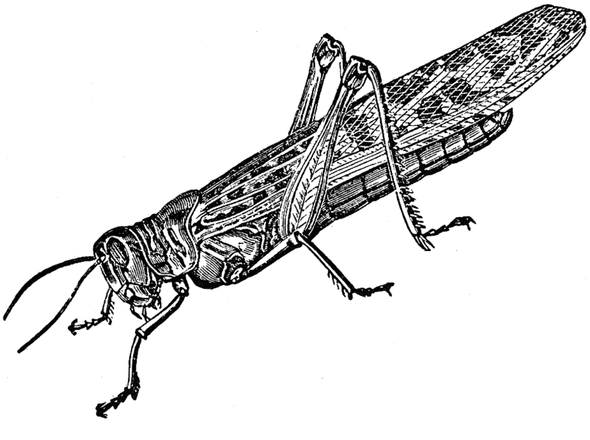
Schmid, G. 1966. Die mollusken des Spitzbergs. Der Spitzberg bei Tübingen, Natur und Landschaftsschutzgebiete. Baden-Würtemburg **3:**596–701.

Stanisic, J. 1997. An area of exceptional land snail diversity: the Macleay Valley, north-eastern New South Wales. Memoirs of the Museum of Victoria **56:**441–448.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. 2nd edition. McGraw-Hill, New York.

Valis, T. 1991. Escarpment climbing history. Pages 3–6 in M. Bracken, J. Barnes, and C. Oates, editors. The escarpment: a climbers guide. Borealis Press, Toronto.

Waldén, H. W. 1981. Communities and diversity of land molluscs in Scandinavian woodlands. I. High diversity communities in taluses and boulder slopes in SW Sweden. Journal of Conchology **30:**351–372.



Animal Biodiversity and Conservation 25.2 (2002) 53

Effects of fire management on the richness and abundance of central North American grassland land snail faunas

J. C. Nekola

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Abstract

Effects of fire management on the richness and abundance of central North American grassland land snail faunas.— The land snail faunas from 72 upland and lowland grassland sites from central North America were analyzed. Sixteen of these had been exposed to fire management within the last 15 years, while the remainder had not. A total of 91,074 individuals in 72 different species were observed. Richness was reduced by approximately 30% on burned sites, while abundance was reduced by 50–90%. One–way ANOVA of all sites (using management type as the independent variable), a full 2–way ANOVA (using management and grassland type) of all sites, and a 2–way ANOVA limited to 26 sites paired according to their habitat type and geographic location, demonstrated in all cases a highly significant (up to $p < 0.0005$) reduction in richness and abundance on fire managed sites. Contingency table analysis of individual species demonstrated that 44% experienced a significant reduction in abundance on fire-managed sites. Only six species positively responded to fire. Comparisons of fire response to the general ecological preferences of these species demonstrated that fully 72% of turf–specialists were negatively impacted by fire, while 67% of duff–specialists demonstrated no significant response. These differences were highly significant ($p = 0.0006$). Thus, frequent use of fire management represents a significant threat to the health and diversity of North American grassland land snail communities. Protecting this fauna will require the preservation of site organic litter layers, which will require the increase of fire return intervals to 15+ years in conjunction with use of more diversified methods to remove woody and invasive plants.

Key words: Land snail, Biodiversity, Conservation, Fire management, Grassland, North America.

Resumen

Efectos de la gestión con fuego sobre la riqueza y abundancia de la fauna de caracoles terrestres de las praderas de América del Norte.— Se analiza la fauna de caracoles terrestres de 72 praderas en mesetas y llanuras de la región central de América del Norte. En 16 de ellas se habían efectuado intervenciones de incendio controlado durante los últimos 15 años, mientras en el resto no. Se observaron un total de 91.074 individuos de 72 especies diferentes. La riqueza en especies estaba reducida en un 30% en las áreas quemadas, mientras que la abundancia de individuos estaba reducida en un 50–90%. Un ANOVA unidireccional de todas las áreas (usando como variable independiente el tipo de intervención), un ANOVA bidireccional completo (usando el tipo de intervención y el tipo de pradera) en todas las áreas y un ANOVA bidireccional limitado a 26 áreas agrupadas según su tipo de hábitat y localización geográfica, demostró en todos los casos una reducción altamente significativa de la riqueza y de la abundancia (hasta $p < 0,0005$) en áreas sometidas a incendio. Un análisis individual de las especies mediante tablas de contingencia demostró que el 44% experimentaron una reducción significativa de su abundancia en las áreas quemadas. Sólo seis especies respondieron positivamente al fuego. Comparando la respuesta al fuego con las preferencias ecológicas generales de estas especies se demostró que al menos el 72% de las especialistas que viven en sustrato herbáceo fueron afectadas negativamente por el fuego mientras que el 67% de las que viven en sustrato húmico no demostraron ninguna respuesta significativa. Estas diferencias fueron altamente significativas ($p = 0,0006$). Así pues, el uso frecuente del fuego representa una amenaza significativa para la salud y diversidad de las comunidades de caracoles terrestres de las praderas de América del Norte. La protección de esta fauna requerirá la preservación de las capas de materia orgánica y la ampliación de los intervalos entre las actuaciones de quema a periodos superiores a 15 años, así como el uso de métodos más diversos para eliminar las plantas leñosas e invasivas.

Palabras clave: Caracol terrestre, Biodiversidad, Conservación, Gestión con fuego, Praderas, América del Norte.

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Introduction

Fire has long been implicated in the maintenance of central North American grassland communities (Weaver, 1954; Curtis, 1959). Numerous native plant species respond to fire by increasing their growth and reproductive rates (Ehrenreich & Aikman, 1963; Kucera & Koelling, 1964; Towne & Owensby, 1984). One of the most direct effects of prairie fire is the removal of the soil mulch layer, which has been implicated in the 'stagnation' of prairie plant communities through the delay of initial spring growth, thinning of grass stem density, and prevention of herbaceous understory development (Weaver & Rowland, 1952; Kucera & Koelling, 1964). Fire is also thought to limit invasion of woody and exotic plants into native prairie habitats (e.g., Pauly, 1985; Roosa, 1984). For these reasons, prescribed fire has become the management tool of choice by prairie conservation groups throughout the midwestern USA (Collins & Wallace, 1990).

However, an increasing body of research suggests that fire is not universally beneficial all prairie biota. Fire depresses growth and reproductive rates of native C_3 prairie plants (Dix, 1960; Hadley, 1970; Hill & Platt, 1975), which make up at least 50% of the native flora north of 44° N (Stowe & Teeri, 1978; Sims, 1988). Fire has also been implicated in the loss and/or reduction of numerous native prairie invertebrate species including Lepidoptera, Homoptera, Hymenoptera, and Araneae (Swengel, 1996, 1998; Harper et al., 2000). The effects of such practices on prairie soil biodiversity are largely undocumented. Combustion of mulch through repeated fire episodes will remove the detritusphere, one of the most important reservoirs for soil biodiversity (Coleman & Crossley, 1996). Harper et al. (2000) documented significant reductions in Collembola following Illinois prairie fires. As the soil fauna represents one of the largest species pools in terrestrial ecosystems (Behan–Pelletier & Newton, 1999), the potential impacts of such processes on total site biodiversity may be large.

Although not as hyper–diverse as bacteria, fungi, nematodes, and arthropods, molluscs still represent one of the more important components of soil biodiversity (Russell–Hunter, 1983). Almost 600 species are known from eastern North America (Hubricht, 1985), with up to 21 taxa co-occurring within 400 cm^2 microhabitats (Nekola & Smith, 1999). Most of these taxa represent generalist detritivores that live in and on dead organic material (Burch & Pearce, 1990)

As almost 90% of snails occur within 5 cm of the soil surface (Hawkins et al., 1998), protection of this fauna will likely be tied to the fate of mulch layers. Disturbances such as logging, recreational or urban development, or bedrock and soil removal cause dramatic changes in woodland snail communities with duff soil surfaces (Nekola, in press a). The impact of fire, and associated detritusphere removal, on snail communities is unclear. Fire has been suggested to negatively influence the faunas of Aegean islands (Welter–Schultes & Williams, 1999), Queensland fens (Stanisic 1996), and Tasmanian woodlands (Regan et al., 2001). However, Frest & Johannes (1995) state that molluscs are able to survive natural fires in northwestern North America, and Theler (1997) argued that xeric prairie faunas in Wisconsin owe their existence to frequent fires that keep grassland areas treeless. Unfortunately, no data was presented by these various authors to validate such conflicting statements.

To evaluate this issue, the richness and abundance of land snails was quantitatively compared between unburned and recently (< 15 year) burned sites in the midwestern USA, including 13 pairs of sites which possess similar habitats and are spatiall proximate. From these, the following questions will be considered: 1. Is there a significant difference in land snail community richness between burned and unburned grasslands? 2. Is there a significant difference in land snail abundance between burned and unburned grasslands? 3. What species show positive, negative, or no response to fire? What ecological factors (if any) may help explain these responses?

Materials and methods

Study Sites

Seventy two grassland sites were surveyed between May 1996–November 2001 for terrestrial molluscs across a 850 km extent of central North America (fig. 1, table 1). Sites are generally centered on northwestern Minnesota and northeastern Iowa. Forty–two occur in Minnesota, 25 in Iowa, and 5 in Wisconsin. Thirty–two sites represent upland habitats (including tallgrass prairie, sand prairie, and bedrock glades), while the remaining 40 are lowland sites (including wet prairie, sedge meadow, and fens). Previous use of fire management on sites was assessed by either observing carbonized woody plant stems or other debris on the ground surface, or through interviews with site managers or other knowledgeable individuals. No use of fire management was noted from 56 sites (88% of total), while 16 (22%) had been subjected to some amount of prescribed burning. Eleven of these burned sites occur in Minnesota, while the remaining five occur in Iowa. The latitude–longitude location of each site was determined using either USGS 7.5 minute topographic maps or a hand–held GPS.

Field Methods

Documentation of terrestrial gastropod faunas from each site was accomplished by hand collection of larger shells and litter sampling for smaller taxa within 100–1,000 m^2 areas that contained examples of all major microhabitats and were thus representative of the larger site. The actual grain size employed was determined by the minimum size necessary to emcompass all microhabitats. Soil litter sampling was primary used as it provides the most complete assessment of grassland faunas (OGGIER et al., 1998). A single site sample consisted of a composite of individual soil litter subsamples of approximately 200 ml collected from appropriate microhabitats. As suggested by EMBERTON et al. (1996), litter collections were made at places of high micromollusc density, with a constant volume (approximately 4 liters) being gathered from each site. Sampling was generally comprised of: 1. Small blocks (ca. 125 cm^3) of turf; 2. Loose soil and leaf litter accumulations under or adjacent to shrubs, cobbles, boulders, and/or hummocks; and 3. Other microsites supporting relatively thick mulch layers.

Laboratory procedures

Samples were slowly and completely dried in either a low–temperature soil oven (ca. 80–95°C) or in full sun in a greenhouse. Dried samples were then soaked in water for 3–24 hours, and subjected to careful but vigorous water disaggregation through a standard sieve series (ASTME 3/8" (9.5 mm), #10 (2.0 mm), #20 (0.85), and #40 (0.425 mm) mesh screens). Sieved sample fractions were then dried and passed again through the same sieve series. These dry, resorted fractions were hand picked against a neutral-brown background. All shells and shell fragments were removed.

All identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht Collection at the Field Museum of Natural History (FMNH), with the total number of shells per species per site being recorded. The total number of unassignable, immature individuals was also counted from each site. All specimens have been catalogued and are housed in the author's collection at the University of Wisconsin–Green Bay. Nomenclature generally follows that of HUBRICHT (1985), with updates and corrections by FREST (1990, 1991) and NEKOLA (in press b). The general ecological preferences (turf specialist, duff–specialist or generalist) of each species is based upon analyses presented in NEKOLA (in press a).

Statistical procedures

Differences in species richness and total shell abundance between burned and unburned grassland sites were analyzed via ANOVA. Initially, 1–way ANOVAs were preformed on the entire dataset. However, the effect of fire may be obscured in this analysis due to confounding effects of habitat type and geographic location. To help control for this, two additional sets of ANOVAs were conducted. First, full 2–way ANOVAs were calculated for all sites using grassland type (upland vs. lowland) and management history (burned vs. unburned) as the independent variables. Second, 13 pairs of sites representing closely similar habitats within the same geographic region, but differing in their fire management history, were selected. These site pairs are (first site is burned, second is unburned): Malmberg Prairie vs. Sandpiper Prairie; Pankratz Mesic Prairie vs. Radium NE; Pankratz Low Prairie vs. Bjornson WMA; Pankratz Fen vs. Faith South; Marcoux WMA vs. Cyr Creek; East Park WMA vs. Goose Lake; Felton Fen 1 vs. Ogema West; Waubun SE vs. Eastlund Lake; Chicog vs. Tansen; Beemis Creek vs. Hampton East; Fayette vs. Decorah Glade; Baty Glade vs. Canton Glade; Brayton–Horsley vs. Stapleton Church. A 2–way ANOVA without interaction was then calculated for these sites, with site pair identity and management type representing independent variables.

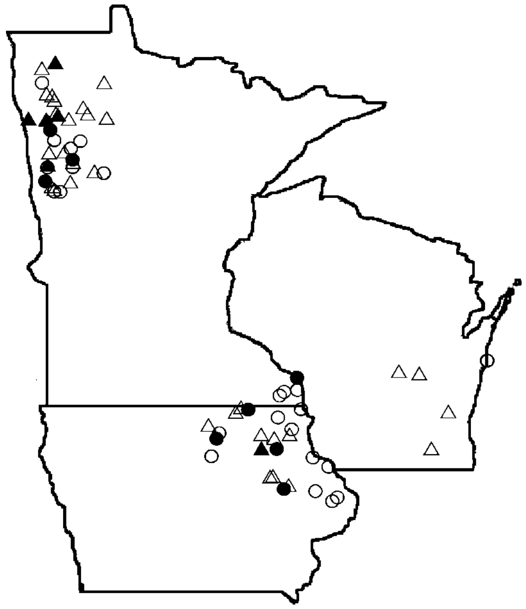


Fig. 1. Map of study region, showing location of surveyed grassland sites: ○ Unburned upland; ● Burned upland; △ Unburned lowland; ▲ Burned lowland.

Fig. 1. Mapa del área de estudio que muestra la localización de las praderas estudiadas: ○ Meseta no quemada; ● Meseta quemada; △ Llanura no quemada; ▲ Llanura quemada.

Table 1. Location, grassland type, management, species richness and total number of collected individuals from sample sites: GT. Grassland type; M. Management; R. Richness; I. Individuals.

Tabla 1. Localización, tipo de pradera, gestión, riqueza de especies y número total de individuos recogidos en cada área de estudio: GT. Tipo de pradera; M. Gestión; R. Riqueza; I. Individuos.

State / County / Site Name	Location	GT	M	R	I
Iowa					
Allamakee County					
Fish Farm Mounds	91°17'12" W – 43°27'13" N	Upland	Unburned	21	632
Williams Creek 3	91°29'1" W – 43°8'1" N	Upland	Unburned	23	2,708
Bremer County					
Brayton–Horsley Fen	92°6'29" W – 42°48'36" N	Lowland	Burned	16	627
Buchanan County					
Rowley Fen	91°51'7" W – 42°22'27" N	Lowland	Unburned	16	3,217
Rowley North Fen	91°51'3" W – 42°22'35" N	Lowland	Unburned	17	3,231
Rowley West Fen	91°54'40" W – 42°22'15" N	Lowland	Unburned	22	2,250
Cerro Gordo County					
Buffalo Slough	93°11'11" W – 43°10'36" N	Lowland	Unburned	19	4,770
Chickasaw County					
Stapelton Church Fen	92°6'14" W – 43°1'35" N	Lowland	Unburned	18	1,065
Clayton County					
Postville Fen	91°33'59" W – 43°2'3" N	Lowland	Unburned	12	252
Turkey River Mounds	91°2'11" W – 42°42'46" N	Upland	Unburned	22	870
Clinton County					
Maquoketa South	90°39'5" W – 42°1'12" N	Upland	Unburned	12	310
Dubuque County					
Roosevelt Road	90°44'30" W – 42°32'55" N	Upland	Unburned	18	375
Fayette County					
Fayette	91°47'28" W – 42°50'11" N	Upland	Burned	13	254
Turner Creek 1 Fen	91°52'11" W – 42°58'15" N	Lowland	Unburned	16	1,071
Floyd County					
Beemis Creek	93°1'18" W – 42°59'39" N	Upland	Burned	8	192
Juniper Hill	92°59'2" W – 43°3'10" N	Upland	Unburned	12	206
Franklin County					
Hampton East	93°8'13" W – 42°43'42" N	Upland	Unburned	15	381
Howard County					
Hayden Prairie	92°23'4" W – 43°26'30" N	Upland	Burned	12	132
Staff Creek Fen	92°30'34" W – 43°26'41" N	Lowland	Unburned	15	1,599
Jackson County					
Hamilton Glade	90°34'9" W – 42°4'23" N	Upland	Unburned	15	340
Jones County					
Canton Glade	90°59'52" W – 42°10'46" N	Upland	Unburned	19	446
Linn County					
Baty Glade	91°39'14" W – 42°11'44" N	Upland	Burned	16	345
Paris Fen	91°35'42" W – 42°13'40" N	Lowland	Unburned	12	1,254

Table 1. (Cont.)

State / County / Site Name	Location	GT	M	R	I
Mitchell County					
Stone School Fen	92°38'11" W – 43°22'49" N	Lowland	Unburned	18	2,926
Winneshiek County					
Decorah Glade	91°46'11" W – 43°18'55" N	Upland	Unburned	18	605
Minnesota					
Becker County					
Audubon South Fen	95°58'47" W – 46°49'58" N	Lowland	Unburned	15	1,816
Callaway North	95°55'22" W – 47°3'57" N	Upland	Unburned	19	362
Greenwater Lake Fen	95°29'59" W – 46°59'20" N	Lowland	Unburned	20	2,132
Ogema West Fen	95°55'59" W – 47°6'32" N	Lowland	Unburned	16	5,001
Straight Lake	95°18'40" W – 46°58'40" N	Upland	Unburned	13	281
Beltrami County					
Fourtown Fen	95°18'21" W – 48°15'56" N	Lowland	Unburned	14	1,403
Clay County					
Barnesville WMA	96°17'34" W –46°43'5" N	Upland	Unburned	11	469
Barnesville WMA Fen	96°17'38" W – 46°43'9" N	Lowland	Unburned	13	436
Bjornson WMA	96°21'24" W – 46°45'44" N	Lowland	Unburned	14	436
Bluestem Prairie	96°28'45" W – 46°51'18" N	Upland	Burned	15	371
Felton Prairie 1 Fen	96°26'21" W – 47°3'51" N	Lowland	Burned	15	2,370
Felton Prairie 2 Fen	96°26'20" W – 47°4'0" N	Lowland	Unburned	14	3,131
Felton Prairie	96°26'1" W – 47°3'34" N	Upland	Unburned	5	63
Tansen	96°11'17" W – 46°42'14" N	Upland	Unburned	10	146
Clearwater County					
Bagley Lake Fen	95°14'35" W – 47°45'41" N	Lowland	Unburned	9	126
Filmore County					
Vesta Creek	91°45'0" W – 43°40'5" N	Upland	Unburned	21	1,151
Houston County					
Twin Pines Farm	91°22'45" W – 43°44'48" N	Upland	Unburned	24	591
Yucatan Twp.	91°38'28" W – 43°43'23" N	Upland	Unburned	20	765
Mahnomen County					
Eastlund Lake	95°47'5" W – 47°26'41" N	Upland	Unburned	13	490
Mahnomen North	95°58'8" W – 47°21'27" N	Upland	Unburned	18	806
Waubun SE	95°54'55" W – 47°9'57" N	Lowland	Unburned	18	2,915
Waubun SE	95°55'4" W – 47°10'5" N	Upland	Burned	8	220
Marshall County					
East Park WMA	96°16'44" W – 48°31'57" N	Lowland	Burned	14	735
Florian WMA	96°33'21" W – 48°26'33" N	Lowland	Unburned	17	3,923
Radium NE	96°32'38" W – 48°16'49" N	Upland	Unburned	12	493
Norman County					
Faith South	96°5'12" W – 47°15'42" N	Lowland	Unburned	16	3,047
Prairie Smoke Dunes	96°18'22" W – 47°27'44" N	Upland	Unburned	3	19
Sandpiper Prairie	96°24'22" W – 47°14'43" N	Lowland	Unburned	12	1,261

Table 1. (Cont.)

