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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 than 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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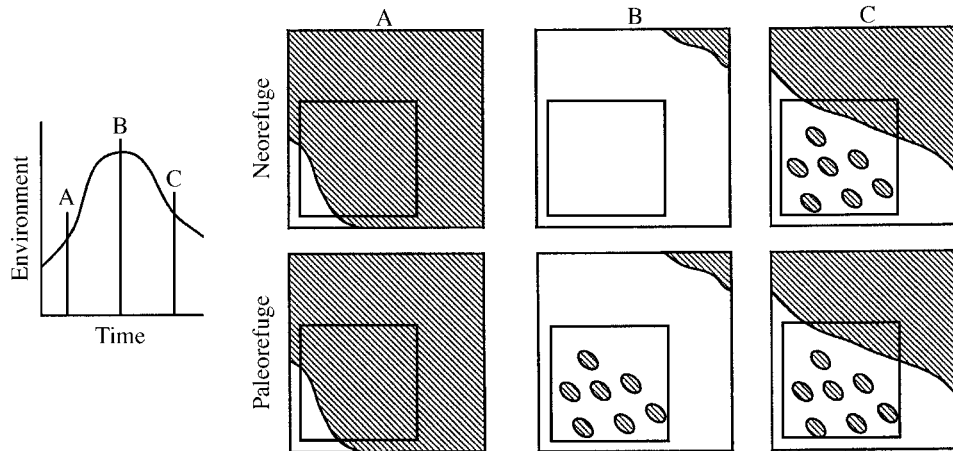


FIG. 1. Diagrammatic representation of the development of paleorefugia and neorefugia. At time period A, environmental conditions are conducive to the existence of a particular habitat (shaded). After critical environmental change (time period B), this habitat has retreated completely from the focal 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 contemporary 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 frag-

ments (MacArthur and Wilson 1967, Diamond 1975, Bierngaard 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 nun-tacks (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 frag-

mented following the close of Wisconsinan glaciation (paleoreugia). The importance of immigration in the development of the biota of young volcanic islands (neoreugia) 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 paleoreugia, whereas immigration will most influence the species composition of neoreugia. 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 paleoreugia than in neoreugia. Paleoreugia can be expected to have steeper species–area curves than neoreugia, because for a given-size island the paleoreuge will be approaching equilibrium number through species loss, whereas the neoreuge will be approaching this number through species accretion. Paleoreugia 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, Bierregaard et al. 1992). The species richness of neoreugia, 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, paleoreugia can be expected to have less variance around the species–area curve than neoreugia. This prediction may be violated for neoreugia 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 neoreugia than in paleoreugia. I expect this as propagule movement (and hence immigration rate) is largely a function of barrier width (Okubo and

Levin 1989). Thus, less-isolated neoreugia should have access to a larger propagule pool than more-isolated ones. This result would not be anticipated from paleoreugia 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 paleoreugia richness when recolonization from nearby sites (Brown and Kodric-Brown 1977) is important.

(3) Species richness should decrease over ecological time scales in paleoreugia, while increasing over similar time scales in neoreugia. Extinction, or “relaxation” (sensu Diamond 1975), should eliminate taxa from paleoreugia, 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 neoreugia 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 neoreugia and paleoreugia will converge. As time increases, immigration between neoreugia 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 paleoreugia, the stochastic loss of species may eventually lower site richness to levels anticipated for neoreugia. 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 neoreugia than for paleoreugia. 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, Fotheringham 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 paleoreugia 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 paleoreugia should be low within regions. However, because immigration is required for development of neoreugia 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.

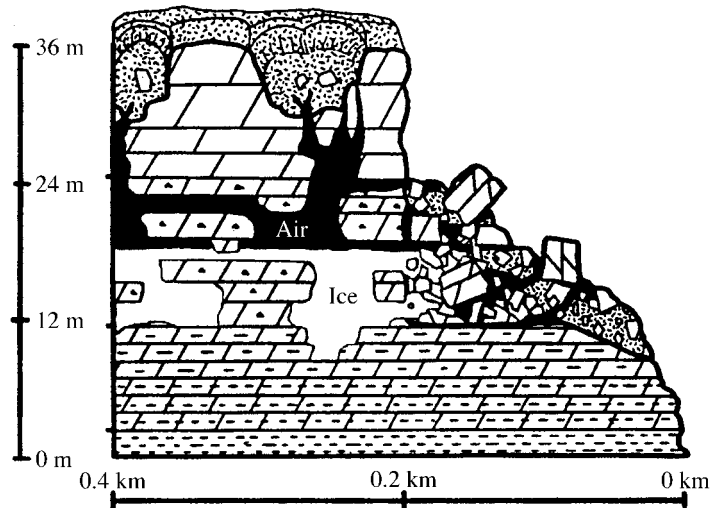
As is true for many ecological processes that operate over large spatial and temporal extents, collection of data to test these hypotheses may be difficult, or in some cases impossible. And, even if appropriate data exist, it may be equally difficult to control for confounding factors (Brown 1995). This 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 a 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, 1986a, 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

