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REVIEW

Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective

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Summary

1. Are local ecological communities ever saturated with species? That is, do they ever reach a point where species from the regional pool are unable to invade the local habitat because of exclusion by resident species?
2. We review the theoretical evidence for saturation in various community models and find that non-interactive models predict the absence of saturation as expected, but that interactive models do not uniformly predict saturation.
3. Instead, models where coexistence is based on niche space heterogeneity predict saturation, whereas those where coexistence is based upon spatial heterogeneity yield mixed predictions.
4. Thus, theory says that species interactions are a necessary but not sufficient condition for local saturation in ecological time.
5. We then argue that unsaturated (Type I) assemblages are likely to be ubiquitous in nature and that even saturated (Type II) assemblages may not show hard limits to richness over evolutionary time-scales.
6. If local richness is not often saturated, then regional richness is freed from local constraint, and other limits on regional richness (which, in turn, limit local richness) become important, including phylogenetic diversification over evolutionary time-scales.
7. Our speculations inevitably suggest that the principal direction of control for species richness is from regional to local. If correct, then the key to community structure may lie in extrinsic biogeography rather than in intrinsic local processes, making community ecology a more historical science.

Key-words: species richness, ecological community, saturation, local richness, regional richness, community classification.

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Introduction

An interactive community is one in which strong biotic interactions take place among species at the same trophic level within a local habitat. In a non-interactive community, local interactions are feeble or absent. Traditionally, interactive communities held a central place in the development of community theory, but evidence suggests that real communities lie on a continuum from interactive to non-interactive (e.g. Ross 1957; Caswell 1976; Rathcke 1976; Taylor 1979; Price 1980; Strong, Lawton & Southwood 1984; Schoener 1986, 1989; Ricklefs 1987; Lawton & Gaston 1989; Mahdi, Law & Willis 1988; Compton, Lawton & Rashbrook 1989) and that for some groups such as phytophagous insects, non-interactive communities may be the norm (Strong, Lawton & Southwood 1984).

The terms 'local' and 'regional' refer to the spatial scales at which ecological and biogeographic processes, respectively, predominate. Thus predation, parasitism, competition, and abiotic fluctuation or disturbance are played out within local arenas, whereas long-distance dispersal, speciation, widespread extinction, and fluctuation in species' distributions take place across broad geographic regions

Biogeographic regions generally extend over continental or subcontinental areas, but local arenas must be small enough that individuals can move among populations in different local habitats. The scale of the local habitat depends upon the taxon in question. It may be a 100 m^2 old field for an assemblage of herbivorous insects, a 1-ha pond for dragonflies or salamanders, or a several hectare woodland for a guild of foliage-gleaning birds. The scale of the local habitat will generally increase for taxa having larger body sizes and wider home ranges.

The distinction between local and regional spatial scales is important because the relative impact of ecological vs. biogeographical processes on community structure depends in part on the intensity of interactions within the local habitat. In an interactive community, local processes play a key role in structuring the species assemblage. In a non-interactive community, weak biotic interactions are overshadowed by the history of colonization from the surrounding region. Species richness and taxonomic composition of non-interactive communities will thus depend more upon the size and composition of the regional pool of colonists than upon such processes as niche packing and competitive dominance.

It follows that interactive and non-interactive local assemblages should differ in their tendency to be saturated with species. At one extreme on the continuum, non-interactive communities contain excess niche space and therefore will not be saturated. At the other extreme, niche space is limited and interactive communities saturate with species. But interactions alone are *not* sufficient to produce a locally saturated community. A major purpose of this review is to examine theoretical and empirical evidence for saturation in local assemblages of interacting species.

In unsaturated communities, similar habitats with richer regional colonization pools exhibit commensurately richer local assemblages (Type I, Fig. 1), a pattern we call 'proportional sampling'. Proportional sampling means that local richness is dependent upon the regional pool and independent of biotic interactions which may be occurring in a habitat.

Common sense suggests that given a sufficiently large regional pool, all communities must reach an upper limit to local species richness (Type II, Fig. 1). However, it is an open question how frequently such limits are reached in nature. Even if the regional pool is extraordinarily rich, local saturation may still not occur. Species-rich taxa in areas of high regional diversity such as the fynbos heath-flora of Southern Africa (Kruger 1979; Cody 1986; Huntly 1988, 1989) and the Indo-Pacific coral reefs (Ladd 1960; Schilder 1965; Kohn 1967; Stehli & Wells 1971; Goldman & Talbot 1976) often have much higher local diversities than their counterparts elsewhere. The existence of these extremely rich local and regional assemblages raises the question whether even the richest communities (i.e. those in the traditional view, most likely to experience strong biotic interactions) have hard upper limits to the number of coexisting species. If not, then the key to community structure for both interactive and non-interactive assemblages may lie in extrinsic biogeography rather than in intrinsic local processes, making community ecology a more historical science.