State / County / Site Name	Location	GT	M	R	I
Pennington County					
Goose Lake	96°27'44" W – 48°5'37" N	Lowland	Unburned	17	996
Higenbotham WMA	96°17'41" W – 48° 0'22" N	Lowland	Unburned	22	1,114
Sanders Fen	96°21'9" W – 48°3'52" N	Lowland	Unburned	15	2,218
Polk County					
Chicog Prairie	96°23'14" W – 47°35'53" N	Upland	Burned	2	153
Erskine North	96°0'3" W – 47°44'17" N	Lowland	Unburned	19	741
Gulley Fen	95°37'22" W – 47°48'13" N	Lowland	Unburned	19	2,032
Malmberg Prairie	96°49'25" W – 47°43'52" N	Lowland	Burned	7	563
Pankratz Prairie	96°26'37" W – 47°43'23" N	Lowland	Burned	12	314
Pankratz Prairie	96°26'31" W – 47°43'23" N	Upland	Burned	11	159
Pankratz Prairie	96°26'48" W – 47°43'9" N	Lowland	Burned	7	190
Red Lake County					
Crane WMA	95°42'49" W – 47°53'27" N	Lowland	Unburned	15	425
Cyr Creek	96°16'12" W – 47°48'10" N	Lowland	Unburned	22	1,845
Marcoux WMA	96°13'27" W – 47°47'55" N	Lowland	Burned	12	688
Winona County					
Great River Bluffs	91°23'28" W – 43°56'53" N	Upland	Burned	19	788
Wisconsin					
Green Lake County					
Berlin Fen	88°54'20" W – 43°57'47" N	Lowland	Unburned	20	3,454
Manitowoc County					
Point Beach St. Forest	87°30'40" W – 44°11'52" N	Upland	Unburned	4	6
Walworth County					
Bluff Creek Fen	88°40'54" W – 42°48'2" N	Lowland	Unburned	20	1,106
Washington County					
Allenton Fen	88°18'25" W – 43°22'42" N	Lowland	Unburned	20	2,858
Waushara County					
Bass Lake Fen	89°16'59" W – 44°0'16" N	Lowland	Unburned	19	1,466

The central tendencies in these various relationships were graphically represented via box plots. In box plots, the central line represents the median of the sample, the margins of the box represent the interquartile distances, and the fences represent 1.5 times the interquartile distances. For data having a Gaussian distribution, approximately 99.3% of the data will fall inside of the fences (Velleman & Hoaglin, 1981). Outliers falling outside of the fences are shown with asterisks.

The average number of individuals per species per site was determined for burned uplands, unburned uplands, burned lowlands, and unburned lowlands. The average proportion of each species in the total community for each site was calculated for each management/habitat type. These proportions were placed in rank order, and plotted vs. log–transformed frequency to create dominance–diversity curves (Whittaker, 1975).

The response of individual species to fire was analyzed through log–linear modelling, as predicted values in the associated contingency table were sparse (< 5) in more than one–fifth of cells (Zar, 1984). The total number of individuals within all burned or unburned sites was compared to a null expectation of equal occurrence

Table 2. List of encountered species, with their average abundances from burned and unburned sites. *P*–values are based on log-likelihood ratio tests, with the two–tailed significance threshold being lowered to $p = 0.000347$ to account for the 72 tested species. General ecological preferences are based on Nekola (in press a). Turf–specialists represent those species demonstrating at least a $p < 0.05$ preference to sites with a friable upper A soil horizon supporting few living plant roots. Turf specialists represent those species demonstrating at least a $p < 0.05$ preference to sites with an upper A soil horizon that is bound together with living plant roots. Species without preferences were too infrequently encountered by Nekola (in press a) to be statistically assigned: AvU. Average unburned; Abb. Abundance burned; Ecp. Ecological preference (T. Turf; D. Duff; G. Generalist.)

Tabla 2. Lista de especies detectadas, con sus abundancias medias en áreas quemadas y no quemadas. Los valores de P *se basan en tests de cociente de probabilidad logarítmica, con el umbral de significación de doble cola reducido hasta* $p = 0,000247$ *para las 72 especies estudiadas. Las preferencias ecológicas generales se basan en* Nekola *(in press a). Las especies que viven en sustrato herbáceo presentan una preferencia de al menos* $p < 0,05$ *por las zonas con horizonte de tierra friable superior A provisto de escasas raíces de plantas vivas. Las especies que viven en sustrato herbáceo presentan una preferencia de al menos* $p < 0,05$ *por las zonas cuyo horizonte se mantiene unido por raíces de plantas vivas. Las especies sin preferencias resultaron excesivamente infrecuentes según* Nekola *(in press a) para consignarlas estadísticamente: AvU. Medias en áreas no quemadas; Abb. Abundancia en áreas quemadas; Ecp. Preferencia ecológica (T. Sustrato herbáceo; D. Sustrato húmico; G. Generalista.)*

Species	AvU	Abb	*P*–value	Ecp
Negative responses				
Carychium exiguum (Say, 1822)	273.607	90.250	0.0000000	T
Carychium exile H. C. Lea, 1842	5.196	0.000	0.0000000	D
Catinella exile (Leonard, 1972)	58.446	1.625	0.0000000	T
Catinella "vermeta"	1.482	0.000	0.0000001	T
Deroceras laeve (Müller, 1774)	4.036	1.188	0.0000050	G
Discus cronkhitei (Newcomb, 1865)	16.143	5.000	0.0000000	G
Euconulus alderi (Gray, 1840)	43.054	8.375	0.0000000	T
Gastrocopta contracta (Say, 1822)	21.232	5.875	0.0000000	G
Gastrocopta holzingeri (Sterki, 1889)	36.196	17.938	0.0000000	D
Gastrocopta pentodon (Say, 1821)	9.661	4.875	0.0000072	D
Gastrocopta procera Gould, 1840	2.304	0.000	0.0000000	T
Gastrocopta rogersensis Nekola & Coles, 2001	5.518	0.062	0.0000000	T
Gastrocopta similis (Sterki, 1909)	21.518	4.125	0.0000000	T
Gastrocopta tappaniana (C. B. Adams, 1842)	112.929	33.375	0.0000000	T
Hawaiia minuscula (A. Binney, 1840)	36.286	23.062	0.0000000	G
Helicodiscus n. sp.	1.071	0.062	0.0001509	T
Nesovitrea binneyana (Morse, 1864)	1.500	0.000	0.0000001	D
Nesovitrea electrina (Gould, 1841)	80.179	22.688	0.0000000	T
Oxyloma retusa (I. Lea, 1834)	21.268	8.750	0.0000000	T
Pomatiopsis lapidaria (Say, 1817)	1.196	0.000	0.0000021	–
Punctum minutissimum (I. Lea, 1841)	26.286	10.500	0.0000000	D
Punctum n. sp.	41.982	12.625	0.0000000	T
Punctum vitreum H. B. Baker, 1930	16.536	2.812	0.0000000	D
Stenotrema leai leai (A. Binney)	2.696	0.375	0.0000004	T
Striatura milium (Morse, 1859)	0.714	0.000	0.0002470	G
Strobilops affinis Pilsbry, 1893	74.911	4.312	0.0000000	T
Triodopsis multilineata (Say, 1821)	1.571	0.062	0.0000016	G
Vallonia pulchella (Müller, 1774)	23.321	11.688	0.0000000	T

Tabla 2. (Cont.)

Species	AvU	Abb	*P*–value	Ecp
Vertigo elatior Sterki, 1894	41.875	5.875	0.0000000	T
Vertigo milium (Gould, 1840)	59.357	36.375	0.0000000	T
Vertigo morsei Sterki, 1894	3.589	0.375	0.0000000	T
Vitrina limpida Gould, 1850	1.143	0.000	0.0000035	G
No response				
Anguispira alternata (Say, 1817)	0.018	0.000	0.5622176	D
Catinella avara (Say, 1824)	7.286	8.000	0.5185276	T
Cochlicopa lubrica (Müller, 1774)	0.464	0.000	0.0031253	D
Cochlicopa lubricella (Porro, 1838)	1.714	1.938	0.6798546	G
Columella simplex (Gould, 1841)	0.071	0.188	0.4068651	D
Discus catskillensis (Pilsbry, 1898)	0.357	0.000	0.0095467	D
Euconulus fulvus (Müller, 1774)	3.429	1.625	0.0040433	D
Euconulus polygyratus (Pilsbry, 1899)	0.018	0.000	0.5622176	D
Gastrocopta abbreviata (Sterki, 1909)	0.000	0.062	0.2039785	–
Gastrocopta armifera (Say, 1821)	1.232	1.188	0.9197258	G
Glyphyalinia indentata (Say, 1823)	2.732	3.250	0.4543545	D
Haplotrema concavum (Say, 1821)	0.411	0.000	0.0054455	G
Hawaiia n. sp.	2.571	1.750	0.1616094	T
Helicodiscus inermis H. B. Baker, 1929	0.679	1.812	0.0089186	–
Helicodiscus parallelus (Say, 1817)	5.393	6.438	0.2831711	G
Helicodiscus shimeki Hubricht, 1962	0.286	0.000	0.0204383	D
Helicodiscus singleyanus (Pilsbry, 1890)	0.375	1.125	0.0247064	G
Hendersonia occulta (Say, 1831)	0.036	0.062	0.7606162	D
Mesodon clausus clausus (Say, 1821)	0.054	0.000	0.3154693	D
Oxyloma peoriensis (Wolf in Walker, 1892)	0.125	0.000	0.1251903	–
Pupoides albilabris (C. B. Adams, 1821)	8.393	7.062	0.2324971	T
Stenotrema barbatum (Clapp, 1904)	0.107	0.000	0.1557229	D
Stenotrema fraternum fraternum (Say, 1824)	0.054	0.062	0.9262276	D
Succinea indiana Pilsbry, 1905	0.000	0.188	0.0277912	–
Succinea ovalis Say, 1817	0.143	0.188	0.7834904	D
Triodopsis alleni (Wetherby in Sampson, 1883)	0.071	0.000	0.2464148	D
Vallonia gracilicosta Reinhardt, 1883	11.500	11.062	0.7459095	D
Vertigo arthuri (von Martens, 1884)	0.643	0.000	0.0005065	–
Vertigo gouldi (A. Binney, 1843)	0.018	0.000	0.5622176	D
Vertigo nylanderi Sterki, 1909	0.036	0.000	0.4124393	T
Vertigo ovata Say, 1822	5.750	4.000	0.0472312	T
Vertigo tridentata Wolf, 1870	0.375	0.062	0.0738709	D
Zonitoides arboreus (Say, 1816)	4.143	4.625	0.5650976	D
Zonitoides nitidus (Müller, 1774)	0.464	0.000	0.0031253	T
Positive response				
Gastrocopta corticaria (Say, 1816)	0.732	3.500	0.0000003	D
Strobilops labyrinthica (Say, 1817)	9.661	22.375	0.0000000	D
Vallonia costata (Müller, 1774)	1.804	6.438	0.0000000	G
Vallonia parvula Sterki, 1892	8.250	13.250	0.0001267	T
Vallonia perspectiva Sterki, 1892	2.143	5.625	0.0000055	D
Vertigo pygmaea (Draparnaud, 1801)	0.000	0.562	0.0001385	G

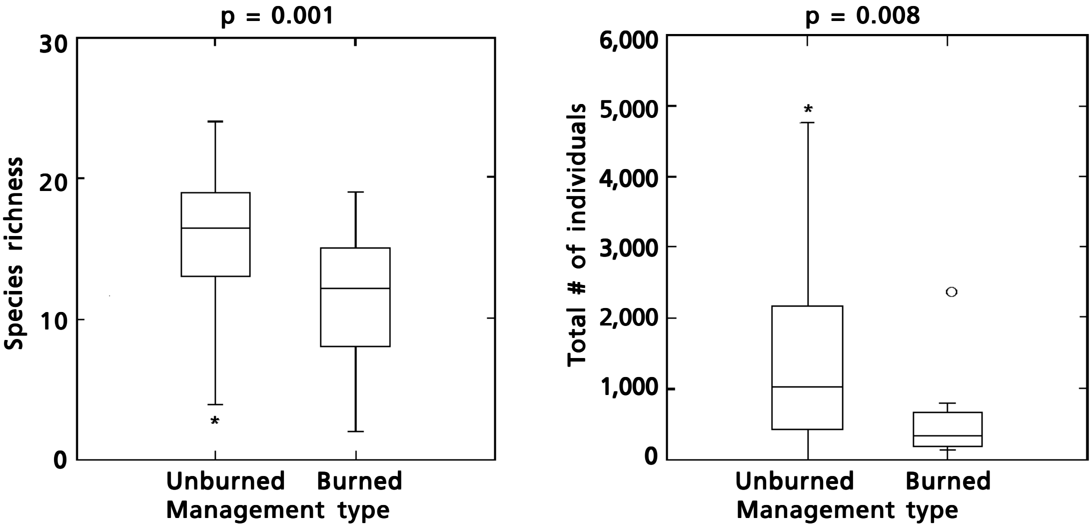


Fig. 2. Box–plot diagram of the response of species richness and abundance to management type on all sampled sites.

Fig. 2. Diagrama de la respuesta en riqueza y abundancia de especies al tipo de actuación desarrollado en todas las áreas estudiadas.

frequency. This null expectation was calculated by assigning 88% of all encountered individuals to unburned sites, with the remaining 22% to burned sites. This procedure was necessary as the number of unburned vs. burned sites was not balanced (88% vs. 22%). A two–tailed significance threshold was employed so that species with positive and negative responses to fire could both be identified. As these analyses were repeated for each species, a Bonferroni correction was used to adjust the significance threshold. Differences between fire responses across the three general ecological preference types were documented via a contingency table, with significance being estimated using both log–linear modelling and Fisher's Exact test.

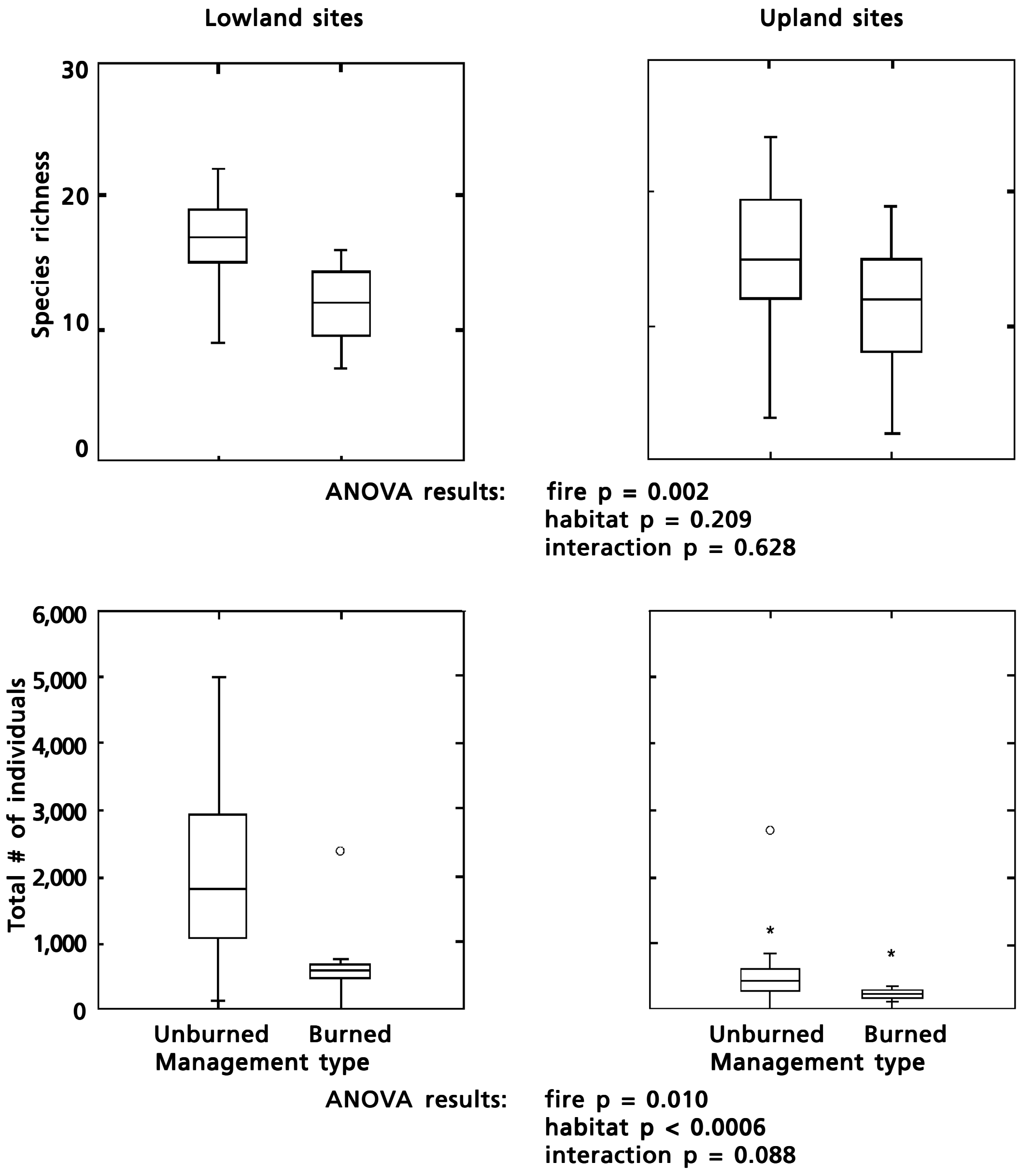
Results

These grassland habitats were generally found to support a diverse and abundant land snail fauna. A total of 91,074 individuals in 72 different species were recovered from the 72 surveyed sites (tables 1, 2). The number of species per each 4 l litter sample ranged from two (Chicog gravel prairie) to 24 (Twin Pines Farm sandstone glade). Average richness ranged from roughly 15 in upland sites, to 17 in lowland. Snail abundance per site ranged from 6 (Point Beach State Forest dunes) to 5,001 (Ogema West fen). Average abundance ranged from roughly 500 in upland sites to 2,000 in lowlands.

One–way ANOVA, using all sites, demonstrated that both species richness ($p = 0.001$) and abundance ($p = 0.008$) were significantly lower on sites that had experienced fire management (fig. 2). Median species richness was approximately 18 on unburned vs. 12 on burned sites. Likewise, median shell abundance was 1,000 on unburned vs. 300 on burned sites.

Full 2–way ANOVA, using all sites and considering both management type and habitat type (upland vs. lowland) as independent variables, demonstrated a highly significant ($p = 0.002$) reduction (approximately 30%) in species richness in both upland and lowland sites (fig. 3). Habitat type and the interaction between habitat and fire history were not significant predictors ($p = 0.209$ and $p = 0.628$, respectively). Likewise, a significant ($p = 0.010$) reduction in shell abundance (50–70%) was noted on burned sites (fig. 3). In this case, however, habitat type was a more significant ($p < 0.0005$) predictor, with lowlands having 4–10 times the number of shells as uplands. Additionally, a marginally significant ($p = 0.088$) interaction between management and habitat was observed, with the reduction appearing to be roughly 50% greater in lowlands.

Two–way ANOVA restricted to the 26 paired sites (fig. 4) demonstrated that even after blocking of variation due to site pair identity, a significant reduction in richness ($p < 0.0005$) and abundance ($p = 0.015$) still occurred on fire–managed sites.



ANOVA results: fire p = 0.002
habitat p = 0.209
interaction p = 0.628

ANOVA results: fire p = 0.010
habitat p < 0.0006
interaction p = 0.088

Fig. 3. Box–plot diagram of the response of species richness and abundance to management and habitat type on all sampled sites.

Fig. 3. Diagrama de la respuesta en riqueza y abundancia de especies al tipo de actuación desarrollado y el hábitat en todas las áreas estudiadas.

Comparison of dominance–diversity diagrams for these sites (fig. 5) demonstrates that both burned upland and lowland sites have truncated curves, with the rarest 40–50% of species being much less common as compared to unburned sites. However, the more common species appear to have largely similar dominance–diversity diagrams.