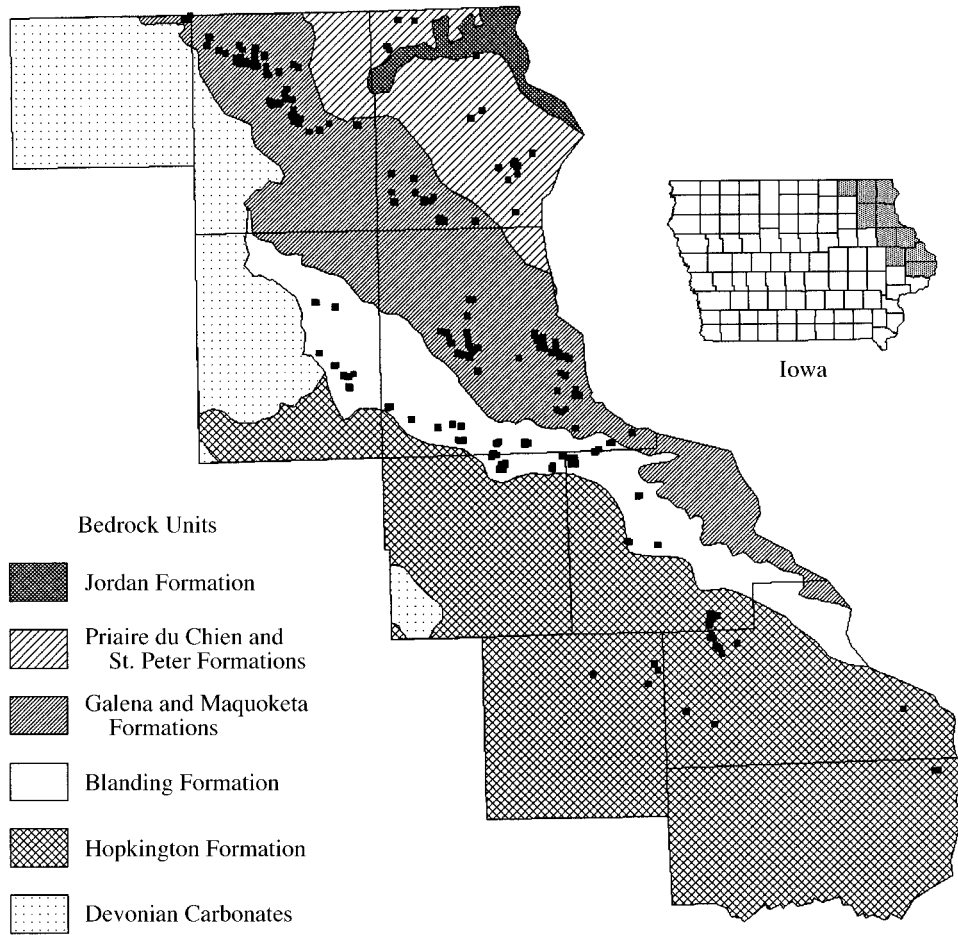


FIG. 3. Distribution of algific talus slopes and major bedrock units in northeastern Iowa, USA.

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 paleoreugia 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-*