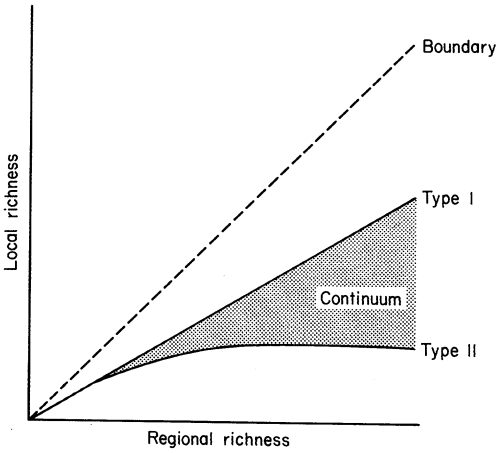

Fig. 1. Two theoretical curves for the relationship between local and regional richness in ecological communities. In Type I communities, local richness is independent of biotic interactions occurring in the local habitat and increases proportionately with regional richness, a pattern we call 'proportional sampling'. In Type II communities, biotic interactions limit local richness which then saturates and becomes independent of regional richness. Real communities probably fall on a continuum between these two extremes.

We intend to address the saturation question here by arguing that Type I assemblages are ubiquitous and that even Type II assemblages may not show hard limits to diversity over evolutionary time-scales. First, we review various community theories concerned with the maintenance of local richness in ecological time. The theories chosen are not a complete list, but are representative of the range of existing models. Some of these theories predict saturation whereas others do not. Then, we review the empirical evidence for saturation in real communities. Finally, we shift to an evolutionary context and review the factors contributing to regional richness, the role of evolution in setting hard limits to species richness, and the probable independence of regional proliferation of biotas from local constraint. The literature on many of these topics is very large; our selection is illustrative, not exhaustive, and emphasizes the theoretical framework at the expense of a complete review of empirical examples.

A classification of communities

Theoretical models of communities may be classified on a continuum from interactive to non-interactive, depending upon the amount of unused niche space available.

NON-INTERACTIVE COMMUNITIES

In non-interactive communities, substantial open niche space is created by reduced population levels due to fluctuations in the abiotic environment, certain types of enemy interactions, or other types of density-independent mortality, as well as barriers to invasion by new colonists coupled with the limited ability (through morphological or other 'design constraints') of residents to expand niches (Price 1984; Strong, Lawton & Southwood 1984 (pp. 112–113); Lawton & Gaston 1989). As a result, competitive displacement, niche shifting, and density compensation are rare and empty niches are common. Population regulation is possible, as long as species are independent and do not share the same regulatory factors.

Caswell (1976) developed what appear to have been the first non-interactive community models to predict the structure of non-interactive assemblages of species (see also May 1979). Caswell's Model I is the most purely non-interactive; it assumes that all species respond to abiotic conditions identically, and that all biotic interactions among species are absent. Colonization by new species is a random process that is independent of the number of species already present. Once a new species enters the community, its birth rate and death rate are linear and equal, and the resulting population dynamics of each species is completely independent of all others. Niches space is always open since there is no limit on the number of individuals summed over all species that can coexist in the community.

INTERACTIVE COMMUNITIES

At the other extreme, in interactive communities, the niche space is filled or nearly filled, resulting in strong interactions between species on the same trophic level, either directly, or indirectly via shared resources and enemies. Coexistence in the presence of these interactions is the major problem encountered by members of these communities. Interactive community models can be of many types (e.g. Schoener 1986), but generally fall into two categories, *niche heterogeneity* and *spatio-temporal heterogeneity*. This grouping is unconventional and somewhat oversimplified (cf. Schoener 1986; Chesson 1991) but the models in each category have sufficient in common to make the grouping logical and convenient for our purposes. Niche hererogeneity models are permutations and elaborations of 'Gause's paradigm' in which coexistence is favoured by species differences in one or more niche dimensions. In consequence, realized niches may be smaller than fundamental niches, and the assemblages will exhibit niche shifting, density compensation, and few empty niches. Niche space can be partitioned with respect to resources (including 'apparent competition' for enemy-free space (Holt 1977; Jeffries & Lawton 1984)), or physical gradients, and can occur in space (MacArthur 1972; Tilman 1986) or time (Chesson & Huntly 1989). Wiens (1989) provides a critical review.

In spatio-temporal heterogeneity models, there are at least five ways in which the number of coexisting species is enhanced compared with limits to coexistence predicted by simple niche heterogeneity models in a homogeneous world (see Shorrocks (1990), Hanski (1990) and Chesson (1991) for recent reviews):

1. by having roughly the same competitive abilities when competition is intense, coupled with unpredictable recruitment via chance disturbance (Sale 1977; Hubbell & Foster 1986);
2. by reducing the intensity of interspecific relative to intraspecific competition via aggregated utilization of fragmented environments (Shorrocks & Rosewell 1986);
3. by periodic disturbance coupled with slow population growth rates (Connell 1978; Huston 1979);
4. by combinations of 'fugitive' (or 'supertramp') species and competitively superior species (e.g. Hutchinson 1951; Skellam 1951; Diamond 1975);
5. by spatial variation in the risk of attack on new population recruits by specialist predators (Janzen 1970; Armstrong 1989).