Contingency table analysis of individual species responses to fire (table 2) indicate that 32 (44%) experience a significant reduction in abundance on fire–managed sites, even following use of a Bonferroni–corrected two–tailed significance threshold (p = 0.000347). Only six species (8%) demonstrated positive responses to fire, while the remaining 34 (47%) demonstrated no

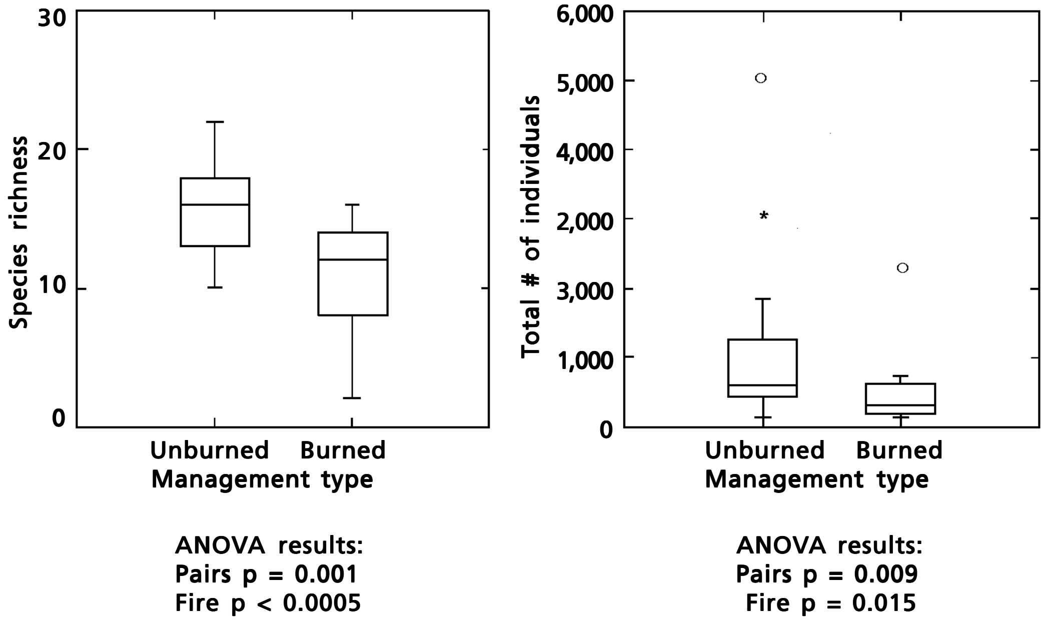


Fig. 4. Box–plot diagram of the response of species richness and abundance to management on 26 sites paired by habitat type and geographic location.

Fig. 4. Diagrama de la respuesta en riqueza y abundancia de especies a la actuación desarrollada en 26 áreas emparejadas según el tipo de hábitat y localización geográfica.

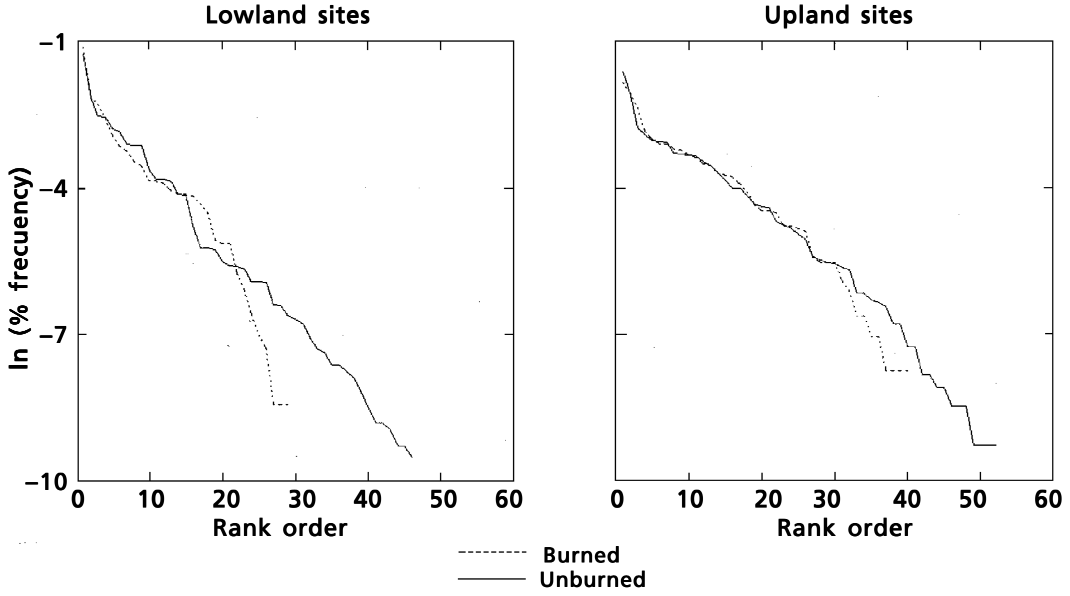


Fig. 5. Dominance–diversity curve for upland/lowland sites which have been burned/unburned.

Fig. 5. Curva de la dominancia–diversidad para las mesetas/llanuras que hayan sido quemadas/ no quemadas.

significant changes in population size. Contingency table analysis of ecological preference vs. fire response indicated that fully 72% of turf–specialists were negatively impacted by fire (table 3). However, only 22% of duff–specialists exhibited negative responses. While 67% of duff–specialists demonstrated no significant response to fire only 24% of turf–specialists were unaffected. Generalist species demonstrated little discernable trend to fire, with seven decreasing, two increasing, and five with no response. Log–likelihood ratio and Fisher's Exact tests both indicated these differences as being highly significant (p = 0.0006 and p = 0.004, respectively).

Table 3. Contingency table analysis of fire response vs. general ecological preferences. Log–likelihood ratio *p* = 0.000634; Fisher's Exact Test *p* = 0.004 (Ecological preferences: T. Turf; D. Duff; G. Generalist.)

Tabla 3. Análisis de la tabla de contingencia de la respuesta al fuego frente a las preferencias ecológicas generales. Logaritmo de la razón de verosimilitudes p *= 0,000634; Test exacto de Fisher* p *= 0,004 (Preferencias ecológicas: T. Sustrato herbáceo; D. Sustrato húmico; G. Generalista.)*

	Ecological preferences		
Fire response	T	D	G
Negative	18	6	7
None	6	18	5
Positive	1	3	2

Discussion

These data clearly indicate that fire management causes significant reductions in land snail community richness and abundance in both upland and lowland grasslands throughout a significant section of the tallgrass prairie biome in central North America. At a species–level, fire most strongly impacts the rarest species, and causes significant population reductions in 44% of the 72 encountered taxa. These negative impacts were most strongly felt in turf–specialists, where almost 75% experienced significant reductions. Thus, statements regarding the benign nature of fire on snail populations (FREST & JOHANNES, 1995), and the beneficial impact of fire on North American grassland faunas (THELER, 1997) can be proven false. Rather, frequent use of fire management appears to represent a significant threat to the health and diversity of North American grassland land snails.

It is not possible through these analyses to definitively identify the factors that directly lead to these impacts. However, at least part of the answer must lay in grassland detritusphere removal. This will lead to direct mortality, as the great majority of land snails are limited to this layer (HAWKINS et al., 1998). As land snail abundance (BERRY, 1973), diversity (CAIN, 1983; LOCASCIULLI & BOAG, 1987), and composition (CAMERON & MORGAN–HUWS, 1975; BAUER et al., 1996; BARKER & MAYHILL, 1999) is often positively correlated with litter depth, detritusphere removal would be expected to have a strong negative impact on land snail community structure.

Redevelopment of an equilibrium thickness of organic detritus takes at least five years in southern Plains grasslands (KUCERA & KOELLING, 1964), with even longer intervals being required in more northern locations (HILL & PLATT, 1975). The optimal interval between fires for land snails might be even longer, depending upon the time required for more refractory plant debris (such as lignified grass stems) to break down, allowing a complete suite of decompositional microhabitats to develop. Litter architecture is known to effect snail community composition in forests of Virginia (BURCH, 1956), British Columbia (CAMERON, 1986), and Puerto Rico (ÁLVAREZ & WILLIG, 1993) and grasslands of England (YOUNG & EVANS, 1991). It should thus not be surprising that in the current data set, sites burned up to 15 years ago have maintained lowered land snail richness and abundance as compared to unburned sites.

As grassland land snails presumably evolved in conjunction with natural fire regimes, it is also intriguing to note that turf–specialists experienced the most severe negative impacts to fire. If fire was a common process structuring central North American grasslands, evolution should have selected for individuals that were more tolerant of, or favored by, this disturbance. Like other native grassland invertebrate groups (SWENGEL, 1996; HARPER et al., 2000), land snails in the presettlement landscape may have been able to tolerate fires by being able to easily recolonize from source pools in adjacent unburned areas. Even when such adjacent source pools are present, recolonization may take over a dozen years (MÄND et al., 2001). In modern landscapes, where grasslands are highly fragmented and surrounded by agricultural, urban, or forest habitats, such recolonization has become much more difficult. Thus, turf–specialist taxa may continue to decrease in burned grasslands due to a lack of recolonization sources, while generalist and duff-specialist woodland taxa, which are more common in the surrounding landscape, may be able to maintain their populations through mass effect (SHMIDA & ELLNER, 1984).

The depression of land snail richness and abundance following fire episodes, the length of time required to redevelop a mature detritusphere, and the greater sensitivity of turf–specialist taxa to fire casts doubt on the wide–

held belief (e.g., Pauly, 1985) that North American grasslands should be burned at 2–6 year intervals. Rather, these data support the contention that presettlement return intervals ranged between 20–30 years (Sims, 1988). These data also strongly suggest that other factors, such as large herbivore grazing (Collins et al., 1998) and periodic drought (Borchert, 1950), may have also played essential roles in keeping prairies treeless, as these processes do not lead to the wholesale detritusphere removal.

Protecting the health of North American grassland land snail populations will require the preservation of mulch layers on sites. Such efforts will also help protect a large percentage of the entire grassland soil biota. The detritusphere can only be protected if more realistic fire return intervals (20–30 years) are adopted by conservation agencies, and used in conjunction with more diversified approaches towards woody and invasive plant removal. Activities like grazing, haying, and hand cutting/pulling will not cause widespread removal of the detritusphere, and should thus be more compatible with land snail (and soil biodiversity) conservation.

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References

Álvarez, J. & Willig, M. R., 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, 25: 100–110.

Barker, G. M. & Mayhill, P. C., 1999. Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru Ecological District, northeastern New Zealand. *Journal of Biogeography*, 26: 215–238.

Bauer, B., Joshi, J., Schmid, B., Hänggi, A., Borcard, D., Stary, J., Pedroli–Christen, A., Thommen, G. H., Luka, H., Rusterholz, H. P., Oggier, P., Ledergerber, S. & Erhardt, A., 1996. Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. *Revue Suisse de Zooligie*, 103: 801–833.

Behan–Pelletier, V. & Newton, G., 1999. Linking soil biodiversity and ecosystem function–the taxonomic dilemma. *Bioscience*, 49: 149–153.

Berry, F. G., 1973. Patterns of snail distribution at Ham Street Woods National Nature Reserve, East Kent. *Journal of Conchology*, 28: 23–35.

Bouchert, J. R., 1950. The climate of the central North American grassland. *Annals of the Association of American Geographers*, 40: 1–39.

Burch, J. B., 1956. Distribution of land snails in plant associations in eastern Virginia. T*he Nautilus*, 70: 60–64.

Burch, J. B. & Pearce, T. A., 1990. Terrestrial Gastropoda. *In: Soil biology guide*: 201–309 (D. L. Dindal, Ed.). John Wiley & Sons, New York.

Cain, A. J., 1983. Ecology and ecogenetics of terrestrial molluscan populations. In: *The Mollusca, Volume 6, Ecology*: 597-647 (W. D. Russell–Hunter, Ed.). Academic Press, New York.

Cameron, R. A. D., 1986. Environment and diversities of forest snail faunas from coastal British Columbia. *Malacologia*, 27: 341–355.

Cameron, R. A. D. & Morgan–Huws, D. I., 1975. Snail faunas in the early stages of a chalk grassland succession. *Biological Journal of the Linnean Society*, 7: 215–229.

Coleman, D. C. & Crossley, D. A. Jr., 1996. *Fundamentals of soil ecology*. Academic Press, New York.

Collins, S. L., Knapp, A. K., Blair, J. M. & Steinauer, E. M., 1998. Modulation of diversity by grazing and mowing on native tallgrass prairie. *Science*, 280: 745–747.

Collins, S. L. & Wallace, L. L., 1990. *Fire in North American tallgrass prairie*. University of Oklahoma Press, Norman, Oklahoma.

Curtis, J. T., 1959. *The vegetation of Wisconsin*. U. Wisconsin Press, Madison.

Dix, R. L., 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. *Ecology*, 41: 49–56.

Ehrenreich, J. H. & Aikman, J. M., 1963. An ecological study of the effect of certain management practices on native prairie in Iowa. *Ecological Monographs*, 33: 113–134.

Emberton, K. C., Pearce, T. A. & Randalana, R., 1996. Quantitatively sampling land–snail species richness in Madagascan rainforests. *Malacologia*, 38: 203–212.

Frest, T. J., 1990. *Final report, field survey of Iowa spring fens, contract #65–2454*. Iowa Department of Natural Resources, Des Moines.

– 1991. *Summary status reports on eight species of candidate land snails from the Driftless Area (Paleozoic Plateau), Upper Midwest*. Final Report, Contract #301–01366, USFWS Region 3, Ft. Snelling, Minnesota.

Frest, T. J. & Johannes, E. J., 1995. *Interior Columbia Basin mollusc species of special concern.* Final Report, Contract #43–0E00–4–9112, Interior Columbia Basin Ecosystem Management Project, Walla Walla, Washington.

Hadley, E. B., 1970. Net productivity and burning responses of native eastern North Dakota prairie communities. *American Midland Naturalist*, 84: 121–135.

HARPER, M. G., DIETRICH, C. H., LARIMORE, R. L. & TESSENE, P. A., 2000. Effects of prescribed fire on prairie Arthropods: an enclosure study. *Natural Areas Journal*, 20: 325–335.

HAWKINS, J. W., LANKESTER, M. W. & NELSON, R. R. A., 1998. Sampling terrestrial gastropods using cardboard sheets. *Malacologia*, 39: 1–9.

HILL, G. R. & PLATT, W. J., 1975. Some effects of fire upon a tallgrass prairie plant community in northwestern Iowa. In: *Prairie: a multiple view*: 103–113 (M. K. Wali, Ed.). University of North Dakota Press, Grand Forks.

HUBRICHT, L., 1985. The distributions of the native land molluscs of the eastern United States. *Fieldiana*, n.s., 24: 1–191.

KUCERA, C. L. & KOELLING, M., 1964. The influence of fire on composition of central Missouri prairie. *American Midland Naturalist*, 72: 142–147.

LOCASCIULLI, O. & BOAG, D. A., 1987. Microdistribution of terrestrial snails (Stylommatophora) in forest litter. *Canadian Field Naturalist*, 101: 76–81.

MÄND, R., EHLVEST, A. & KIRISTAJA, P., 2001. Land snail in an afforested oil–shale mining area. *Proceedings of the Estonian Academy of Sciences, Biology and Ecology*, 50: 37–41.

NEKOLA, J. C. (in press a). Large–scale Terrestrial Gastropod Community Composition Gradients in the Great Lakes region of North America. *Journal of Biogeography*.

– (in press b). Terrestrial gastropod fauna of northeastern Wisconsin and the southern Upper Peninsula of Michigan. *American Malacological Bulletin*.

NEKOLA, J. C. & SMITH, T. A., 1999. Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. *Malacologia,* 41: 253–269.

OGGIER, P., ZSCHOKKE, S. & BAUR, B., 1998. A comparison of three methods for assessing the gastropod community in dry grasslands. *Pedobiologia*, 42: 348–357.

PAULY, W. R., 1985. *How to manage small prairie fires*. Dane County Environmental Council, Madison, Wisconsin.

REGAN, T. J., REGAN, H. M., BONHAM, K., TAYLOR, R. J. & BURGMAN, M. A., 2001. Modelling the impact of timber harvesting on a rare carnivorous land snail (*Tasmaphena lamproides*) in northwest Tasmania, Australia. *Ecological Modelling*, 139: 253–264.

ROOSA, D. M., 1984. Fury on the prairie. *Iowa Conservationist*, 43: 13.

RUSSELL–HUNTER, W. D., 1983. Overview: planetary distribution of and the ecological constraints upon the mollusca. In: *The Mollusca, Volume 6, Ecology*: 1–27 (W. D. Russell–Hunter, Ed.). Academic Press, New York.

SHMIDA, A. & ELLNER, S., 1984. Coexistence of plant species with similar niches. *Vegetatio*, 58: 29–55.

SIMS, P. L., 1988. Grasslands. In: *North American terrestrial vegetation*: 266–286 (M. G. Barbour & W. D. Billings, Eds.). Cambridge University Press, New York.

STANISIC, J., 1996. New land snails from boggomoss environments in the Dawson Valley, south-eastern Queensland (Eupulmonata: Charopidae and Camaenidae). *Memoirs of the Queensland Museum*, 39: 343–354.

STOWE, L. G. & TEERI, J. A., 1978. The geographic distribution of C_4 species of the Dicotyledonae in relation to climate. *American Naturalist*, 112: 609–621.

SWENGEL, A. B., 1996. Effects of fire and hay management on the abundance of prairie butterflies. *Biological Conservation*, 76: 73–85.

– 1998. Comparisons of butterfly richness and abundance measures in prairie and barrens. *Biodiversity and Conservation*, 7: 1,639–1,659.

THELER, J. L., 1997. The modern terrestrial gastropod (land snail) fauna of western Wisconsin's hill prairies. *The Nautilus*, 110: 111–121.

TOWNE, G. & OWENSBY, C., 1984. Long–term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *Journal of Range Management*, 37: 392–397.

VELLEMAN, P. F. & HOAGLIN, D. C., 1981. *Applications, basics, and computing of exploratory data analysis*. Addison–Wesley Press, Reading, Massachusetts.

WEAVER, J. E., 1954. *North American prairie*. Johnson Publishing Company, Lincoln, Nebraska.

WEAVER, J. E. & ROWLAND, N. W., 1952. Effects of excessive natural mulch on development, yield, and structure of native grassland. *Botanical Gazette*, 114: 1–19.

WELTER–SCHULTES, F. W. & WILLIAMS, M. R., 1999. History, island area and habitat availability determine land snail species richness of Aegean islands. *Journal of Biogeography*, 26: 239–249.

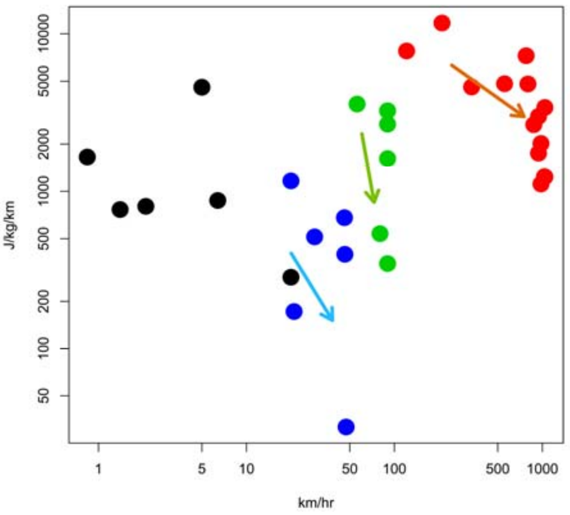
WHITTAKER, R. H., 1975. *Communities and ecosystems*. MacMillan Publishing, New York.

YOUNG, M. S. & EVANS, J. G., 1991. Modern land mollusc communities from Flat Holm, South Glamorgan. *Journal of Conchology*, 34: 63–70.

ZAR, J. H., 1984. *Biostatistical analysis*. Prentice–Hall, Inc., Englewood Cliffs, New Jersey.