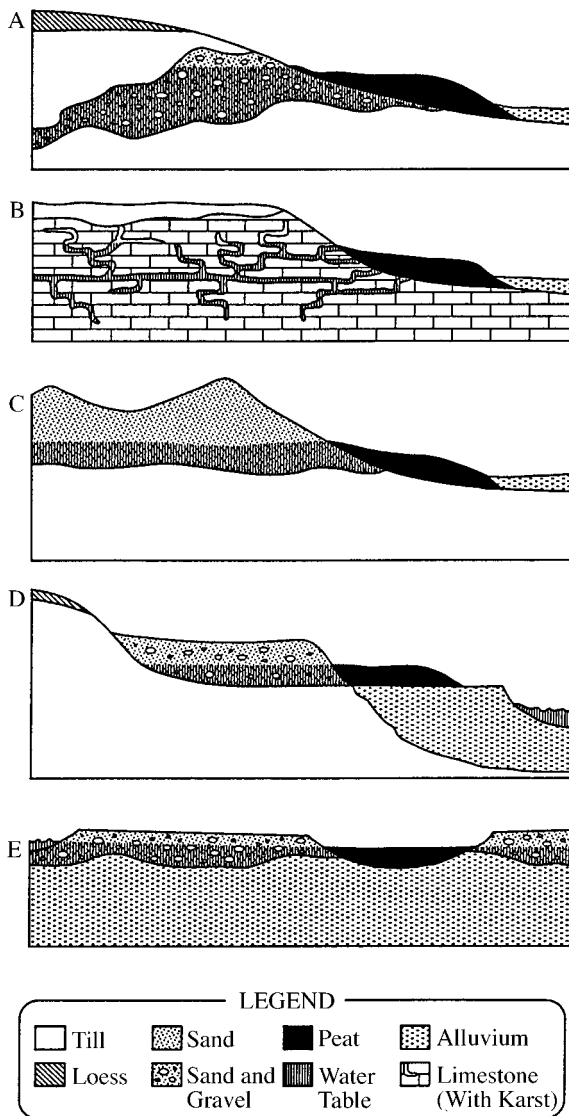


FIG. 4. Cross section of the five geologic features that give rise to fen formation in northeastern Iowa: (A) pre-Illinoian till sites, with groundwater seepage emanating from sand and gravel lenses interbedded between till units; (B) bedrock sites, with groundwater seepage emanating from fractured carbonate, 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. pedicularis*, *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