Spatio-temporal heterogeneity and/or environmental uncertainty are important conditions for coexistence in all of these models, although as far as we are aware, they have not previously been gathered together in this way.

In (1), species persist because random walks to extinction are exceedingly slow (Hubbell & Foster 1986) and the probability of propagules gaining access to spatio-temporally shifting colonization sites is independent of population size (Sale 1977). In (2) and (3), aggregation on spatio-temporally ephemeral resources or disturbance can reduce average resource utilization by the superior competitors, allowing inferior competitors to invade and persist. Competition coefficients may be high and local competition intense, but the average level of competition is reduced by probabilistic refuges or reduced population levels. In periodically disturbed communities, a dynamic equilibrium is possible between the rate of population reduction and the rate of competitive displacement within single patches (Huston 1979). Fugitive (supertramp) species (4) coexist regionally with superior competitors because they are better at colonizing new environmental patches (Skellam 1951; Diamond 1975).

In (5), the density of a given species is limited by minimum spatial distances among individuals mediated through specialist predators. Safe sites invadable by a species are places some minimum distance from patches occupied by adults of that same species (Armstrong 1989). Sites safe from predators are thus fragmented and move idiosyncratically through time and space.

A THREE-WAY CLASSIFICATION OF COMMUNITIES

Figure 2 is one of several ways to summarize relationships among various community models in terms of niche heterogeneity, spatial heterogeneity, and the fullness of the niche space (on a three-dimensional figure it is difficult to incorporate temporal heterogeneity: the figure is illustrative, not all-embracing, and the temporal component of spatio-temporal heterogeneity has been omitted).

Non-interactive communities may incorporate varying degrees of both niche and spatial heterogeneity and are drawn, for convenience, at an intermediate position on both axes. Niche heterogeneity and spatial heterogeneity models occupy opposite corners of the space. The Huston (1979) model occupies the niche and spatial uniformity corner because it is characterized by temporal rather than spatial or niche heterogeneity. Connell's (1978) model incorporates both, so it is shifted toward the spatial heterogeneity corner relative to Huston's.

Limits to local species richness

THEORETICAL PREDICTIONS

As expected, Caswell's non-interactive model of community assembly predicts that given an infinitely large regional pool, there are no upper limits on the richness of the local community. Local richness depends only upon the length of time the community has existed and over which colonization has occurred (Caswell 1976).

Do all interactive models predict limits to local richness? In trying to answer this question, it is convenient, and important, to distinguish between *ecological* and *evolutionary* time, and between *saturation* and *hard limits* to local diversity. Given a species pool with defined characteristics (niche widths, competition coefficients, intrinsic rates of increase, etc.) local communities may saturate with species. That is, some species from the regional pool may be unable to invade the community; and species entering the community early in its development may be excluded by later invaders (Lawton 1987; Drake 1990a, b, 1991), as envisaged in Type II assemblages (Fig. 1). Moreover, the level of saturation may be strongly influenced by the sequence of species invasion during community assembly. In a series of computer simulations, Drake (1990b) has shown that the equilibrium number of a species at saturation can vary two-fold, depending upon the sequence of random species drawn from an unchanging regional pool. But saturation over ecological time from a given species pool is not necessarily the same as there being hard limits to species richness of local assemblages over evolutionary time. If the characteristics of species in the regional pool change, by long distance immigration of new taxa, or by evolution, changes in critical parameters may permit more species to coexist locally (see also (Wilson 1969). That is, the asymptote in Type II communities could drift up, toward some ultimate hard limit over evolutionary time. We return to the problem of hard limits to local diversity in evolutionary time below. First, we focus on whether or not interactive models necessarily predict saturated, Type II communities in ecological time for a given regional pool.

In broad terms, and for a given species pool, niche heterogeneity models predict saturation, but spatio-temporal heterogeneity models are a mix (Table 1). Among niche heterogeneity models, traditional equilibrium communities such as MacArthur's (1972) and Tilman's (1986) are saturated in the strictest sense. The number of species is set by the number of distinct niches, i.e. by limits to similarity of niche space utilization of coexisting species. Species composition and relative abundance are stable and are resistant to invasion from that pool. The temporal niche model of Chesson & Huntly (1989) also predicts saturation, but here the overlaps occur in time rather than space, and coexistence is enhanced by increased environmental variability (niche heterogeneity; Chesson & Warner 1981). Limits to richness thus occur along a time axis and are set by limits to similarity of environmental response, by each species. Niche distributions are measured along a temporal axis, so species relative abundances will shift through time.