Section VII: Human macroecology and sustainability

The goal of creating a human society which exists in a sustainable fashion with the finite Earth requires not only that our actions be assessed for individual farms, villages, and cities, but also collectively across humanity. However, such a macroecological perspective is largely missing from sustainability studies. Because human civilization is a complex adaptive system which is maintained far from thermodynamic equilibrium, it requires energy inputs via vast quantities of increasingly exhausted fossil fuel stocks. It also requires other essential and non-substitutable commodities such as metal ores, radio-nucleotides, rare earths, phosphate fertilizer, arable land, and fresh water that are becoming evermore scarce. The dynamics of such systems are highly unpredictable. Small perturbations can cause wholesale changes, including total collapse. Ensuring that global civilization does not suffer this fate will require that valuable insights from the natural – and not just social – sciences be considered. Our most recent paper is a ecological consideration of the history food storage and transportation, published in *Bioscience* in the summer of 2015 (see right). The next project considers the ecological dynamics of human innovation, in particular whether high population density cities are needed to generate the technological advancements needed to support the ever growing human population.



Relationship between energetic costs and speed for goods transportation fueled by animal metabolism (black dots) and extrametabolic processes in marine (blue), terrestrial (blue), and aerial (red) domains. The trajectory of the relationship over time is shown within each of the latter three groups by best-fit vectors.

Representative Publications
[number of citations as of October 27, 2017]

Hammond, S.T., J.H. Brown, J.R. Burger, T.P. Flanagan, T.S. Fristoe, N. Mercado-Silva, **J.C. Nekola** & J.G. Okie. 2015. Food spoilage, storage and transport: implications for a sustainable future. *Bioscience*. 65:758–768. **[12]**

Brown, J.H., J.R. Burger, W.R. Burnside, M. Chang, A.D. Davidson, T.S. Fristoe, M.J. Hamilton, S.T. Hammond, A. Kodric-Brown, N. Mercado-Silva, **J.C. Nekola** & J.G. Okie. 2014. Macroecology meets macroeconomics: resource scarcity and global sustainability. *Ecological Engineering.* 65:24-32. **[32]**

Nekola, J.C., C.D. Allen, J.H. Brown, J.R. Burger, A.D. Davidson, T.S. Fristoe, M.J. Hamilton, S.T. Hammond, A. Kodric-Brown, N. Mercado-Silva & J.G. Okie. 2013. The Malthusian-Darwinian dynamic and the trajectory of civilization. *Trends in Ecology and Evolution.* 28:127-130. **[41]**

Nekola, J.C., J.H. Brown, A. Kodric-Brown & J.G. Okie. 2013. Global sustainability vs. the MDD: a response to Rull. *Trends in Ecology and Evolution.* 28: 444. **[3]**

Burger, J.R., J.H. Brown, C.D. Allen,, W.R. Burnside, A.D. Davidson, T.S. Fristoe, M.J. Hamilton, N. Mercado-Silva, **J.C. Nekola**, J.G. Okie & W. Zuo. 2012. The macroecology of sustainability. *PLoS Biology*. 10:e1001345. **[84]**

Brown, J.H., W.R. Burnside, A.D. Davidson, J.P. DeLong, W.C. Dunn, M.J. Hamilton, **J.C. Nekola**, J.G. Okie, N. Mercado-Silva, W.H. Woodruff & W. Zuo. 2011. Energetic Limits to Economic Growth. *Bioscience*. 61:19-26. **[179]**

Smith, V.H., G.D. Tilman & **J.C. Nekola**. 1999. Eutrophication impacts of excess nutrient inputs on fresh water, marine, and terrestrial ecosystems. *Environmental Pollution.* 100: 179-196. **[2017]**

Forum: Science & Society

The Malthusian–Darwinian dynamic and the trajectory of civilization

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Two interacting forces influence all populations: the Malthusian dynamic of exponential growth until resource limits are reached, and the Darwinian dynamic of innovation and adaptation to circumvent these limits through biological and/or cultural evolution. The specific manifestations of these forces in modern human society provide an important context for determining how humans can establish a sustainable relationship with the finite Earth.

Malthus, Darwin, and population dynamics

In 1798 Thomas Malthus laid out the concept of exponential population growth that became the foundation of demography and population biology. He noted that the 'increase of population is necessarily limited by the means of subsistence.' Population growth can thus continue only as long as environmental conditions remain favorable. As numbers increase, sooner or later environmental limits cause birth rates to decrease and/or death rates to increase, ultimately leading to an end to population growth. These concepts profoundly influenced Charles Darwin half a century later: because more offspring are born than can survive, only the fittest individuals reproduce and pass their superior traits on to their offspring. The result is adaption or innovation in the form of either genetic or cultural evolution.

The Malthusian dynamic pushes a population to increase until it reaches its environmental limits. The Darwinian dynamic pushes against these limits by incorporating new traits and technologies that enhance survival and reproduction. There are restrictions to this Malthusian–Darwinian Dynamic (MDD), however: it is logically, physically, and biologically impossible for exponential growth to continue indefinitely within a finite world.

Ecological and historical perspective on the rise of human civilization

Humans are an exceptional species. Our population has increased almost continuously from less than a million individuals in sub-Saharan Africa 50 000 years ago to a current population of 7 billion spanning the entire globe. The human population is projected to reach between 9 and 10 billion by 2050 [1]. In the process, humans have created complex social, technological, and economic systems. We have transformed the atmosphere, water, land, and biodiversity of the planet. We have become the most dominant single species the earth has ever seen. Our success to date is a consequence of our ability to continually develop new innovations that push back environmental limits and to transfer this information across generations (Figure 1). Operating in this way, the MDD has led to rapid cultural evolution and made possible the transition from hunter–gatherer to agricultural to industrial–technological–informational economies.

A central feature of human ecology has been the positive feedback between growth and innovation. As populations grew and aggregated into larger and more complex social groups, more information was acquired and processed. This led to new technologies that further pushed back ecological limits, allowing for continued population growth. The result has been an ascending spiral of exponential processes feeding back on each other: population growth and aggregation begot technological innovation, which in turn allowed for more resource extraction and a greater ability to overcome ecological constraints, begetting still more population growth and socioeconomic development [2].

Our ability to evade local resource shortages and population crashes through trade, migration, and innovation has allowed for continued growth not just of the global population but also of its resource use and economic activity [3]. For more than 200 years, so-called Malthusians [4] have argued, however, that this cannot indefinitely continue because essential resources supplied by the finite Earth will ultimately become limiting. This Malthusian perspective has historically been countered by so-called Cornucopians, who have argued that there is no hard limit to human population size and economic activity because human ingenuity and technological innovation provide an effectively infinite capacity to increase resource supply [5].

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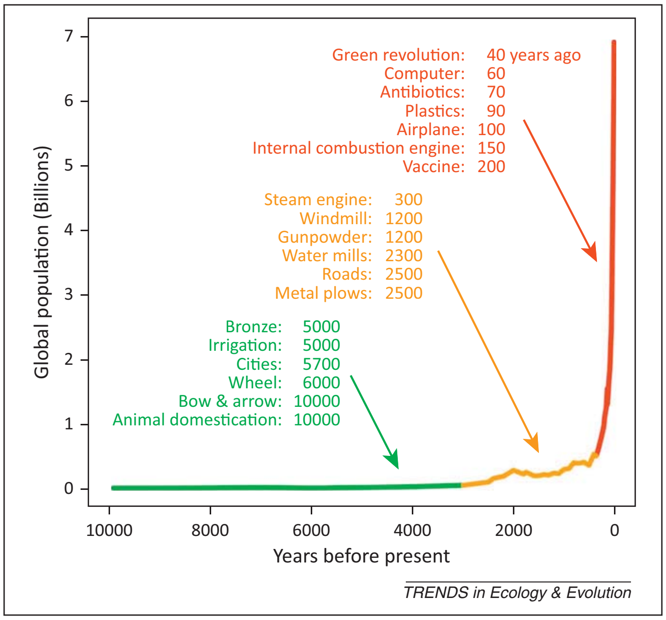

TRENDS in Ecology & Evolution

Figure 1. Global human population over the last 10 000 years. Data are based on estimates from [11], the US census bureau, and http://en.wikipedia.org/wiki/World_population_estimates. Average estimates of population size across these sources are plotted. Examples of major innovations that have helped to expand human carrying capacity (based in part on [12]) are listed for three time periods in years before present (ybp): 10 000–3000 ybp (green), 3000–300 ybp (orange), and 300 ybp–present (red).

Box 1. The MDD and challenges to global sustainability

Although the MDD has spurred innovations and adaptations that have allowed us to colonize the entire planet, it has also shaped our biological makeup, selecting for traits and behaviors that favor selfishness and may ultimately make us ill-equipped to act in concert to address global issues.

Natural selection generates the tendency for individuals to preferentially promote themselves and their families. Social groups often establish acceptable behaviors to minimize the inherent conflict between such individual self-interest and group welfare. Although disobeying group rules can result in increased individual fitness, this is counteracted by the detection and punishment of cheaters by social groups. Whether through luck or drive, some will still manage to possess a disproportionate share of resources. Although the degree of inequality can be moderated, highly asymmetric wealth distributions have proven robust to the best efforts of social philosophies and political movements to impose more egalitarian patterns [13].

All of these factors contribute to the tragedy of the commons, which occurs when selfish individuals reap the benefits from shared resources while spreading the costs across the group [14]. The increase in global atmospheric CO_2 concentrations and the reduction in global fisheries stocks (Figure 2) both represent pressing global environmental issues related to this mechanism. In the case of CO_2 emissions, individuals benefit from using carbon-based energy while global society is burdened by the costs related to increased atmospheric CO_2 concentrations. Similarly, a single fishing vessel has no incentive to curb harvests because the costs of reduced stocks are paid for by humanity as a whole. Efforts to implement and enforce international regulations to moderate these two activities have failed because of the selfishness of countries and individuals in combination with the difficulty of detecting cheating at the global scale [15].

Malthus warned of population and economic collapse in the British Isles because the exponentially increasing population would eventually outstrip linearly increasing food supplies. Although millions did die from widespread famines in Ireland and the Scottish Highlands in the mid-19th century, more widespread starvation was averted because of newly acquired agricultural technologies and emigration of people to overseas colonies [2]. As a result, the British economy did not collapse and by 1900 had become the dominant global empire. In the 1960s and 1970s Malthusians again warned that the global human population was nearing its environmental limits. Outbreaks of famine and disease did occur, but advances in agriculture, medicine, technology, and commerce – most notably the green revolution and economic globalization – pushed back the limits again and our population has more than doubled from approximately three billion in 1960 to more than seven billion today [1].

Our ability to evade previous environmental limits through the MDD should not imply, however, that such outcomes are inevitable. First, although the MDD has served as the engine for our extraordinary success, it also contains within it the potential seeds for our ultimate downfall. Motives driven by the MDD, such as selfishness and cheating, benefit individuals at the expense of society as a whole (Box 1). Second, because natural selection can only operate on current conditions, there is little tendency to recognize approaching environmental limits and curb growth before resources are overexploited [6]. Third, the assertion that adaptation and innovation will always prevent collapse – because they have in the past – is logically untenable and akin to the statistical fallacy of extrapolating beyond a data set. Whether we wish to acknowledge it or not, there are hard limits to innovation: according to the first law of thermodynamics, we cannot create energy or matter; according to the second law of thermodynamics, large energy inputs are required to maintain highly organized systems.

The ruins of Mohenjo Daro, Mesopotamia, Egypt, Greece, Rome, the Maya, Hohokam, Angkor Wat, and Easter Island are enduring evidence that many earlier societies were unable to innovate their way out of local limits and therefore collapsed despite attaining dense populations and advanced cultures. Although the proximate causes of these declines are debated and undoubtedly differ, the ultimate causes lie in an inability to sustain resource supplies and protect against parasites, diseases, and other human groups [7].

Until now, both Malthusians and Cornucopians have been correct: some populations have crashed and cultures have vanished, but our species has endured because these events have been localized. However, behavioral changes and technological innovations over the last century now intricately interconnect us in a single global society. As a result, local perturbations currently have the ability to reverberate across all of humanity. For instance, the 2008 meltdown of the USA real estate and mortgage markets and the 2011 Tōhoku earthquake and tsunami in Japan both led to global interruptions in economic activity, impacting most individuals in some way.

Within the context of our now highly globalized society, the essential question is how much potential exists for the

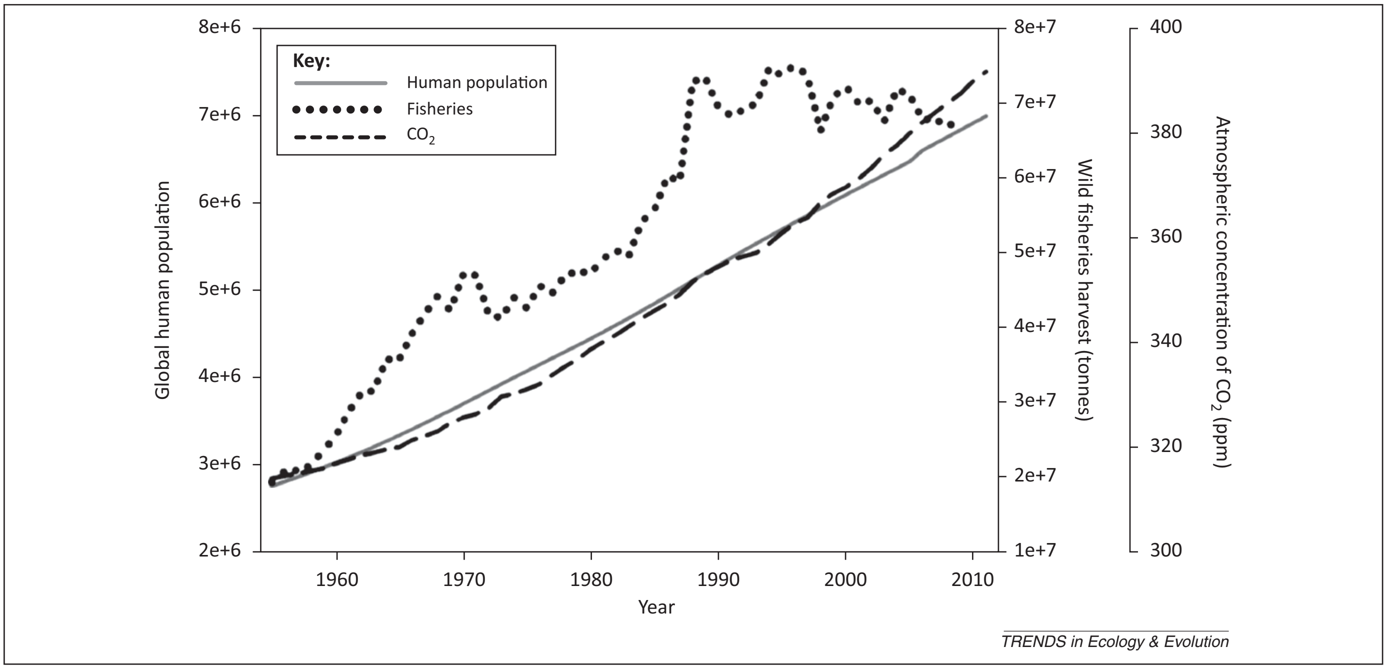

Figure 2. The trajectories of atmospheric CO_2 and wild fisheries harvest in relation to global population since 1955. Note that the increase in CO_2 concentration has accelerated, whereas fisheries harvest reached a peak in the 1990s and has since declined. The world population size is from the World Resources Institute (http://earthtrends.wri.org). The wild fisheries harvest data are from the FAO Fishery Statistical Collection Global Capture Production Database (http://www.fao.org/fishery/statistics/global-capture-production/en) and are limited to diadromous and marine species. Yearly mean CO_2 concentrations as measured at the Mauna Loa Observatory were obtained from ftp://ftp.cmdl.noaa.gov/ccg/co2/trends/co2_annmean_mlo.txt.

Darwinian side of the MDD to allow for continued adaptation and innovation to push back against global scale constraints. Many are now asking questions such as 'What are the limits to growth?' and 'What will happen when these limits are met?' [5,8].

The road forward

We cannot provide definitive answers to these questions. Contemporary human civilization is a complex adaptive system, maintained far from thermodynamic equilibrium largely via the throughput of vast quantities of increasingly exhausted fossil fuel stocks [9]. This system also requires other essential and non-substitutable commodities such as metal ores, radionucleotides, rare earth elements, phosphate fertilizer, arable land, and fresh water that are becoming ever more scarce [10]. The dynamics of such systems are highly unpredictable. Small perturbations can cause wholesale changes, including total collapse.

The bad news is that the MDD has left humans ill prepared to make the necessary ecological and behavioral changes required to avoid civilization collapse. The universal underlying biological imperatives of the MDD lie at the root of many of the most challenging impediments to long-term sustainability: exponential population growth, exploitation of all available resources, and the expression of behaviors that promote the competitive abilities of individuals, their families, and social groups over the species as a whole.

However, the good news is that the MDD may also provide valuable insights into potential solutions from both natural (in particular evolutionary biology and ecology) and social (in particular economics and sociology) science perspectives. We must recognize that a sustainable future will ultimately require: (i) negative population growth for a number of generations, followed by zero growth; (ii) a steady-state economy based on sustainable use of renewable energy and material resources; and (iii) new social norms that favor the welfare of the entire global population over that of specific individuals and groups. It is also essential that we recognize that humanity has not yet evolved the genetic or cultural adaptations needed to accomplish these tasks.

Our exceptional brains give us the ability to appreciate the present situation and envision alternate futures before catastrophe occurs. The challenge will be to facilitate a rapid cultural evolution that, for the good of the entire species, rewards individual sacrifices in fitness and quality of life. Genuine collaboration between natural and social scientists will be essential to inform society as a whole – and policy makers specifically – of this difficult but necessary adaptation required to accommodate our species in a finite and now full world.

References

1 Bongaarts, J. (2009) Human population growth and the demographic transition. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 2985–2990
2 Boserup, E. (1981) *Population and Technological Change*, University of Chicago Press
3 Hall, C.A.S. and Klitgaard, K.A. (2011) *Energy and the Wealth of Nations: Understanding the Biophysical Economy*, Springer
4 Ehrlich, P.R. (1968) *The Population Bomb*, Sierra Club/Ballantine Books
5 Simon, J.L. (1981) *The Ultimate Resource*, Princeton University Press
6 Levin, S.A. (2000) *Fragile Dominion: Complexity and the Commons*, Perseus Publishing
7 Tainter, J.A. (1988) *The Collapse of Complex Societies*, Cambridge University Press
8 Heinberg, R. (2011) *The End of Growth: Adapting to Our New Economic Reality*, New Society Publishers

9 Smil, V. (2008) *Energy in Nature and Society: General Energetics of Complex Systems*, MIT Press

10 Burger, J.R. *et al.* (2012) The macroecology of sustainability. *PLoS Biol.* 10, e1001345

11 Durand, J.D. (1977) Historical estimates of world population: an evaluation. *Popul. Dev. Rev.* 3, 253–296

12 Vermeij, G.J. and Leigh, E.G., Jr (2011) Natural and human economies compared. *Ecosphere* 2, art39

13 Chatterjee, A. *et al.*, eds (2005) *Econophysics of Wealth Distributions*, Springer Verlag

14 Hardin, G. (1968) The tragedy of the commons. *Science* 162, 1243–1248

15 Ostrom, E. *et al.* (1999) Revisiting the commons: local lessons, global challenges. *Science* 284, 278–282

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Essay

The Macroecology of Sustainability

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abstract: The discipline of sustainability science has emerged in response to concerns of natural and social scientists, policymakers, and lay people about whether the Earth can continue to support human population growth and economic prosperity. Yet, sustainability science has developed largely independently from and with little reference to key ecological principles that govern life on Earth. A macroecological perspective highlights three principles that should be integral to sustainability science: 1) physical conservation laws govern the flows of energy and materials between human systems and the environment, 2) smaller systems are connected by these flows to larger systems in which they are embedded, and 3) global constraints ultimately limit flows at smaller scales. Over the past few decades, decreasing per capita rates of consumption of petroleum, phosphate, agricultural land, fresh water, fish, and wood indicate that the growing human population has surpassed the capacity of the Earth to supply enough of these essential resources to sustain even the current population and level of socioeconomic development.

“Sustainability” has become a key concern of scientists, politicians, and lay people—and for good reason. There is increasing evidence that we have approached, or perhaps even surpassed, the capacity of the planet to support continued human population growth and socioeconomic development [1–3]. Currently, humans are appropriating 20%–40% of the Earth’s terrestrial primary production [4–6], depleting finite supplies of fossil fuels and minerals, and overharvesting “renewable” natural resources such as fresh water and marine fisheries [7–10]. In the process, we are producing greenhouse gases and other wastes faster than the environment can assimilate them, altering global climate and landscapes, and drastically reducing biodiversity [2]. Concern about whether current trajectories of human demography and socioeconomic activity can continue in the face of such environmental impacts has led to calls for “sustainability.” A seminal event was the Brundtland commission report [11], which defined “sustainable development (as) development that meets the needs of the present without compromising the ability of future generations to meet their own needs.”