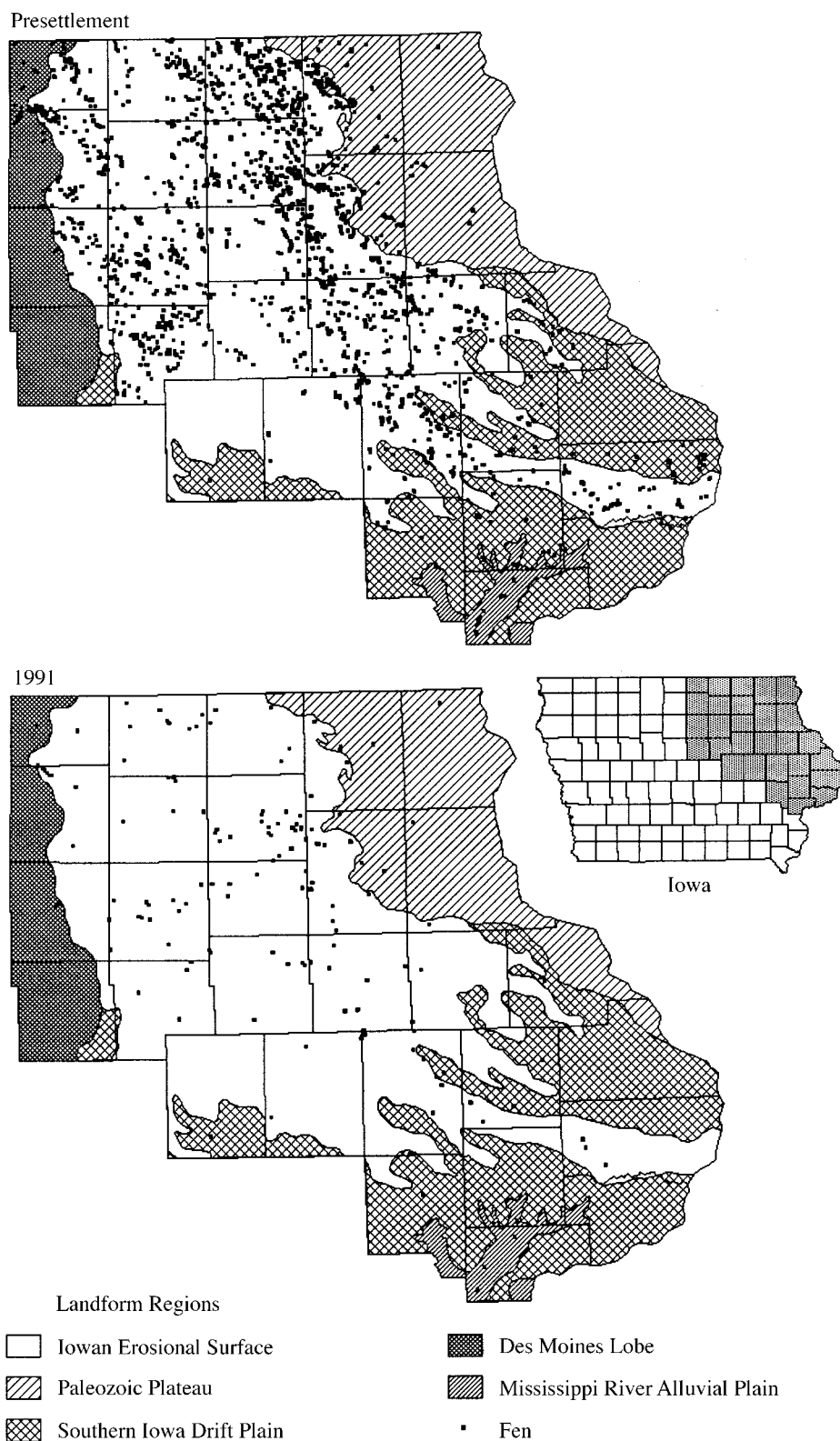


FIG. 5. Presettlement and 1991 distribution of northeastern Iowa fens within major landform boundaries, based on Prior (1991).

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

$$\begin{aligned} & \ln(\text{species richness} + 1) \\ &= \beta_0 + \beta_1(\ln(\text{habitat size})) + \beta_2(\text{habitat type}) \\ &+ \beta_3(\text{habitat type} \times \ln(\text{habitat size})) + \varepsilon \quad (1) \end{aligned}$$

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

$$\begin{aligned} \ln(\text{species richness} + 1) &= \beta_0 + \beta_1(\ln(\text{habitat size})) \\ &+ \beta_2(\text{isolation index}) + \varepsilon \quad (2) \end{aligned}$$

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

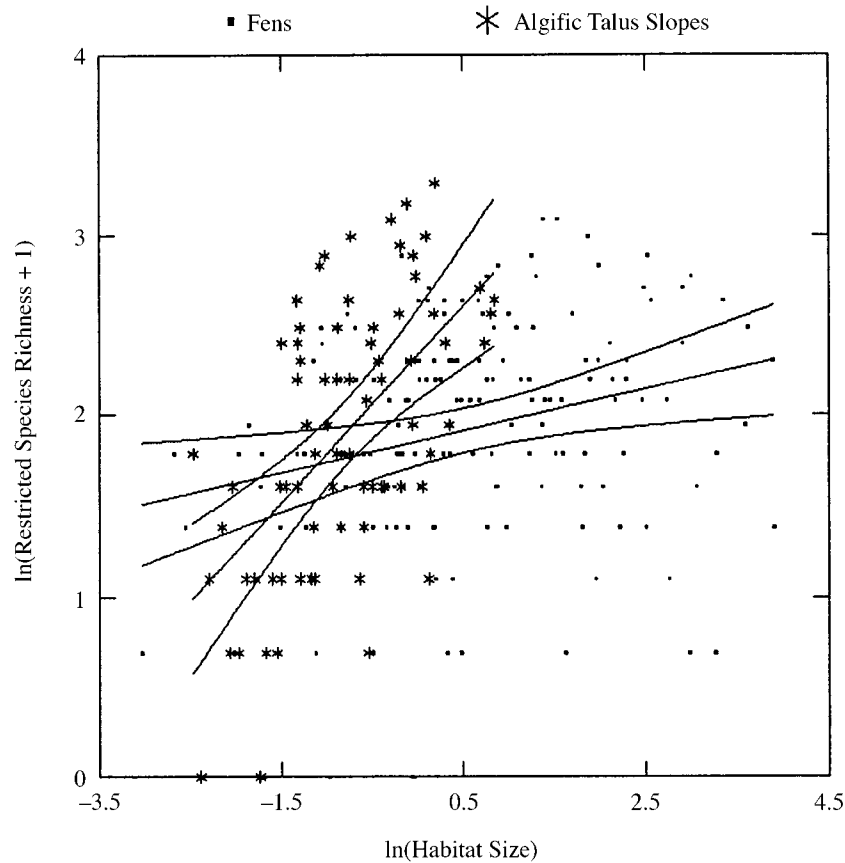


FIG. 6. Species–area curves (Eq. 1). Log-transformed restricted-species richness as a function of log-transformed habitat size for northeastern Iowa algific talus slope and fen habitats. Each group of three curves shows the position of best-fit regression line and 95% confidence interval around the mean 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 in-sample 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.

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 paleoreugia and neoreugia 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 neoreugia in one and a paleoreugia 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. Neoreugia and paleoreugia of very ancient origin may also demonstrate different biogeographic patterns. For instance, some ancient oceanic islands represent neoreugia (like the Hawaiian archipelago, which formed

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.

through volcanic eruptions) whereas others represent paleoreugia (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 neoreugia should allow for stronger species–isolation relationships, and different dispersal-strategy frequencies in their contemporaneous biota as compared to ancient oceanic paleoreugia. Hypotheses regarding paleoreugia and neoreugia 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 paleoreugia and neoreugia 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 prelim-

inary 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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