In spatio-temporal heterogeneity models, the Shorrocks–Rosewell (1986), Connell (1978), and Huston (1979) models predict upper limits to richness, but for somewhat different reasons than MacArthur (1972), Tilman (1986), and Chesson–Huntly (1989). In the Shorrocks–Rosewell model, the limit is set by the degree of spatial aggregation as well as competition coefficients of the constituent species. In Connell (1978) and Huston (1979) it is set by a dynamic balance between the level of disturbance and the rate of competitive elimination of the inferior by the superior competitors. Both communities will collapse to one or a few coexisting species in the absence of mitigating aggregation and disturbance, and thus may be thought of as oversaturated in comparison to classical niche heterogeneity models. In Connell's (1978) model, if the species pool and the frequency, intensity, and scale of disturbance are relatively constant, so too will be the species composition and their relative abundance in the community. Huston's (1979) model resembles Connell's, but without the spatial dimension in which differential dispersal abilities become relevant.

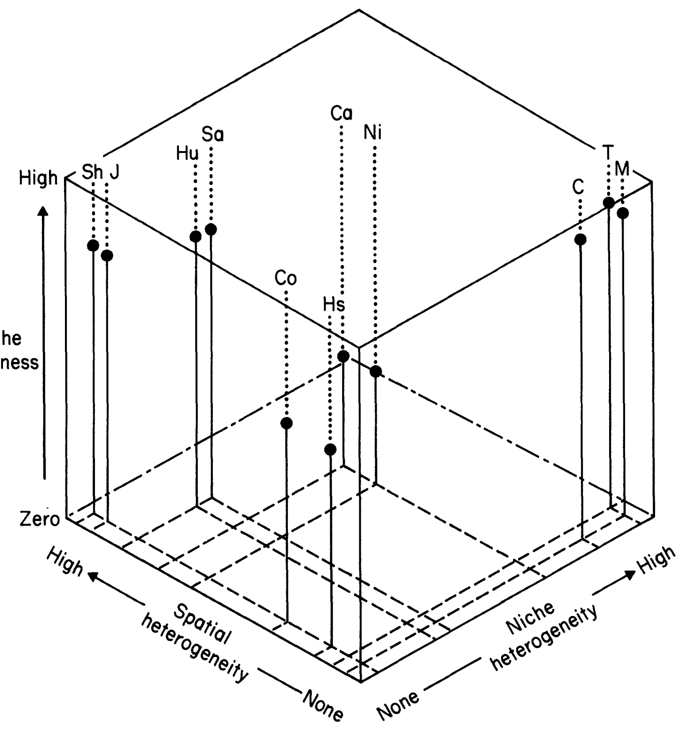

Fig. 2. A three-way classification of community models in terms of niche heterogeneity, spatial heterogeneity, and the fullness of the niche space (saturation; see text). The position of each vertical line on the floor of the cube represents the relative degree of spatial and/or niche heterogeneity built into the assumptions of a particular model. The lines are all slightly set back from the floor-edge because a degree of niche heterogeneity exists in most situations (Chesson 1991). The length of the line on the vertical axis represents the relative fullness of the niche space as surmised from the description of the model. Dashed lines represent unutilized niche space in ecological time. The temporal component of spatio-temporal heterogeneity (see text) was not incorporated into this three-dimensional figure. Sh=Shorrocks & Rosewell 1986; J=Janzen 1970; Armstrong 1989; Ca=Caswell 1976; Co=Connell 1978; Hs=Huston 1979; Hu=Hubbell & Foster 1986; Sa=Sale 1977; C=Chesson & Huntly 1989; T=Tilman 1986; M=MacArthur 1972; N_i=non-interactive (Strong, Lawton & Southwood 1984).

Table 1. Saturation or lack of it, predicted by models of community structure

Model type	Source	Saturation
Non-interactive	Caswell (1976)	No
Interactive		
Niche heterogeneity		
Classical niche	MacArthur (1972)	Yes
Resource ratio	Tilman (1986)	Yes
Temporal niche/subadditivity	Chesson & Huntly (1989)	Yes
Spatio-temporal heterogeneity		
Lottery	Sale (1977)	No
Random walk	Hubbell & Foster (1986)	No
Aggregation	Shorrocks & Rosewell (1986)	Oversaturated
Disturbance	Huston (1979), Connell (1978)	Oversaturated
Specialist predator	Janzen (1970), Armstrong (1989)	No

The Hubbell–Foster (1986) and Sale (1977) models are fundamentally stochastic, so that species composition and relative abundance are unstable, and the resultant communities unsaturated. Limits to richness can arise, but only because habitat space is finite, placing restrictions on the total number of individuals of all species that can occur there. As diversity increases, average population sizes will decrease until local extinction matches the rate of appearance of new species at the site. However, this ‘stochastic equilibrium’ is scale-dependent, because larger habitats will have lower average extinction rates, all else being equal. Average extinction probabilities are likely to be quite low, even for moderately sized habitats (Hubbell & Foster 1986), suggesting that such stochastic communities are unlikely to be saturated in moderate to large-sized habitats at realistic levels of diversity.