One result has been the emergence of the discipline of *sustainability science*. “Sustainability science (is) an emerging field of research dealing with the interactions between natural and social systems, and with how those interactions affect the challenge of sustainability: meeting the needs of present and future generations while substantially reducing poverty and conserving the planet’s life support systems” (*Proceedings of the National Academy of Sciences of the USA* [PNAS], http://www.pnas.org/site/misc/sustainability.shtml). It is the subject of numerous books, at least three journals (*Sustainability Science* [Springer]; *Sustainability*: *Science*, *Practice*, *& Policy* [ProQuest-CSA]; *International Journal of Sustainability Science and Studies* [Polo Publishing]), and a special section of the PNAS. In “A Survey of University-Based Sustainability Science Programs”, conducted in 2007, (http://sustainabilityscience.org/content.html?contentid=1484), the American Association for the Advancement of Science listed 103 academic programs, including 64 in the United States and Canada, and many more have been established subsequently.

Interestingly, despite the above definition, the majority of sustainability science appears to emphasize social science while largely neglecting natural science. A survey of the published literature from 1980 through November 2010 using the Web of Science reveals striking results. Of the 23,535 published papers that include “sustainability” in the title, abstract, or key

Essays articulate a specific perspective on a topic of broad interest to scientists.

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Abbreviations: GDP, gross domestic product

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words, 48% include "development" or "economics". In contrast, only 17% include any mention of "ecology" or "ecological", 12% "energy", 2% "limits", and fewer than 1% "thermodynamic" or "steady state". Any assessment of sustainability is necessarily incomplete without incorporating these concepts from the natural sciences.

Human Macroecology

A macroecological approach to sustainability aims to understand how humans are integrated into and constrained by the Earth's systems [12]. In just the last 50,000 years, *Homo sapiens* has expanded out of Africa to become the most dominant species the Earth has ever experienced. Near-exponential population growth, global colonization, and socioeconomic development have been fueled by extracting resources from the environment and transforming them into people, goods, and services. Hunter-gatherers had subsistence economies based on harvesting local biological resources for food and fiber and on burning wood and dung to supplement energy from human metabolism. With the transition to agricultural societies after the last ice age [13] and then to industrial societies within the last two centuries, per capita energy use has increased from approximately 120 watts of human biological metabolism to over 10,000 watts, mostly from fossil fuels [3,14]. Modern economies rely on global networks of extraction, trade, and communication to rapidly distribute vast quantities of energy, materials, and information.

The capacity of the environment to support the requirements of contemporary human societies is not just a matter of political and economic concern. It is also a central aspect of ecology— the study of the interactions between organisms, including humans, and their environments. These relationships always involve exchanges of energy, matter, or information. The scientific principles that govern the flows and transformations of these commodities are fundamental to ecology and directly relevant to sustainability and to the maintenance of ecosystem services, especially in times of energy scarcity [15]. A macroecological perspective highlights three principles that should be combined with perspectives from the social sciences to achieve an integrated science of sustainability.

Principle 1: Thermodynamics and the Zero-Sum Game

The laws of thermodynamics and conservation of energy, mass, and chemical stoichiometry are universal and without exception. These principles are fundamental to biology and ecology [16–18]. They also apply equally to humans and their activities at all spatial and temporal scales. The laws of thermodynamics mean that continual flows and transformations of energy are required to maintain highly organized, far-from-equilibrium states of complex systems, including human societies. For example, increased rates of energy use are required to fuel economic growth and development, raising formidable challenges in a time of growing energy scarcity and insecurity [3,15,19]. Conservation of mass and stoichiometry means that the planetary quantities of chemical elements are effectively finite [15,18].

Human use of material resources, such as nitrogen and phosphorus, alters flows and affects the distribution and local concentrations in the environment [18]. This is illustrated by the Bristol Bay salmon fishery, which is frequently cited as a success story in sustainable fisheries management [20,21]. In three years for which good data are available (2007–2009), about 70% of the annual wild salmon run was harvested commercially, with one species, sockeye, accounting for about 95% of the catch [22]. From a management perspective, the Bristol Bay sockeye fishery has been sustainable, because annual runs have not declined. Additional implications for sustainability, however, come from considering the effect of human harvest on the flows of energy and materials in the upstream ecosystem (Figure 1). When humans take about 70% of Bristol Bay sockeye runs as commercial catch, this means a 70% reduction in the number of mature salmon returning to their native waters to spawn and complete their life cycles. It also means a concomitant reduction in the supply of salmon to support populations of predators, such as grizzly bears, bald eagles, and indigenous people, all of which historically relied on salmon for a large proportion of their diet [23,24]. Additionally, a 70% harvest means annual removal of more than 83,000 metric tonnes of salmon biomass, consisting of approximately 12,000, 2,500, and 330 tonnes of carbon, nitrogen, and phosphorus, respectively (see Text S1 for sources and calculations). These marine-derived materials are no longer deposited inland in the Bristol Bay watershed, where they once provided important nutrient subsidies to stream, lake, riparian, and terrestrial ecosystems [24–27]. So, for example, one apparent consequence is that net primary production in one oligotrophic lake in the Bristol Bay watershed has decreased "to about 1/3 of its level before commercial fishing" [28]. Seventy percent of Bristol Bay salmon biomass and nutrients are now exported to eastern Asia, western Europe, and the continental US, which are the primary markets for commercially harvested wild Alaskan salmon. Our macroecological assessment of the Bristol Bay fishery suggests that "sustainable harvest" of the focal salmon species does not consider the indirect impacts of human take on critical resource flows in the ecosystem (Figure 1). So the Bristol Bay salmon fishery is probably not entirely sustainable even at the "local" scale.

Principle 2: Scale and Embeddedness

Most published examples of sustainability focus on maintaining or improving environmental conditions or quality of life in a localized human system, such as a farm, village, city, industry, or country ([29,30] and articles following [31]). These socioeconomic systems are not closed or isolated, but instead are open, interconnected, and embedded in larger environmental systems. Human economies extract energy and material resources from the environment and transform them into goods and services. In the process, they create waste products that are released back into the environment. The laws of conservation and thermodynamics mean that the embedded human systems are absolutely dependent on these flows: population growth and economic development require increased rates of consumption of energy and materials and increased production of wastes. The degree of dependence is a function of the size of the economy and its level of socioeconomic development [3]. Most organic farms import fuel, tools, machinery, social services, and even fertilizer, and export their products to markets. A small village in a developing country harvests food, water, and fuel from the surrounding landscape.

Large, complex human systems, such as corporations, cities, and countries, are even more dependent on exchanges with the broader environment and consequently pose formidable challenges for sustainability. Modern cities and nation states are embedded in the global economy, and supported by trade and communication networks that transport people, other organisms, energy, materials, and information. High densities of people and concentrations of socioeconomic activities require massive inputs of energy and materials and produce proportionately large amounts of wastes. Claims that such

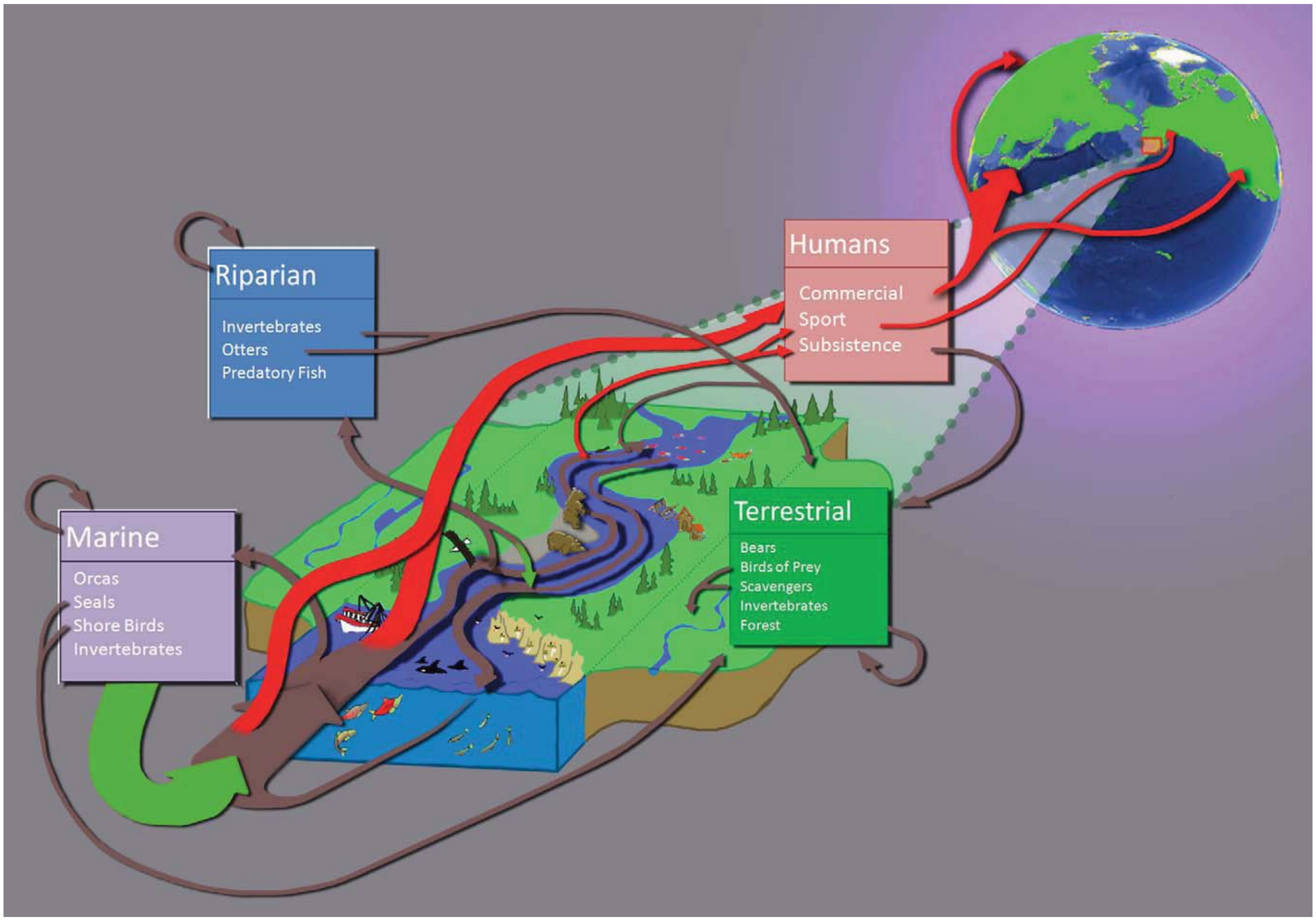

Figure 1. Pictorial illustration of important flows of salmon and contained biomass, energy, and nutrients within and out of the Bristol Bay ecosystem. Brown arrows depict the flows within the ecosystem, green arrows depict inputs due to growth in fresh water or the sea, and red arrows represent human harvest. Seventy percent of salmon are extracted by humans and are no longer available to the Bristol Bay ecosystem.

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systems are "sustainable" usually only mean that they are comparatively "green"—that they aim to minimize environmental impacts while offering their inhabitants happy, healthy lifestyles.

A macroecological perspective on the sustainability of local systems emphasizes their interrelations with the larger systems in which they are embedded, rather than viewing these systems in isolation. Portland, Oregon offers an illuminating example. The city of Portland and surrounding Multnomah County, with a population of 715,000 and a median per capita income of US$51,000, bills itself and is often hailed by the media as "the most sustainable city in America" (e.g., SustainLane.com, 2008). On the one hand, there can be little question that Portland is relatively green and offers its citizens a pleasant, healthy lifestyle, with exemplary bike paths, parks, gardens, farmers' markets, and recycling programs. About 8% of its electricity comes from renewable non-hydroelectric sources (http://apps3.eere.energy.gov/greenpower/resources/tables/topten.shtml). On the other hand, there also can be no question that Portland is embedded in and completely dependent on environments and economies at regional, national, and global scales (Figure 2). A compilation and quantitative analysis of the flows into and out of the city are informative (see Text S1 for sources and calculations). Each year the Portland metropolitan area consumes at least 1.25 billion liters of gasoline, 28.8 billion megajoules of natural gas, 31.1 billion megajoules of electricity, 136 billion liters of water, and 0.5 million tonnes of food, and the city releases 8.5 million tonnes of carbon as CO_2, 99 billion liters of liquid sewage, and 1 million tonnes of solid waste into the environment. Total domestic and international trade amounts to 24 million tonnes of materials annually. With respect to these flows, Portland is not conspicuously "green"; the above figures are about average for a US city of comparable size (e.g., [32]).

A good way to see the embedding problem is to imagine the consequences of cutting off all flows in and out, as military sieges of European castles and cities attempted to do in the Middle Ages. From this point of view and in the short term of days to months, some farms and ranches would be reasonably sustainable, but the residents of a large city or an apartment building would rapidly succumb to thirst, starvation, or disease. Viewed from this perspective, even though Portland may be the greenest and by some definitions "the most sustainable city in America", it is definitely not self-sustaining. Massive flows of energy and materials across the city's boundaries are required just to keep its residents alive, let alone provide them with the lifestyles to which they have become accustomed. Any complete ecological assessment of the sustainability of a local system should consider its connectedness with and dependence on the larger systems in which it is embedded.

Figure 2. Pictorial illustration of important flows of resources into and wastes out of Portland, Oregon. This "most sustainable city in America" depends on exchanges with the local, regional, and global environments and economies in which it is embedded.
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Principle 3: Global Constraints

For thousands of years, humans have harvested fish, other animals, and plants with varying degrees of "sustainability" and lived in settlements that depend on imports and exports of energy and materials. Throughout history, humans have relied on the environment for goods and services and used trade to compensate for imbalances between extraction, production, and consumption at local to regional scales. What is different now are the enormous magnitudes and global scales of the fluxes of energy and materials into and out of human systems. Every year fisheries export thousands of tonnes of salmon biomass and the contained energy and nutrients from the Bristol Bay ecosystem to consumers in Asia, Europe, and the US. Every year Portland imports ever larger quantities of energy and materials to support its lifestyle and economy. Collectively, such activities, replicated thousands of times across the globe, are transforming the biosphere.

Can the Earth support even current levels of human resource use and waste production, let alone provide for projected population growth and economic development? From our perspective, this should be ***the*** critical issue for sustainability science. The emphasis on local and regional scales—as seen in the majority of the sustainability literature and the above two examples—is largely irrelevant if the human demand for essential energy and materials exceeds the capacity of the Earth to supply these resources and if the release of wastes exceeds the capacity of the biosphere to absorb or detoxify these substances.

Human-caused climate change is an obvious and timely case in point. Carbon dioxide has always been a waste product of human metabolism—not only the biological metabolism that consumes oxygen and produces carbon dioxide as it converts food into usable energy for biological activities, but also the extra-biological metabolism that also produces CO_2 as it burns biofuels and fossil fuels to power the maintenance and development of hunter-gatherer, agricultural, and industrial-technological societies. Only in the last century or so, however, has the increasing production of CO_2 by humans overwhelmed the Earth's capacity to absorb it, increasing atmospheric concentrations and warming the planet more each decade. So, for example, efforts to achieve a "sustainable" local economy for a coastal fishing village in a developing country will be overwhelmed if, in only a few decades, a rising sea level caused by global climate change inundates the community. This shows the importance of analyzing sustainability on a global as well as a local and regional scale.

A macroecological approach to sustainability science emphasizes how human socioeconomic systems at any scale depend on the flows of essential energy and material resources at the scale of the biosphere as a whole. The finite Earth system imposes absolute limits on the ecological processes and human activities embedded within it. The impossibility of continued exponential growth of population and resource use in a finite world has long been recognized [33–35]. But repeated failures to reach the limits in the predicted time frames have caused much of the economic establishment and general public to discredit or at least discount Malthusian dynamics. Now, however, there is increasing evidence that humans are pushing if not exceeding global limits [2,3,36,37]. For example, the Global Footprint Network estimates that the ecological footprint, the amount of land required to maintain the human population at a steady state [9], had exceeded the available land area by more than 50% by 2007, and the imbalance is increasing (http://www.footprintnetwork.org/en/index.php/GFN).

Here we present additional evidence that humans have approached or surpassed the capacity of the biosphere to provide essential and often non-substitutable natural resources. Figure 3 plots trends in the total and per capita use of agricultural land, fresh water, fisheries, wood, phosphate, petroleum, copper, and coal, as well as gross domestic product (GDP), from 1961 to 2008. Note that only oil, copper, coal, and perhaps fresh water show consistent increases in total consumption. Consumption of the other resources peaked in the 1980s or 1990s and has since declined. Dividing the total use of each resource by the human population gives the per capita rate of resource use, which has decreased conspicuously for all commodities except copper and coal. This means that production of these commodities has not kept pace with population growth. Consumption by the present generation is already "compromising the ability of future generations to meet their own needs." And this does not account for continued population growth, which is projected to increase the global population to 9–10 billion by 2050 and would result in substantial further decreases in per capita consumption.

Figure 3 shows results consistent with other analyses reporting "peak" oil, fresh water, and phosphate, meaning that global stocks of these important resources have been depleted to the point that global consumption will soon decrease if it has not already done so [10,37]. Decreased per capita consumption of essential resources might be taken as an encouraging sign of increased efficiency. But the increase in efficiency is also a response to higher prices as a result of decreasing supply and increasing demand. We have included plots for copper and coal to show that overall production of ***some*** more abundant commodities has kept pace with population growth, even though the richest stocks have already been exploited. This is typical in ecology: not all essential resources are equally limiting at any given time. Diminishing supplies of some critical