The Janzen–Armstrong model also predicts no saturation. A simple patch model incorporating specialist predators (Armstrong 1989) has shown that specialists can stabilize tree relative abundances in a frequency-dependent manner (cf. Sale 1977; above) for any number of species, but that stability approaches a neutral random walk (cf. Hubbell & Foster 1986) at high diversities. The Janzen–Armstrong model emphasizes that factors preventing self-replacement can produce spatial heterogeneity, permitting the maintenance of ever-richer assemblages.

In sum, it is inevitable that non-interactive local communities conform to Type I (Fig. 1) with local species richness directly proportional to regional species richness. Less obvious is the realization that although some models of interactive communities predict local saturation in ecological time (Type II; Fig. 1), others do not. Theory says that species interactions are a necessary but not sufficient condition for local saturation in ecological time. Hence, interactive communities may conform at one extreme to Type I, and at the other extreme to Type II. Table 1 summarizes a range of community models and their predictions about local saturation (see also Fig. 2).

EVIDENCE

Given these theoretical results, will saturation ever be observed in nature? Scepticism concerning the existence of saturated natural communities has a venerable history in ecology. For example, both J. Grinnell and P. Taylor discussed the question in papers written between 1910 and 1920 (Schoener 1989); both authors conclude that local communities are not necessarily saturated with species, and identify vacant niches. More recently, Whittaker (1977) expressed doubts that local communities can ever be saturated in the sense of a fully packed niche space, and warned that the term 'saturation' may be more confusing than illuminating.

Although we share these concerns, it is certainly possible to test whether there is a ceiling to species richness in local habitats using the method advocated in Fig. 1 (e.g. Terborgh & Faaborg 1980; Lawton 1982; Cornell 1985a, b). In assemblages with no local ceiling, proportional sampling will occur (Type I assemblages: Fig. 1). If assemblages saturate, then local richness may at first increase with increases in regional richness, but will eventually become constant. Data that exhibit constant local richness with increasing regional richness point to a saturated community (Type II assemblages: Fig. 1).

An early test for saturation by this method was performed on bird communities occupying West Indian islands (Terborgh & Faaborg 1980). When the numbers of species in standard samples from matched habitats were plotted against the number of species on each island, a ceiling was apparent, suggesting saturation. Both species interactions and pool exhaustion were explored as possible explanations, but they could not be readily distinguished, making interpretation of the ceiling ambiguous at best. More recently, Wiens (1989) replotted the data from this study and showed pictorially and statistically that proportional sampling explains the pattern nearly as well as the saturation model. Interestingly, Ricklefs (1987) tested assemblages of songbirds in the same archipelago and observed a strong dependence of local richness on regional richness with no hint of a ceiling to local richness. The weight of evidence thus favours proportional sampling as the most plausible description of these island bird assemblages.

In another study involving vertebrates, Tonn *et al.* (1990) reported a ceiling to local species richness in small-lake fish assemblages. However, their conclusions are based on only two data points, making it impossible to tell which model the data support. They are at least as consistent with proportional sampling as they are with the saturation model.

Saturation was first tested with phytophagous insects using assemblages of cynipid gall wasps associated with the Californian oaks (Cornell 1985a, b). The cynipids are a diverse group with over 600 species in North America (Kormbein *et al.* 1979), virtually restricted to the oaks. Distributional ranges of the oaks vary widely, cynipid regional richness correlates strongly with oak distribution in California (Cornell & Washburn 1979; Cornell 1985a), and saturation can be evaluated by correlating local richness with regional richness on oaks with various ranges. When this is done, the data clearly conform to the Type I model (Cornell 1985a, b) indicating that local cynipid assemblages are not saturated.

Stevens (1986) found no correlation between local richness of wood-boring scolytid beetles and the geographic range of their host plants. However, he did report a correlation between regional richness and host range, and concluded that richer regional faunas on widely distributed hosts were mainly due to geographic turnover of local assemblages. This result could imply a ceiling to local richness. However, the scolytids show a significant, albeit noisy linear correlation between local and regional richness (omitting seven host species sampled at only one site) ($Y = 0{\cdot}33X + 0{\cdot}39$. $R^2 = 0{\cdot}26$; $P < 0{\cdot}001$; $n = 40$); quadratic (and all higher order) terms of a curvilinear regression were not significant ($t = -0{\cdot}7$; $P > 0{\cdot}4$) implying that scolytids are also Type I assemblages.

More recently, Lawton (1990a, b) has used the method to test for a ceiling in the richness of local herbivore assemblages associated with bracken. Bracken has a worldwide distribution, but varies from region to region in the extent of its geographic distribution. Furthermore, in those regions where bracken has a wider distribution, greater numbers of herbivores are associated with the plant. Species pools thus vary from place to place.

When the number of bracken herbivores in local samples is correlated with the size of the regional pool, again one observes proportional sampling indicating no saturation. This is a particularly satisfying result, because previously gathered information about the system such as the prevalence of empty niches and the lack of density-compensation (Lawton 1982, 1984; Lawton & Gaston 1989; Compton, Lawton & Rashbrook 1989) suggests that bracken assemblages are non-interactive, and as such they should be unsaturated.

Hawkins & Compton (1992) plotted local against regional richness of South African fig wasps and their parasitoids, and demonstrated a slight curvilinear relationship in the former and striking proportional sampling in the latter. The curve for the fig wasps did not come close to an asymptote, leading the authors to conclude that both groups are unsaturated. This study is notable for the quantity of data collected, and is the first rigorous test for saturation in the third trophic level.

Finally, Zwolfer (1987) and Lewinsohn (1991) correlated the number of insect species in flower heads of temperate and tropical Asteraceae respectively with several host attributes. Using path analysis, they demonstrated a strong correlation between local richness in flower heads and the size of the regional pool, again suggesting such assemblages are unsaturated.

Data for parasite communities in Amphibia (Aho 1990) and fish (Aho & Bush, in press) do not support proportional sampling, and appear more consistent with Type II assemblages. These data on parasite assemblages from vertebrate hosts appear to be substantially different from the proportional sampling model revealed by studies of insect herbivores on host-plants, and provide the best evidence currently available for Type II assemblages.

As far as we are aware, these are the only data sets complete enough to test for saturation by the method advocated in Fig. 1. Some studies with fewer data may support the saturation model, e.g. ants, sclerophyll vegetation (Westoby 1985); invetebrates in grass beds (Heck 1979); crustaceans on coral heads (Abele 1984); fish on coral heads (Bohnsack & Talbot 1980). Others suggest proportional sampling, e.g. freshwater ciliates (Taylor 1979); leafminers on oaks (Opler 1974); coral reef fish (Westoby 1985). However, none of these results are sufficiently rigorous to allow unambiguous rejection of either model.

CAVEATS

Proportional sampling does not necessarily mean that the community is non-interactive. Although the absence of a ceiling is characteristic of and strongly suggests a non-interactive system, communities where all of the species interact strongly can show the same pattern, as the theoretical discussion above makes plain. All that proportional sampling indicates is that regardless of the nature of local interactions, they are not sufficient to limit local species richness. Supporting evidence on lack of density-compensation, or other evidence from manipulations is required to confirm that a community is non-interactive.

Of course, some portions of the community may be more interactive than others. At one extreme, a community may comprise a core of strongly interacting species, and a second group of weakly interacting tramp species. Tramp diversity may increase as the regional pool gets larger, producing a Type I pattern even though strong interactions limit the diversity of core species. It may thus be desirable in some cases to refine the search for limits on local richness by focusing on species groups most likely to interact (e.g. Cornell 1985a). It is a moot point how the more limited set of species might be identified a priori without a great deal of detailed information on the natural history of the system.

It is also important to note that the unequivocal statistical detection of a Type II pattern in real data does not necessarily provide an unambiguous test for saturation. Additional observations and/or experiments may be needed to distinguish true saturation from stocastic equilibrium or 'pseudosaturation'. A stochastic equilibrium is simply a balance of colonization and extinction rates that is independent of species interactions (i.e. a non-interactive equilibrium; Wilson 1969). Pseudosaturation results when the true size of the regional pool is overestimated. The regional pool may be overestimated if it includes species specialized to habitats other than the one of interest, or if it is drawn from an excessively large geographic region, so that the species included in it can never reach or colonize the local community under study. If the overestimates are proportionally larger for putatively larger regional pools, a spurious Type II pattern will be generated (Cornell 1985b, 1991).

Interactions among the constituent species are a central requirement for true saturation, Thus, evidence for density compensation, niche shifting, the absence of identifiable empty niches, and/or high ratios of core vs. tramp species would support true saturation. High ratios of tramp species and/or rapid species turnover independent of observable interaction among newly arriving and disappearing species would support stochastic equilibrium, whereas, low turnover coupled with lack of niche shifting, lack of density-compensation, and obvious empty niches would support pseudosaturation.