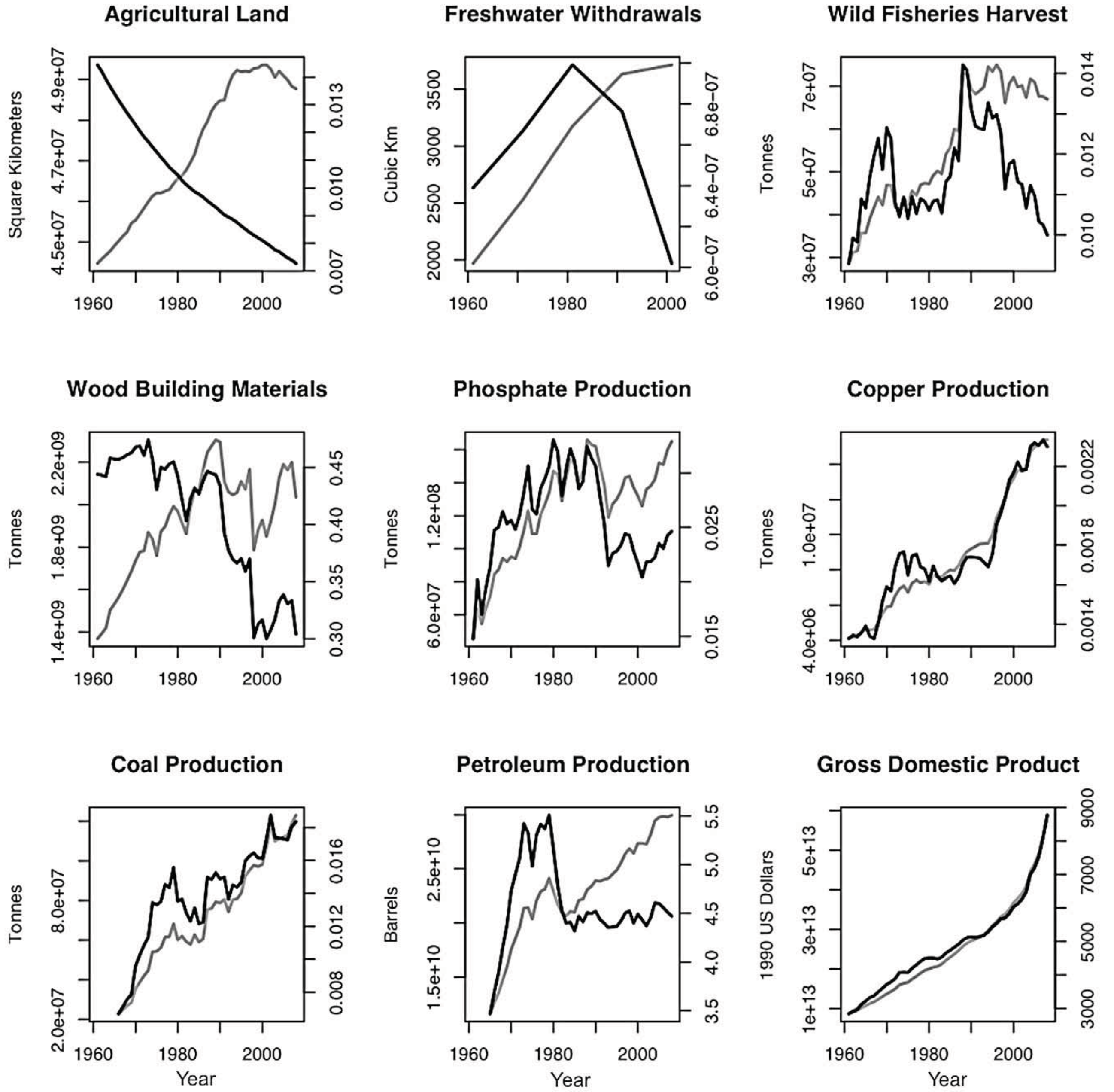

Figure 3. Global trends in total and per capita consumption of resources and GDP from 1961 to 2008. Total global use/production is represented by the grey line using the axis scale on the left side of each diagram. Per capita use/production is represented by the black line using the axis scale on the right side of each diagram. Per capita values represent the total values divided by global population size as reported by the World Resources Institute (http://earthtrends.wri.org/). The *y*-axes are untransformed and scaled to allow for maximum dispersion of variance. Individual sources for global use/production values are as follows: Agricultural land in square-km is from the World Development Indicators Database of the World Bank (http://data.worldbank.org/data-catalog/world-development-indicators) and represents the sum of arable, permanent crop, and permanent pasture lands (see also [46]). Freshwater withdrawal in cubic-km from 1960, 1970, 1980, and 1990 is from UNESCO (http://webworld.unesco.org/water/ihp/db/shiklomanov/part%273/HTML/Tb_14.html) and for 2000 from The Pacific Institute (http://www.worldwater.org/data.html). Wild fisheries harvest in tonnes is from the FAO Fishery Statistical Collection Global Capture Production Database (http://www.fao.org/fishery/statistics/global-capture-production/en) and is limited to diadromous and marine species. Wood building material production in tonnes is based on the FAO ForeSTAT database (http://faostat.fao.org/site/626/default.aspx), and represents the sum of compressed fiberboard, pulpwood+particles (conifer and non-conifer [C & NC]), chips and particles, hardboard, insulating board, medium density fiberboard, other industrial roundwood (C & NC), particle board, plywood, sawlogs+veneer logs (C & NC), sawnwood (C & NC), veneer sheets, and wood residues. Phosphate, copper, and combustible coal production in tonnes is based on World Production values reported in the USGS Historical Statistics for Mineral and Material Commodities (http://minerals.usgs.gov/ds/2005/140/). Global coal production data is limited to 1966–2008. Petroleum production in barrels from 1965 to 2008 is based on The Statistical Review of World Energy (http://www.bp.com/sectiongenericarticle800.do?categoryId=9037130&contentId=7068669) and represents all crude oil, shale oil, and oil sands plus the liquid content of natural gas where this is separately recovered. These data are reported in 1,000 barrels/day units, and were transformed to total barrels produced per year. GDP in 1990 US dollars are from the World Resources Institute (http://earthtrends.wri.org/). All data were accessed May 15–June 15, 2011.
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resources, such as oil, phosphorus, arable land, and fresh water, jeopardize the capacity to maintain even the current human population and standard of living.

What are the consequences of these trends? Many economists and sustainability scientists suggest that there is little cause for concern, at least in the short term of years to decades. They give several reasons: i) the finite stocks have not been totally exhausted, just depleted; there are still fish in the sea, and oil, water, phosphate, copper, and coal in the ground; they are just getting harder to find and extract; ii) conservation and substitution can compensate for depletion, allowing economies to grow and provide for increases in population and standard of living; iii) production depends more on the relationship between supply and demand as reflected in price than on absolute availability; and iv) the socioeconomic status of contemporary humans depends not so much on raw materials and conventional goods as on electronic information, service industries, and the traditional economic variables of money, capital, labor, wages, prices, and debt.

There are several reasons to question this optimistic scenario. First, the fact that GDP has so far kept pace with population does not imply that resource production will do likewise. Indeed, we have shown that production of some critical resources is not keeping pace. Second, there is limited or zero scope to substitute for some resources. For most of them, all known substitutes are inferior, scarcer, and more costly. For example, there is no substitute for phosphate, which is an essential requirement of all living things and a major constituent of fertilizer. No other element has the special properties of copper, which is used extensively in electronics. Despite extensive recycling of copper, iron, aluminum, and other metals, there is increasing concern about maintaining supplies as the rich natural ores have been depleted (e.g., [38], but see [39]). Third, several of the critical resources have interacting limiting effects. For example, the roughly constant area of land in cultivation since 1990 indicates that modern agriculture has fed the increasing human population by achieving higher yields per unit area. But such increased yields have required increased inputs of oil for powering machinery, fresh water for irrigation, and phosphate for fertilizer. Similarly, increased use of finite fossil fuels has been required to synthesize nitrogen fertilizers and to maintain supplies of mineral resources, such as copper, nickel, and iron, as the richest ores have been depleted and increased energy is required to extract the remaining stocks. An optimistic scenario would suggest that increased use of coal and renewable energy sources such as solar and wind can substitute for depleted reserves of petroleum, but Figure 3 shows a similar pattern of per capita consumption for coal as for other limiting resources, and the capacity of renewables to substitute for fossil fuels is limited by thermodynamic constraints due to low energy density and economic constraints of low energy and monetary return on investment [40–43]. Fourth, these and similar results (e.g., [3]) are starting to illuminate the necessary interdependencies between the energetic and material currencies of ecology and the monetary currencies of economics. The relationship between decreasing supply and increasing demand is causing prices of natural resources to increase as they are depleted, and also causing prices of food to increase as fisheries are overharvested and agriculture requires increasing energy and material subsidies [2,8,43]. The bottom line is that the growing human population and economy are being fed by unsustainable use of finite resources of fossil fuel energy, fertilizers, and arable land and by unsustainable harvests of "renewable resources" such as fish, wood, and fresh water. Furthermore, attaining sustainability is additionally complicated by inevitable yet unpredictable changes in both human socioeconomic conditions and the extrinsic global environment [44]. Sustainability will always be a moving target and there cannot be a single long-term stable solution.

Most sustainability science focuses on efforts to improve standards of living and reduce environmental impacts at local to regional scales. These efforts will ultimately and inevitably fail unless the global system is sustainable. There is increasing evidence that modern humans have already exceeded global limits on population and socioeconomic development, because essential resources are being consumed at unsustainable rates. Attaining sustainability at the global scale will require some combination of two things: a decrease in population and/or a decrease in per capita resource consumption (see also [45]). Neither will be easy to achieve. Whether population and resource use can be reduced sufficiently and in time to avoid socioeconomic collapse and attendant human suffering is an open question.

Critics will point out that our examination of sustainability from a macroecological and natural science perspective conveys a message of "doom and gloom" and does not offer "a way forward". It is true that humanity is faced with difficult choices, and there are no easy solutions. But the role of science is to understand how the world works, not to tell us what we want to hear. The advances of modern medicine have cured some diseases and improved health, but they have not given us immortality, because fundamental limits on human biology constrain us to a finite lifespan. Similarly, fundamental limits on the flows of energy and materials must ultimately limit the human population and level of socioeconomic development. If civilization in anything like its present form is to persist, it must take account of the finite nature of the biosphere.

Conclusion

If sustainability science is to achieve its stated goals of "dealing with the interactions between natural and social systems" so as to "[meet] the needs of present and future generations while substantially reducing poverty and conserving the planet's life support systems", it must take account of the ecological limits on human systems and the inherently ecological nature of the human enterprise. The human economy depends on flows of energy and materials extracted from the environment and transformed by technology to create goods and services. These flows are governed by physical conservation laws. These flows rarely balance at local or regional scales. More importantly, however, because these systems are all embedded in the global system, the flows of critical resources that currently sustain socioeconomic systems at these scales are jeopardized by unsustainable consumption at the scale of the biosphere. These ecological relationships will determine whether "sustainability" means anything more than "green", and whether "future generations [will be able] to meet their own needs".

Supporting Information

Text S1 Supplementary data. Calculations for salmon nutrient inputs to terrestrial and riparian ecosystems.
(DOCX)

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References

1. Goodland R (1995) The concept of environmental sustainability. Ann Rev Ecol System 26: 1–24.
2. Rockström J, Steffen W, Noone K, Persson A, Chapin FS 3rd, et al. (2009) A safe operating space for humanity. Nature 461: 472–475.
3. Brown JH, Burnside WR, Davidson AD, DeLong JP, Dunn WC, et al. (2011) Energetic limits to economic growth. BioScience 61: 19–26.
4. Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277: 494–499.
5. Imhoff ML, Bounoua L, Ricketts T, Loucks C, Harriss R, et al. (2004) Global patterns in human consumption of net primary production. Nature 429: 870–873.
6. Haberl H, Erb KH, Krausmann F, Gaube V, Bondeau A, et al. (2007) Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proc Natl Acad Sci U S A 104: 12942–12947.
7. Pauly D, Watson R, Alder J (2005) Global trends in world fisheries: impacts on marine ecosystems and food security. Phil Trans Roy Soc B 360: 5–12.
8. Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314: 787–790.
9. Wackernagel M, Rees WE (1996) Our ecological footprint: reducing human impact on the earth. New Society Publications.
10. Gleick PH, Palaniappan M (2010) Peak water limits to freshwater withdrawal and use. Proc Natl Acad Sci U S A 107: 11155–11162.
11. Brundtland GH (1987) Our common future. World Commission on Environment and Development.
12. Burnside WR, Brown JH, Burger O, Hamilton MJ, Moses M, et al. (2012) Human macroecology: linking pattern and process in big picture human ecology. Biol Rev 87: 194–208.
13. Day JW Jr, Boesch DF, Clairain EJ, Kemp GP, Laska SB, et al. (2007) Restoration of the Mississippi Delta: lessons from hurricanes Katrina and Rita. Science 315: 1679–1684.
14. Moses ME, Brown JH (2003) Allometry of human fertility and energy use. Ecol Let 6: 295–300.
15. Day JW Jr, et al. (2009) Ecology in times of scarcity. BioScience 59: 321–331.
16. Odum HT (1971) Environment, power and society. New York: Wiley-Interscience.
17. Odum HT (2007) Environment, power, and society for the twenty-first century: the hierarchy of energy. Columbia University Press.
18. Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton: Princeton University Press.
19. Czúcz B, Gathman JP, Mcpherson GUY (2010) The impending peak and decline of petroleum production: an underestimated challenge for conservation of ecological integrity. Con Biol 24: 948–956.
20. Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proc Natl Acad Sci U S A 100: 6564–6568.
21. Hilborn R (2006) Salmon-farming impacts on wild salmon. Proc Natl Acad Sci U S A 103: 15277.
22. ADG&F (2010) Alaska historical commercial salmon catches, 1878–2010. Alaska Department of Game and Fish, Division of Commercial Fisheries.
23. Coupland G, Stewart K, Patton K (2010) Do you never get tired of salmon? Evidence for extreme salmon specialization at Prince Rupert harbour, British Columbia. J Anthro Arch 29: 189–207.
24. Cederholm CJ, Kunze MD, Murota T, Sibatani A (1999) A Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries 24: 6–15.
25. Gende SM, Edwards RT, Willson MF, Wipfli MS (2002) Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52: 917–928.
26. Naiman RJ, Bilby RE, Schindler DE, Helfield JM (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5: 399–417.
27. Schindler DE, Scheuerell MD, Moore JW, Gende SM, Francis TB, et al. (2003) Pacific salmon and the ecology of coastal ecosystems. Front Ecol Enviro 1: 31–37.
28. Schindler DE, Leavitt PR, Brock CS, Johnson SP, Quay PD (2005) Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology 86: 3225–3231.
29. International Council for Science (2002) Science and technology for sustainable development. Paris: International Council for Science.
30. Millenium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press.
31. Turner BL, Lambin EF, Reenberg A (2007) The emergence of land change science for global environmental change and sustainability. Proc Natl Acad Sci U S A 104: 20666–20671.
32. Hillman T, Ramaswami A (2010) Greenhouse gas emission footprints and energy use benchmarks for eight US cities. Environ Science & Tech 44: 1902–1910.
33. Malthus TR (1798) An essay on the principle of population. Prometheus.
34. Ehrlich PR (1968) The population bomb. New York.
35. Meadows DH (1972) The limits of growth. A report for The Club of Rome.
36. Holdren JP (2008) Science and technology for sustainable well-being. Science 319: 424–434.
37. Nel WP, Van Zyl G (2010) Defining limits: energy constrained economic growth. Applied Energy 87: 168–177.
38. Gordon RB, Bertram M, Graedel TE (2006) Metal stocks and sustainability. Proc Natl Acad Sci U S A 103: 1209–1214.
39. Kesler SE, Wilkinson BH (2008) Earth's copper resources estimated from tectonic diffusion of porphyry copper deposits. Geology 36: 255.
40. Fargione J, Hill J, Tilman D, Polasky S, Hawthorne P (2008) Land clearing and the biofuel carbon debt. Science 319: 1235–1238.
41. Hall CAS, Day JW (2009) Revisiting the limits to growth after peak oil. American Scientist 97: 230–237.
42. Smil V (2008) Energy in nature and society: general energetics of complex systems. MIT Press.
43. The Royal Society (2009) Reaping the benefits: science and the sustainable intensification of global agriculture. London: The Royal Society.
44. Milly PC, Betancourt J, Falkenmark M, Hirsch RM, Kundzewicz ZW, et al. (2008) Stationarity is dead: whither water management? Science 319: 573–574.
45. Cohen JE (1996) How many people can the earth support? WW Norton & Company.
46. Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, et al. (2011) Solutions for a cultivated planet. Nature 478: 337–342.

Energetic Limits to Economic Growth

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The human population and economy have grown exponentially and now have impacts on climate, ecosystem processes, and biodiversity far exceeding those of any other species. Like all organisms, humans are subject to natural laws and are limited by energy and other resources. In this article, we use a macroecological approach to integrate perspectives of physics, ecology, and economics with an analysis of extensive global data to show how energy imposes fundamental constraints on economic growth and development. We demonstrate a positive scaling relationship between per capita energy use and per capita gross domestic product (GDP) both across nations and within nations over time. Other indicators of socioeconomic status and ecological impact are correlated with energy use and GDP. We estimate global energy consumption for alternative future scenarios of population growth and standards of living. Large amounts of energy will be required to fuel economic growth, increase standards of living, and lift developing nations out of poverty.

Keywords: energy, economic growth, economy, human macroecology, scaling

The human species has an interesting duality. On the one hand, *Homo sapiens* is just another species, subject to the same scientific laws as the millions of other animals, plants, and microbes. On the other hand, humans are unique. No other species in the history of Earth has achieved such ecological dominance and created such complex socioeconomic systems. Because of this duality, humans have been studied by both natural and social scientists, but often from very different perspectives (Arrow et al. 2004).

In just a few thousand years the human population has colonized the entire world and grown to almost 7 billion. Humans now appropriate 20% to 40% of terrestrial annual net primary production, and have transformed the atmosphere, water, land, and biodiversity of the planet (Vitousek et al. 1997, Haberl et al. 2007). For centuries some have questioned how long a finite planet can continue to support near-exponential population and economic growth (e.g., Malthus 1798, Ehrlich 1968, Meadows et al. 1972). Recent issues such as climate change, the global decline in population growth rate, the depletion of petroleum reserves and resulting increase in oil prices, and the recent economic downturn have prompted renewed concerns about whether longstanding trajectories of population and economic growth can continue (e.g., Arrow et al. 2004). These serious issues fall within the purview of both the natural and social sciences—especially ecology and economics.

This article integrates perspectives from physics, ecology, and economics with an analysis of extensive global data to show how scientific laws governing the flows of energy in the biosphere affect socioeconomic activity. Our purpose is neither to pit ecology against economics nor to predict future population and economic trends; rather, we use theoretical perspectives from thermodynamics, allometry, and metabolic ecology (McMahon and Bonner 1983, Schneider and Kay 1995, Brown et al. 2004) and empirical approaches from macroecology (Brown 1995) to document energetic constraints on human ecology that have important implications for modern humans.

The central role of energy

Economic growth and development require that energy and other resources be extracted from the environment to manufacture goods, provide services, and create capital. The central role of energy is substantiated by both theory and data.

Key theoretical underpinnings come from the laws of thermodynamics: first, that energy can be neither created nor destroyed, and second, that some capacity to perform useful work is lost as heat when energy is converted from one form to another. Complex, highly organized systems, including human economies, are maintained in states far from thermodynamic equilibrium by the continual intake and transformation of energy (Soddy 1926, Odum 1971, Georgescu-Roegen 1977, Ruth 1993, Schneider and Kay 1995, Hall et al. 2001, Chen 2005, Smil 2008).

Empirically, the central role of energy in modern human economies is demonstrated by the positive relationship between energy use and economic growth (Shafiee and Topal 2008, Smil 2008, Payne 2010). Here, we take a macroecological perspective and quantify statistical relationships between energy use and economic activity for 220 nations over 24 years, using data from the International Energy Agency (IEA; *www.iea.org/stats/index.asp*) and World Resources Institute (WRI; *http://earthtrends.wri.org/index.php*). Per capita energy consumption for each country is calculated as the sum of human biological metabolism plus the energy obtained from

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all other sources. Individual biological metabolism was estimated from data on daily caloric intake for each country and converted to watts per individual. Energy use from all other sources, including fossil fuels and renewable energy supplies, was obtained from the IEA. For our measure of economic activity, we used the WRI's data for gross domestic product (GDP), the market value of all goods and services produced within a country per year (Mankiw 2006). Both energy use and GDP are expressed on a per capita basis. So, per capita GDP can be thought of as an index of an average individual's share of his or her country's economy, and per capita energy use as the power required to sustain that level of economic activity.

Figure 1 shows the relationship between energy use and GDP plotted on logarithmic axes, with each colored line indicating the trajectory for a single country over the period 1980–2003. A regression through the mean GDP, G for mean energy consumption and E for each country over the 24-year period, accounts for 76% of the variation. The fitted regression describes the scaling of per capita energy use with per capita GDP as a power law: $E = 4.13G^{0.76}$ (figure 1; see also figure S1c in supplemental online materials at *http://caliber.ucpress.net/doi/suppl/10.1525/bio.2011.61.1.7*). The sublinear slope, 0.76, indicates that the rate of per capita energy consumption associated with greater economic activity increases less rapidly than GDP itself. Countries with larger economies take advantage of economies of scale and new technologies to use energy more efficiently on a per capita basis (Hoffert et al. 1998). For example, there is both a positive relationship and an economy of scale between economic growth and the amount of infrastructure, such as roads, pipelines, and power lines, that distributes energy resources (Easterly and Rebelo 1993). The relationship between energy use and GDP holds across countries spanning the entire range of economic development from poorest to richest, encompassing two orders of magnitude in both energy use (100 to 10,000 watts) and wealth ($500 to $50,000).

A similar trend occurs within countries over time. The vast majority of nations we analyzed (74%) increased both energy use and GDP from 1980 to 2003 and exhibited positive correlations across the 24 years (mean slope = 0.59; 95% confidence interval = 0.45–0.72; figure 2; see also figure S1 at *http://caliber.ucpress.net/doi/suppl/10.1525/bio.2011.61.1.7*). Countries notable for sustained recent development, such as

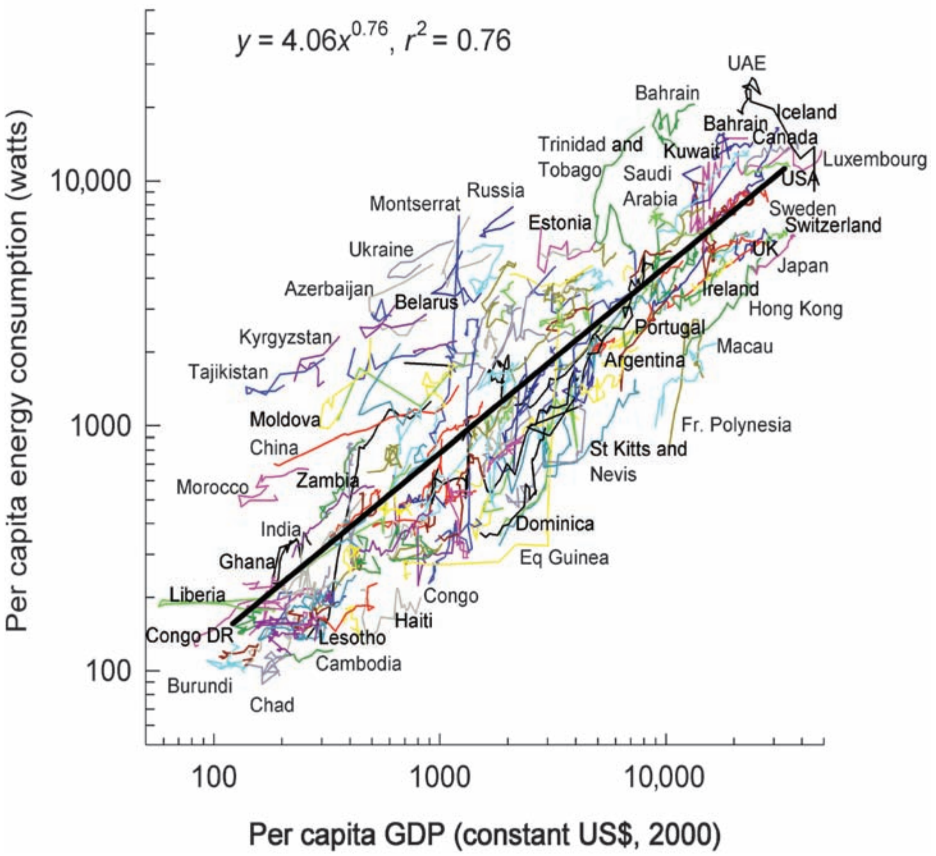

*Figure 1. The relationship between per capita energy use and per capita gross domestic product (GDP; in US dollars) of countries, plotted on logarithmic axes, from 1980 to 2003. Note that the slope or exponent, 0.76 (95% confidence interval: 0.69–0.82), is close to three-quarters, which is the canonical value of the exponent for the scaling of metabolic rate with body mass in animals. If per capita GDP is taken as the size of an average individual's economy and per capita energy use as the rate of energy consumption required to support that economy, this relationship may not be coincidental. Total per capita energy consumption is calculated as the caloric intake of humans (about 130 watts) plus the energy derived from all other sources, including fossil fuels and renewables. The thin colored lines show trends for individual countries from 1980 to 2003. The thick black line is a regression model fit to the mean values for each nation during this period. GDP data are from the World Resources Institute (*http://earthtrends.wri.org/index.php*). Total energy consumption data are calculated from the sum of energy consumption from eating (data from the World Resources Institute) plus all other sources of energy consumed for other purposes such as utilities, manufacturing, and transportation. Source: Data are from the International Energy Agency at* www.iea.org/stats/index.asp.

China and India, show trajectories of continually increasing energy use. The patterns in figures 1 and 2 are consistent with the increasing energy use that fueled socioeconomic development throughout history (Tainter 1988, Smil 2008). For example, from 1850 to 2000, while the global human population grew fivefold, world energy use increased 20-fold and fossil fuel use rose more than 150-fold (Holdren 2008).

The relationship between energy use and GDP depicted in figure 1 raises several important issues. One is the considerable variation around the regression line: Countries with similar per capita GDPs differ by more than an order of magnitude in per capita energy consumption. We did not analyze this residual variation quantitatively, although it would be illuminating to do so. For example, several oil-exporting nations (e.g., the United Arab Emirates, Bahrain, Tajikistan, and Azerbaijan) are consistent outliers, with high values of energy use relative to GDP. We hypothesize that much of this energy is used to extract oil that is then exported to and consumed by industrialized nations. Although the United States is among the countries with highest per capita energy use, several other developed countries have comparably high values. We hypothesize that in some of them, such as Iceland, Sweden, and Norway, large quantities of energy are used to heat houses and workplaces during cold winters at high latitudes.

Additionally, some of the variation in figure 1 may reflect error or a lack of standardization in the ways different countries have calculated energy use and GDP. The data sources that we used (IEA and WRI), although probably the best available, have their limitations. The original data are self-reported by the countries, and some of the abrupt, seemingly inexplicable changes in the trajectories in figure 1 may simply reflect errors or changing methods of estimating energy use, GDP, or both. One strength of our macroecological approach (Brown 1995), however, is that the hundreds of data points distributed over orders of magnitude variation mean that modest errors and other sources of uncontrolled noise in the data do not obscure the strong signals that are manifest in the robust patterns within and across countries over time.

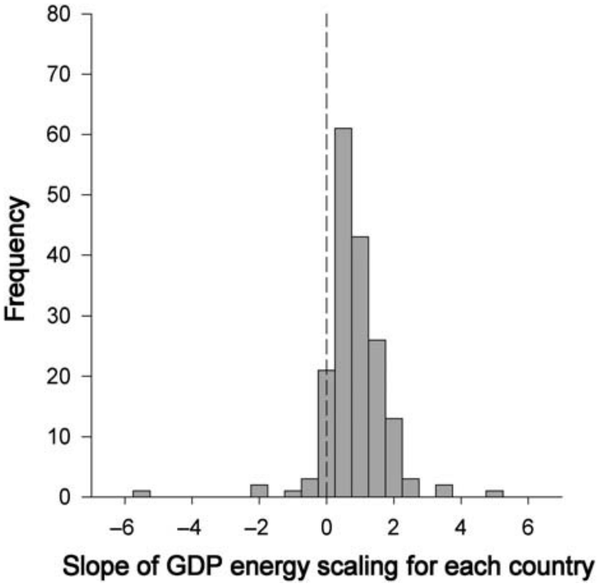

*Figure 2. The frequency distribution of exponents (slopes from log-log plots) of economic trajectories of per capita energy use as a function of per capita gross domestic product (GDP) within countries over the time series from 1980 to 2003. The average slope is approximately 0.6 and nearly all countries showed positive growth over the 24-year period. Source: Data are from the World Resources Institute (*http://earthtrends.wri.org/index.php*) and the International Energy Agency (*www.iea.org/stats/index.asp*).*

Another question is, what are the independent and dependent variables? Does energy use support economic development or does economic development drive energy consumption? Financial and energy economists have used econometric techniques to analyze time series of energy consumption and economic growth within countries in an effort to assess causal relationships, but they have reached no clear consensus about whether energy use causes economic growth, or vice versa (see Mahadevan and Asafu-Adjaye 2007, Payne 2010). By analogy to biological allometry, we plotted per capita energy use as the dependent variable and per capita GDP as the independent variable; this is analogous to plotting the rate of energy use of an animal as a function of its body size. The exponent for the scaling of energy use as a function of GDP, 0.76, is reminiscent of the three-quarter-power scaling of metabolic rate with body mass in animals (Kleiber 1961, McMahon and Bonner 1983). This may not be coincidental. In a very real sense both animals and economies have "metabolisms." Both consume, transform, and allocate energy to maintain complex adaptive systems far from thermodynamic equilibrium. The energy and other resources that sustain these systems are supplied by hierarchically branching networks, such as the blood vessels and lungs of mammals and the oil pipelines, power grids, and transportation networks of nations. Models of these networks suggest that three-quarter-power scaling optimizes distribution of resources (West et al. 1997, Banavar et al. 2010).

Some may be concerned that the relationships in figures 1 and 2 are "just correlations" that do not necessarily imply any underlying mechanism or causality. We disagree. All science is ultimately based on correlations—between dependent and independent variables, model predictions and empirical measurements, or experimental treatments and controls. Any mechanism or causation comes from logical inference. We infer that energy limits economic activity through direct causal mechanisms. The evidence for this inference is presented above and comes from three sources: (1) theory, the application of the second law of thermodynamics to complex adaptive systems; (2) data, the robust relationship between per capita energy use and per capita GDP across both space (the 220 nations of the world) and time (24 years); and (3) analogy, the similarity between biological and socioeconomic metabolism. We find the last to be especially compelling. Just as a body has a metabolism that burns food energy to survive and grow, a city or national economy has a metabolism that must burn fuel in order to sustain itself and grow. Just as higher metabolic rates are required to sustain and grow larger, more complex bodies (Kleiber 1961, McMahon and Bonner 1983), so higher rates of energy consumption are required to sustain and grow larger, more developed economies that provide greater levels of technological development and higher standards of living.

Quantitative relationships among energy use, GDP, and other socioeconomic indicators

Some may be concerned that the relationships in figures 1 and 2 do not reflect what is "really important," which might be some aspect of quality of life rather than GDP. However, nearly all measures of economic activity and standard of living are closely correlated with both GDP and energy use (figure 3; for additional variables, see figure S2 in the supplemental online materials at *http://caliber.ucpress.net/doi/suppl/10.1525/bio.2011.61.1.7*). These include measures of nutrition, education, health care, resource use, technology, and innovation. These relationships are not surprising and reflect mechanistic underpinnings. It takes money and energy to train engineers, MDs, and PhDs; to produce vaccines, drugs, and medical equipment; and to construct and maintain road, rail, airplane, cell phone, and Internet networks, hospitals and research centers, parks and conservation areas, and modern buildings and cities. The ecological footprint, an aggregate measure of per capita resource consumption and waste production, also increases with energy use and GDP (figure 3; Dietz et al. 2007). Figure 3 shows that it has not been possible to increase socially desirable goods and services substantially without concomitantly increasing the consumption of energy and other natural resources and without increasing environmental impacts that now include climate change, pollution, altered biogeochemical cycles, and reduced biodiversity.

Energetic implications for future economic growth

These empirical patterns, together with their theoretical underpinnings, raise the question of whether economic growth and associated increases in human population, resource use, technological development, and standard of living can continue their present trajectories (Grossman and Krueger 1995, Ausubel 1996). In figure 4 we develop some quantitative scenarios. We caution that these are not intended to be predictions of the future; rather, they are extrapolations of the power-law relationship shown in figure 1 to estimate the quantity of energy that would be required to support different global populations and levels of economic development. So, for example, raising the current global population to the standard of living in the United States would require a nearly fivefold increase in the rate of energy consumption, from 17 to 77 terawatts (1 terawatt $= 10^{12}$ watts). Population growth must also be considered in any future scenario. To support a projected global population of 9.5 billion in 2050 with an average standard of living equivalent to the current US lifestyle would require about 268 terawatts, 16 times the current global energy use. Even maintaining this increased population at the more modest Chinese standard of living would require 2.5 times more energy than is used today (figure 4).

There are good reasons, however, such simple scenarios based on extrapolations of current population and economic trends may be imprecise. Our calculations incorporate the economy of scale implicit in the nonlinear scaling of energy use with GDP, but do not take into account many potentially important factors, such as greater efficiency that may be triggered by energy shortages; technological innovations that may increase energy supplies; and socioeconomic, demographic, and behavioral changes. Indeed, the global human socioeconomic system is complex, poised far from thermodynamic equilibrium by high rates of energy input and transformation. Such systems have unpredictable nonlinear dynamics, making it nearly impossible to predict very far into the future (Schneider and Kay 1995).

One thing is clear: If the relationships depicted in figures 1–3 characterize fundamental causal relationships among the rate of energy use, level of economic activity, and standard of living, then additional economic growth and development will require some combination of (a) increased energy supply, (b) decreased per capita energy use, and (c) decreased human population. We consider each in turn.

Increased energy supply. The sources of energy that may be used to support future economic growth include finite stocks of fossil fuels as well as nuclear, renewable, and other proposed but unproven technologies. Fossil fuels currently provide 85% of humankind's energy needs (figure 5), but they are effectively fixed stores that are being depleted rapidly (Heinberg 2003, IEA 2008, Hall and Day 2009). Conventional nuclear energy currently supplies only about 6% of global energy; fuel supplies are also finite, and future developments are plagued by concerns about safety, waste storage, and disposal (Nel and Cooper 2009). A breakthrough in nuclear fusion, which has remained elusive for the last 50 years, could potentially generate enormous quantities of energy, but would likely produce large and unpredictable socioeconomic and environmental consequences. Solar, hydro, wind, and tidal renewable energy sources are abundant, but environmental impacts and the time, resources, and expenses required to capture their energy limit their potential (Hall and Day 2009). Biofuels may be renewable, but ecological constraints and environmental impacts constrain their contribution (Fargione et al. 2008). More generally, most efforts to develop new sources of energy face economic problems of diminishing returns on energy and monetary investment (Hall et al. 1986, Tainter 1988, Allen et al. 2001, Tainter et al. 2003).

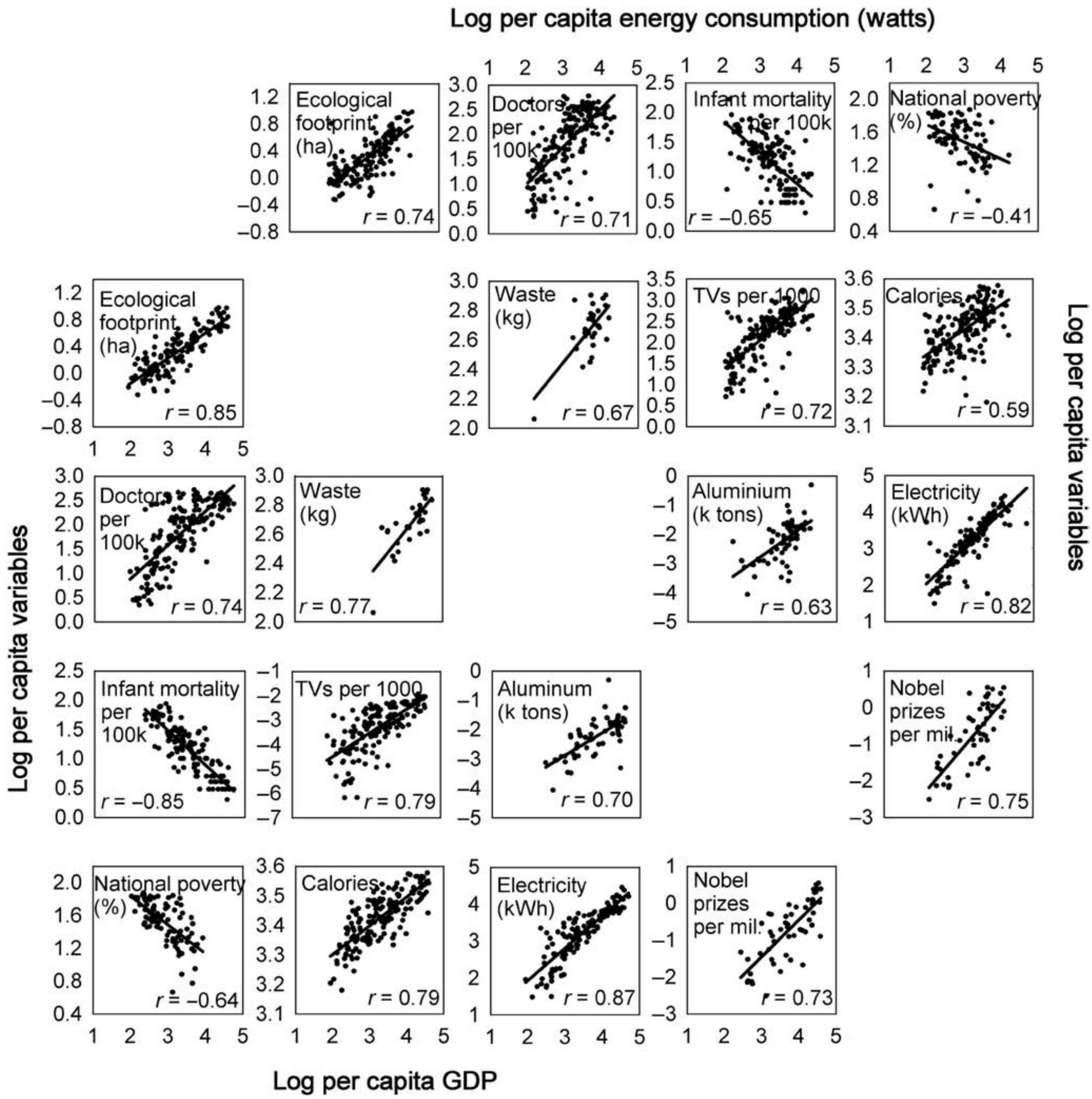

*Figure 3. Variables reflecting socioeconomic status and standard of living are strongly correlated with per capita energy use (upper panels) and per capita gross domestic product (GDP; lower panels). The variables include measures of health and wellness (population growth rate, doctors per 100,000 people, life expectancy, infant mortality, caloric intake, national poverty), energy use (electricity [kilowatt hours], residential energy [kilograms of oil equivalent]), resource consumption (meat, televisions, aluminum [kilotons], waste [kilograms]), intellectual and technological contributions (Nobel Prizes, patents), and ecological impacts (ecological footprint [in hectares]). All correlations (*r*) are significant (*P* < 0.05). Data sources are provided in supplemental online materials.*

Decreased per capita energy use. The Malthusian-Darwinian dynamic that has shaped the evolution of human behavior and demography has created powerful tendencies for individuals and societies to exploit all available resources and use all available technologies to enhance personal status, biological fitness, and societal wealth (Lotka 1922). Poor people migrate to cities and to other countries to improve their prospects. Citizens of developing countries such as China and India are not usually satisfied with the status quo, and understandably want to live like those in the de-

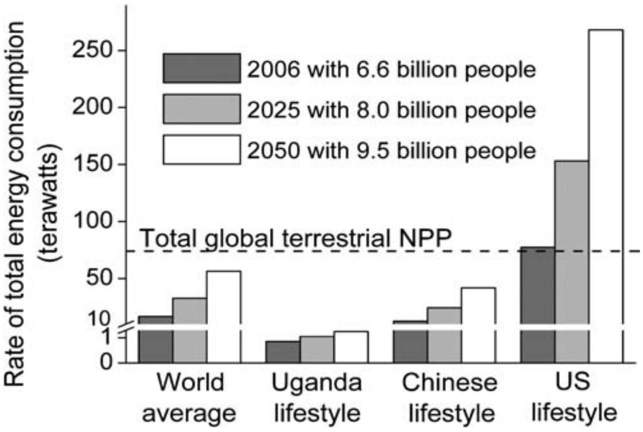

Figure 4. Current and projected global energy consumption based on alternative scenarios of population growth (2006, 2025, and 2050) and standard of living (equivalent to contemporary Uganda, China, and United States). Dashed line is total global terrestrial net primary productivity (NPP), 75 terawatts (Haberl et al. 2007). Data sources and calculation methods can be found in supplemental online materials.

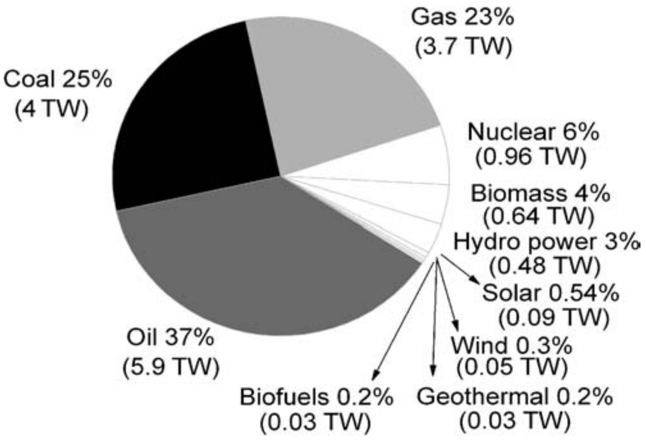

Figure 5. Sources of energy currently consumed by the global human economy. Total annual consumption is approximately 15.9 terawatts (TW, 1 terawatt = 10^{12} watts), of which about 85% comes from fossil fuels, 6% from nuclear energy, and the remaining 9% from solar, hydro, wind, and other renewable sources (BP 2009, REN21 2009).

veloped world. People in the richest nations are reluctant to sacrifice economic growth—much less give up their automobiles, electronics, and organ transplants—so that people in poorer countries can have bicycles, personal computers, and flu shots.