Evolutionary time

The richness of regional biotas has increased steadily since at least the Mesozoic (Sepkowski *et al.* 1981; Niklas, Tiffney & Knoll 1983; Strong, Lawton & Southwood 1984; Benton 1985, 1987; Knoll 1986; Signor 1990; Valentine 1990). The clear implication of these results is that local (alpha) community diversity must also have increased in evolutionary time, or that beta diversity — the turnover of species from place to place — has increased. Available data suggest that both processes are involved (Knoll 1986; Sepkowski 1988), with evidence that not only total faunal richness, but also local richness in comparable communities has risen steadily for at least 100 million years (Sepkowski *et al.* 1981). Much of this increase may involve occupation and radiation into vacant niches (Walker & Valentine 1984), not least because periods of mass extinction create huge 'holes' in the niche space (Stanley 1987). As new biotas evolve to fill them, original patterns of niche utilization rarely return. At any given point in ecological time, opportunities always exist for the invasion of appropriately adapted species into unoccupied niches, and the subdivision of existing niches.

We expect Type I local assemblages to accumulate species as the size of the regional pool increases over evolutionary time. At the other extreme of the continuum, what evidence is there that a plateau in local species richness (saturation in ecological time) remains fixed, if the size and species' characteristics of the regional pool changes? That is, are hard limits to local diversity maintained over evolutionary time? If they are, there are limits to the subdivision of niche space; if they are not, niche space can be ever more finely divided over evolutionary time.

Empirical evidence is equivocal, but suggests that for some taxa, at least, richness of local assemblages increases over evolutionary time in geologically stable habitats that have not been subjected to climatic extremes. Although geological time in itself may be neither necessary nor sufficient to produce high species diversity (Pianka 1989; Fryer & Iles 1972), long evolutionary time periods coupled with favourable genetic and environmental conditions can result in prolific adaptive radiations of key taxa. Extremely rich local assemblages with a long, relatively undisturbed evolutionary history include Lake Baikal gammarid amphipods (Brooks 1950), and the fynbos heathland of South Africa (Cody 1986; Huntley 1988; Kruger 1979). The fynbos combines high (but not exceptional) point (alpha) diversity within local assemblages with unusually high beta diversity, involving very fine habitat partitioning among closely related taxa (Cowling *et al.* 1989). The problems with all such examples is that we do not know whether the contemporary communities, rich as they are, conform to Type I or Type II (e.g. Cowling *et al.* 1989); nor are the ecological processes maintaining local diversity well understood in terms of the idealized models illustrated in Fig. 2.

In theory, a number of scenarios may link local richness and regional richness over evolutionary time (Fig. 3). Case (a) (upper graph) is for Type I assemblages; Case (b) (lower graph) is for the opposite extreme (Type II assemblages). In both cases, an initial number of species, x, in the regional pool increases to $x + n$ ($n >$ or $= 1$), either by long-distance immigration, or speciation. In Type I assemblages, simple proportional sampling suggests that regional and local richness follow trajectory (ii). But if the new species in the regional pool are better dispersers, local richness may increase supra proportionately (i). On the other hand, if the new species are superior competitors, even though local communities are not initially saturated with species, it is conceivable that local richness may fall, confronted with the new invaders.

In Type II systems, local richness may remain unchanged as regional richness increases (ii), implying hard limits to local diversity. Alternatively, changes in species characteristics (competition coefficients, niche-widths, intrinsic rates of increase, etc.) may permit an increase in local diversity (i) (i.e. there are no hard limits); or local diversity may actually fall if particularly aggressive competitors enter the system (iii).

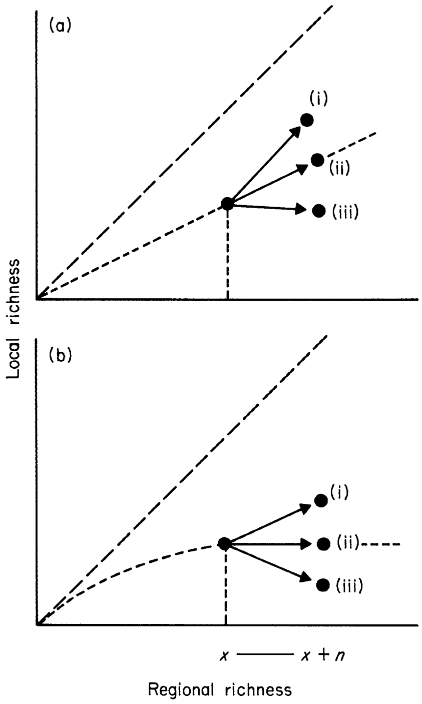

Fig. 3. Possible changes in local richness (i, ii, iii) in (a) Type I communities and (b) Type II communities, as a function of increases in regional richness (x to $x + n$) over evolutionary time. Changes in species characteristics affecting their dispersal characteristics and the nature of their interactions over evolutionary time make the direction of change in local richness in response to a change in regional richness largely unpredictable.