Decreased human population. With growing standards of living and rates of energy use, parents tend to invest more resources in fewer children (Moses and Brown 2003). This trade-off between the number and quality of offspring contributes to demographic transitions, where family size and the rate of population growth decrease with increasing economic development (Thompson 1929). The global population growth rate has declined in the last decade, but only a few developed countries currently have zero or negative population growth (WRI, *http://earthtrends.wri.org/index.php*). The relationship between family size and per capita energy use suggests that five times the current rates of energy supply will be required to achieve a global level of socioeconomic development capable of stabilizing the human population without infringing on the freedom of individuals to have as many children as they choose (Moses and Brown 2003, DeLong et al. 2010).

The bottom line is that an enormous increase in energy supply will be required to meet the demands of projected population growth and lift the developing world out of poverty without jeopardizing current standards of living in the most developed countries. And the possibilities for substantially increasing energy supplies are highly uncertain. Moreover, the nonlinear, complex nature of the global economy raises the possibility that energy shortages might trigger massive socioeconomic disruption. Again, consider the analogy to biological metabolism: Gradually reducing an individual's food supply leads initially to physiological adjustments, but then to death from starvation, well before all food supplies have been exhausted.

Mainstream economists historically have dismissed warnings that resource shortages might permanently limit economic growth. Many believe that the capacity for technological innovation to meet the demand for resources is as much a law of human nature as the Malthusian-Darwinian dynamic that creates the demand (Barro and Sala-i-Martin 2003, Durlauf et al. 2005, Mankiw 2006). However, there is no scientific support for this proposition; it is either an article of faith or based on statistically flawed extrapolations of historical trends. The ruins of Mohenjo Daro, Mesopotamia, Egypt, Rome, the Maya, Angkor, Easter Island, and many other complex civilizations provide incontrovertible evidence that innovation does not always prevent socioeconomic collapse (Tainter 1988, Diamond 2004).

Conclusions

We are by no means the first to write about the limits to economic growth and the fundamental energetic constraints that stem directly from the laws of thermodynamics and the principles of ecology. Beginning with Malthus (1798), both ecologists and economists have called attention to the essential dependence of economies on natural resources and have pointed out that near-exponential growth of the human population and economy cannot be sustained indefinitely in a world of finite resources (e.g., Soddy 1922, Odum 1971, Daly 1977, Georgescu-Roegen 1977, Cleveland et al. 1984, Costanza and Daly 1992, Hall et al. 2001, Arrow et al. 2004, Stern 2004, Nel and van Zyl 2010). Some ecological economists and systems ecologists have made similar theoretical arguments for energetic constraints on economic systems (e.g., Odum 1971, Hall et al. 1986). However, these perspectives have not been incorporated into mainstream economic theory, practice, or pedagogy (e.g., Barro and Sala-i-Martin 2003, Mankiw 2006), and they have been downplayed in consensus statements by influential ecologists (e.g., Lubchenco et al. 1991, Palmer et al. 2004, ESA 2009) and sustainability scientists (e.g., NRC 1999, Kates et al. 2001, ICS 2002, Kates and Parris 2003, Parris and Kates 2003, Clark 2007).

Our explicitly macroecological and metabolic approach uses new data and analyses to provide quantitative, mechanistic, and practically relevant insights into energetic limits on economic growth. We hope the evidence and interpretations presented here will call the attention of scientists, policymakers, world leaders, and the public to the central but largely underappreciated role of energetic limits to economic growth.

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References cited

Allen TFH, Tainter JA, Pires JC, Hoekstra TW. 2001. Dragnet ecology—“Just the facts, ma’am”: The privilege of science in a postmodern world. BioScience 51: 475–485.

Arrow K, Dasgupta P, Goulder L, Daily G, Ehrlich P, Heal G, Levin S, Schneider S, Starrett D, Walker B. 2004. Are we consuming too much? Journal of Economic Perspectives 18: 147–172.

Ausubel JH. 1996. Can technology spare the Earth? American Scientist 84: 166–178.

Banavar JR, Moses ME, Brown JH, Damuth J, Rinaldo A, Sibly RM, Maritan A. 2010. A general basis for quarter power scaling in animals. Proceedings of the National Academy of Sciences 107: 15816–15820.

Barro RJ, Sala-i-Martin X. 2003. Economic Growth. 2nd ed. MIT Press.

[BP] British Petroleum. 2009. BP Statistical Review of World Energy June 2006. BP. (11 October 2010; *www.bp.com/liveassets/bp_internet/globalbp/globalbp_uk_english/reports_and_publications/statistical_energy_review_2006/STAGING/local_assets/downloads/spreadsheets/statistical_review_full_report_workbook_2006.xls*)

Brown JH. 1995. Macroecology. University of Chicago Press.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. Ecology 85: 1771–1789.

Chen J. 2005. The Physical Foundation of Economics: An Analytical Thermodynamic Theory. World Scientific.

Clark WC. 2007. Sustainability science: A room of its own. Proceedings of the National Academy of Sciences 104: 1737–1738.

Cleveland CJ, Costanza R, Hall CAS, Kaufmann RK. 1984. Energy and the U.S. economy: A biophysical perspective. Science 225: 890–897.

Costanza R, Daly HE. 1992. Natural capital and sustainable development. Conservation Biology 6: 37–46.

Daly HE. 1977. Steady-state Economics. Freeman.

DeLong JP, Burger O, Hamilton MJ. 2010. Current demographics suggest that future energy supplies will be inadequate to slow human population growth. PLoS ONE 5: e13206. doi:10.1371/journal.pone.0013206

Diamond J. 2004. Collapse: How Societies Choose to Fail or Succeed. Viking Adult.

Dietz T, Rosa EA, York R. 2007. Driving the human ecological footprint. Frontiers in Ecology and the Environment 5: 13–18.

Durlauf SN, Johnson PA, Temple JRW. 2005. Growth econometrics. Pages 555–677 in Aghion P, Durlauf SN, eds. Handbook of Economic Growth. Elsevier.

Easterly W, Rebelo S. 1993. Fiscal policy and economic growth: An empirical investigation. Journal of Monetary Economics 32: 417–458.

Ehrlich P. 1968. The Population Bomb. Ballantine.

[ESA] Ecological Society of America. 2009. Ecological Impacts of Economic Activities. ESA. (14 October 2010; *www.esa.org/pao/economic_activities.php*)

Fargione J, Hill J, Tilman D, Polasky S, Hawthorne P. 2008. Land clearing and the biofuel carbon debt. Science 319: 1235–1238.

Georgescu-Roegen N. 1977. The steady state and ecological salvation: A thermodynamic analysis. BioScience 27: 266–270.

Grossman GM, Krueger AB. 1995. Economic growth and the environment. Quarterly Journal of Economics 110: 353–377.

Haberl H, Erb K-H, Krausmann F, Gaube V, Bondeau A, Plutzar C, Gingrich S, Lucht W, Fischer-Kowalski M. 2007. Quantifying and mapping the human appropriation of net primary production in Earth’s terrestrial ecosystems. Proceedings of the National Academy of Sciences 104: 12942–12947.

Hall CAS, Day JW Jr. 2009. Revisiting the limits to growth after peak oil. American Scientist 97: 230–237.

Hall CAS, Cleveland CJ, Kaufmann RK. 1986. Energy and Resource Quality: The Ecology of the Economic Process. Wiley.

Hall C, Lindenberger D, Kümmel R, Kroeger T, Eichhorn W. 2001. The need to reintegrate the natural sciences with economics. BioScience 51: 663–673.

Heinberg R. 2003. The end of the oil age. Earth Island Journal 18: 3.

Hoffert MI, et al. 1998. Energy implications of future stabilization of atmospheric CO_2 content. Nature 395: 881–884.

Holdren JP. 2008. Science and technology for sustainable well-being. Science 319: 424–434.

[ICS] International Council for Science. 2002. Report of the Scientific and Technological Community to the World Summit on Sustainable Development (WSSD). ICS. Report no. 1.

[IEA] International Energy Agency. 2008. World Energy Outlook 2008. Organisation for Economic Co-operation and Development and IEA.

Kates RW, Parris TM. 2003. Long-term trends and a sustainability transition. Proceedings of the National Academy of Sciences 100: 8062–8067.

Kates RW, et al. 2001. Environment and development: Sustainability science. Science 292: 641–642.

Kleiber M. 1961. The Fire of Life: An Introduction to Animal Energetics. Wiley.

Lotka AJ. 1922. Contribution to the energetics of evolution. Proceedings of the National Academy of Sciences 8: 147–151.

Lubchenco J, et al. 1991. The sustainable biosphere initiative: An ecological research agenda: A report from the Ecological Society of America. Ecology 72: 371–412.

Mahadevan R, Asafu-Adjaye J. 2007. Energy consumption, economic growth and prices: A reassessment using panel VECM for developed and developing countries. Energy Policy 35: 2481–2490.

Malthus TR. 1798. An Essay on the Principle of Population. Prometheus.

Mankiw NG. 2006. Macroeconomics. 6th ed. Worth.

McMahon TA, Bonner JT. 1983. On Size and Life. Scientific American Library.

Meadows DH, Meadows DL, Randers J, Behrens WW. 1972. The Limits to Growth: A Report for the Club of Rome’s Project on the Predicament of Mankind. Earth Island.

Moses ME, Brown JH. 2003. Allometry of human fertility and energy use. Ecology Letters 6: 295–300.

[NRC] National Research Council. 1999. Our Common Journey. The National Academies Press.

Nel WP, Cooper CJ. 2009. Implications of fossil fuel constraints on economic growth and global warming. Energy Policy 37: 166–180.

Nel WP, van Zyl G. 2010. Defining limits: Energy constrained economic growth. Applied Energy 87: 168–177.

Odum HT. 1971. Environment, Power and Society. Wiley.

Palmer M, et al. 2004. Ecology: Ecology for a crowded planet. Science 304: 1251–1252.

Parris TM, Kates RW. 2003. Characterizing a sustainability transition: Goals, targets, trends, and driving forces. Proceedings of the National Academy of Sciences 100: 8068–8073.

Payne JE. 2010. Survey of the international evidence on the causal relationship between energy consumption and growth. Journal of Economic Studies 37: 53–95.

[REN21] Renewable Energy Policy Network for the 21st Century. 2006. Renewables, Global Status Report: 2006 Update. REN21 Steering Committee.

Ruth M. 1993. Integrating Economics, Ecology, and Thermodynamics. Springer.

Schneider ED, Kay JJ. 1995. Order from Disorder: The Thermodynamics of Complexity in Biology. Pages 161–172 in Murphy MP, O'Neill LAJ, eds. What Is Life: The Next Fifty Years. Reflections on the Future of Biology. Cambridge University Press.

Shafiee S, Topal E. 2008. An econometrics view of worldwide fossil fuel consumption and the role of US. Energy Policy 36: 775–786.

Smil V. 2008. Energy in Nature and Society: General Energetics of Complex Systems. MIT Press.

Soddy F. 1922. Cartesian Economics: The Bearing of Physical Science upon State Stewardship. Hendersons.

———. 1926. Wealth, Virtual Wealth, and Debt: The Solution of the Economic Paradox. Omni.

Stern DI. 2004. Economic growth and energy. Pages 35–78 in Encyclopedia of Energy, vol 2. Academic Press.

Tainter JA. 1988. The Collapse of Complex Societies. Cambridge University Press.

Tainter JA, Allen THF, Little A, Hoekstra TW. 2003. Resource transitions and energy gain: Contexts of organization. Conservation Ecology 7: 4.

Thompson WS. 1929. Population. American Journal of Sociology 34: 959–975.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. Science 277: 494–499.

West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling laws in biology. Science 276: 122–126.

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CONCLUDING REMARKS

What does ‘mechanism’ mean within an ecological context? It is interesting to note the strongly negative reactions of some ecologists to even the idea that stochastic process may underlie a number of classic ecological patterns. There appear to be two main reasons ecologists have tended to reject stochastic mechanism when attempting to explain ecological pattern: they are ‘too’ random and they ‘have nothing to do with ecology’.

With regards to the first critique, why should pattern-producing random process not be considered a type of mechanism? This bias against stochastic models may be partly driven by the field of ecology having historically adopted a definition of ‘mechanism’ used by biological, molecular and cellular biologists, in which mechanism is quite explicit, concrete and deterministic – this protein bumps into that protein causing a conformation change and exposing an enzymatic site. But physics has seen a progression from deterministic laws such as those of Newton to the stochastic techniques and laws of Heisenberg and Schrödinger. Now as molecular and cellular biologists have begun scaling up into systems biology, stochastic models are of increasing importance. Why should ecology be any different? Perhaps the increasing incorporation of stochasticity is a sign of disciplinary maturity. Stochastic models should be seen as just another class of possible explanatory models that should be judged on their ability to elucidate our understanding of and make novel predictions about ecological systems.

Although almost never verbalized, it also seems likely that considerable resistance to stochastic thinking is also based on the “it has nothing to do with ecology” argument. Ecology is relatively unique as a field because many scientists choose their discipline not because they are enamored with the process of science but also because they are enthralled with the organisms they study and the landscapes those organisms live in. Few physicists felt a loss at reducing atoms to randomly colliding abstractions, but many ecologists feel a loss at similarly reducing organisms to grist for an abstract, general principle like the central limit theorem or maximum entropy. But therein lies an irreconcilable problem: many of the patterns ecologists like to hold up as their own, such as the species abundance distribution, species area relationship or distance decay of similarity are in fact frequently repeated across entirely non-ecological systems such as geology, meteorology, economics, computer science, sociology, and the arts. Are we willing to throw these essential ecological descriptors away as not being truly ‘ecological’? Or, should we be willing to accept mechanisms that are general enough to be common between all these fields?

Through my eclectic research program, I have rounded up my ‘blind men’ (the various fields that I conduct active research in) and asked them to report back on the nature of this thing called ‘ecology’. When viewed across multiple fields and types of observation, some general perspectives come into view – perspectives which are generally not articulated by practitioners in the field. Yet they appear to help define ‘ecology’:

(1) ***The more general the pattern the more likely its ultimate cause lies in statistical mechanics.*** In ecological subdisciplines like community ecology and macroecology – which by their vary nature consider hundreds to billions of interacting individuals and dozens to thousands of species – it is highly probable that almost all emergent pattern is

generated from principles of statistical mechanics. This realization underlies the fact that the distribution of species abundance is very similar to the distribution of drinking glass longevities and Cowboy Junkies song performances.

(2) ***Conversely, the smaller the system under investigation, and the more specific / idiosyncratic its patterns, the more likely it is governed by system-restricted process.*** Process restricted to purely ecological process (i.e. the interactions between individuals and their environment) is most apt to operate at the small scale including few interacting individuals and species and may not be generalizable. While typically such research has been dismissed (especially by theorists) as 'natural history' and 'just-so stories' yet it remains the most likely path to identifying ecological mechanism.

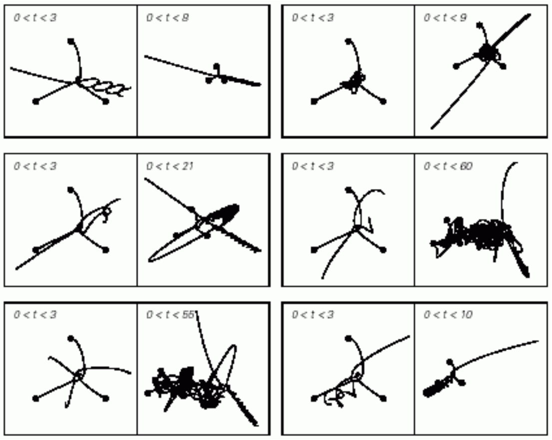
(3) ***The presence of deterministic mechanistic process at the small scale does not mean that the sum across all such processes at larger scales will not be stochastic.*** While the evolutionary trajectory for a given species or clade and the explicit makeup of a particular individual ecological community may well be explained via deterministic, mechanistic ecological process, the emergent patterns created across the larger system including these components may well take on patterns indicative of stochastic process. This will happen when individual mechanistic processes – and their individual/species-specific parameters – are themselves randomly distributed.

(4) ***The existence of universal patterns cannot be used to test for underlying mechanism beyond that of stochastic logic.*** The paradox that the same statistical distributions can be generated in model communities from complete resource competition or neutral models is explained by realizing both generate dynamical complexities, and it is these which generate expected patterns. In competition models complexity arises as multiple agents, each with individualistic resource utilization and dispersal functions, interact in an elaborate network with multiple other agents often over multiple temporal and spatial scales. Such interactions can be made even more complicated, but also more realistic, by inclusion of some degree of stochasticity in resource requirements and dispersal processes. In neutral models complexity arises as multiple agents, each with a unique community and metacommunity frequency, undergo a lottery process of replacement in space. These interactions are further complicated as new species are supplied to the system across multiple scales via dispersal and speciation.

(5) ***Important mechanistic insights may be gained by looking for differences in the parameterized values and functional form of universal distributions, and deviations of pattern from universal expectations.*** For instance, in the case of the species area relationship, it has long been recognized that differences in slope on continents vs. across archipelagos conveys information about the mechanisms that generate and maintain diversity. Similarly, distance decay rates provide vital information about niche characteristics and dispersal capacities in relation to the environmental template of spatial and temporal variation. So, for example, isolated spruce-fir forests of the Appalachians demonstrate an almost 3-fold greater DD rate as compared to continuous northern taiga, and large-fruited, more dispersal-limited plant species have almost twice the DD rate as compared to smaller-seeded taxa. And the shape of the distance decay relationship

informs about whether samples were collected within the same (power-law) or across different (exponential) communities. Important insights may also be gained by identifying domains where universal expectations are not generated, such as the lower than expected frequency of rare and abundant organisms in ecological communities vs. other complex systems.

(6) ***Efforts to accurately predict ecological outcomes, even at small deterministic scales, must be held with great suspect.*** The mathematics for >2 interacting individuals is highly complicated and falls within the framework of the Three Body Problem in astrophysics, which shows there is no single general outcome emerging from the gravitational interaction of 3 or more bodies (see right panel). Accurate prediction in such systems is entirely dependent upon exact knowledge of starting parameters, and as shown by the Heisenberg Uncertainty Principle and Observer Effects, such knowledge is impossible to obtain. While qualitative forecasts may be possible, precise, quantitative predictions of individual events pose great challenges. For example, it might be possible to predict qualitatively how community-wide species abundance distributions will be altered by invasions of multiple exotic species. It will be much more difficult, however, to predict the relative abundance and extent of spatial distribution of each exotic and native species. Indeed, such an effort may be as Quixotic as attempting to predict the exact date and magnitude of the next earthquake in the San Francisco Bay area or the price of a given stock in 2050. As in weather forecasting, while some level of short-term predictability will often be possible due to understanding current drivers, recent trajectories, and spatial/temporal autocorrelations, predictions will necessarily become increasingly imprecise as the forecast period increases. Rather than emphasizing prediction, ecologists perhaps should spend more effort on understanding the mechanisms and events that have conspired to generate current and past patterns. Even when it may be practically impossible to predict the future trajectory of a system, by looking backward it may be possible to deduce quite accurately when and how specific mechanisms came into play. In complex, human systems mechanisms are deduced by historians who analyze post hoc the particular combination of initial conditions and drivers that generated pattern. Similarly, community ecologists could enhance their understanding of the spatial and tempral patterns of biodiversity by becoming better natural historians, and using post hoc analysis to decipher how past events that have left a lasting influence on current conditions. While it may not be possible to predict future events with precision, by studying systems over time community ecologists may be able to establish what factors caused a particular outbreak of hantavirus or bird flu or simply whether Schrödinger's Cat survived.



(7) ***Statistical mechanics is not physics even though physicists got there first.*** Statistical mechanics simply represents the fundamental rules of logic for systems made of a large number of quasi-independent and variable parts. While this exists for physical systems (for instance the speed, trajectory, and atomic weights of gas molecules) it is even more applicable for ecological systems where agents possess many additional degrees of freedom. In some ways statistical mechanics may become even more fully expressed in ecological systems as compared to the simpler systems expressed by electrons, gasses, and fluids.

(8) ***When searching for mechanism for a given ecological pattern, we must first consider processes larger than ecology.*** These include: mathematical logic; statistical mechanics (mathematical logic of large stochastic systems); physical laws; and chemical laws. What is left unexplained after this ***may*** be due to explicit ecological process (the interaction of organisms with themselves and the physical environment).