The fynbos flora has recently suffered catastrophic reduction in local diversity, due to the invasion of the region by alien plants from Mediterranean climates elsewhere in the world (Stirton 1978; Huntley 1988). Regional diversity has increased, but local diversity has fallen, either as visualized in Fig. 3b (iii) or, less likely, Fig. 3a (iii). As well as emphasizing that increases in the size of the regional pool can lead to reductions in local diversity, rather than an increase, the invasion of the fynbos by alien plant species serves to illustrate that there is nothing unique about this habitat that guarantees high local diversity. It is a product of particular species' characteristics evolved over a very long period of time. Similar remarks apply to loss of diversity in other species-rich systems due to changes in the composition of the regional pool (e.g. Miller 1989).

It is difficult to test the alternative models displayed in Fig. 3. One approach is to see if comparable ecological systems in different parts of the world, with different evolutionary histories do, or do not converge in species richness of local assemblages. This requires other, confounding variables to be factored out, and despite a long history, has yielded equivocal results (e.g. Pianka 1986; Schluter 1986, and references therein).

Overall, the mixed theoretical predictions for interactive communities and the likelihood that many communities may be non-interactive, argues that saturation in ecological time ought to be rare in real systems, and that the size of local assemblages should be strongly dependent on the size of regional pools. The number of species in a given regional pool may increase over evolutionary time, changing average local richness, but the proportional nature of the relationship need not change (Fig. 3). Indeed, we believe that proportional sampling (Fig. 3aii) is the most likely outcome, and that it ought to be viewed as the null hypothesis for communities; the focus of research on what determines species richness of ecological communities should therefore be shifted to mechanisms which set limits on regional richness.

Regional richness

The interplay between local and regional richness is not simply that local communities are samples of the regional pool of species; by definition, the regional pool of a species is the sum of the species in local assemblages. Dependent and independent variables are therefore hard to define. In general, if local diversity is saturated, then regional diversity may in some sense be limited by local processes. The limit would be most obvious if habitats from place to place in the region are essentially uniform with the same set of species adapted to live in each. Beta diversity would then be low, and local and regional diversity would converge (Fig. 4). More likely, habitats in the region will be subtly different, and the impact of local processes on regional diversity will be softer and less obvious. Each habitat will have a different species composition, beta diversity will be high, and limits to regional richness will be set by the number of distinct habitats, each supporting a saturated assemblage (Fig. 4). The presence of different but ecologically equivalent species in identical habitats within the region can raise the limits on regional richness to some extent (Shmida & Wilson 1985), depending upon the prevalence of such species. Moreover, high regional richness due to the above-mentioned habitat heterogeneity can 'feed back' to the local community, enhancing local richness as well. This may occur via mass or source–sink effects (Shmida & Wilson 1985; Pulliam 1988) whereby species become established in habitats where they are not self-maintaining because of a high rate of propagule influx from more favourable source areas. As a result, local communities will become 'oversaturated', complicating the direction of cause and effect between local and regional richness.

If local richness is not often saturated, as is likely if our arguments are correct, then other limits on regional richness, which in turn, limit local richness, must be sought. Several factors operating at ecological time-scales outside the local community may enhance regional richness, including habitat heterogeneity, high productivity, and habitat stability (Shmida & Wilson 1985). At evolutionary time-scales, questions often asked by systematists such as, 'Where do species come from?' and 'Why do certain taxa radiate extensively?' suggest profitable approaches to the problem. Conditions which encourage rapid diversification in lineages over evolutionary time-scales will result in large regional richness, and may ultimately set its limit. The evolution of high regional diversity in particular taxa may have more to do with accidents of geology, for

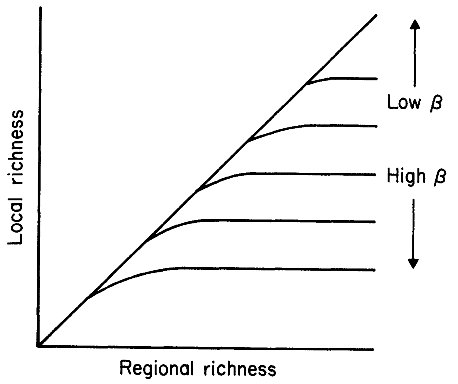

Fig. 4. Changes in the relationship between local and regional richness in saturated communities with changes in the degree of habitat heterogeneity and thus beta diversity. As habitat heterogeneity increases, beta diversity increases, and saturation occurs at a progressively smaller proportion of the regional pool.

example continental drift, than with the ecology of species' interactions acting over evolutionary time.

In the classical view (Simpson 1953; Hutchinson 1959), rapid diversification is encouraged by the creation of an extensive open niche space or adaptive zone. Species proliferate in the new zone via niche differentiation, thus diversification can be related back in some sense to local ecological conditions. Recent attempts to rigorously test the adaptive zone hypothesis for the origins of phytophagy in several insect taxa show a strong correlation between adoption of phytophagy and diversification (Mitter, Farrell & Wiegmann 1988). However, species proliferation into a new adaptive zone need not require niche differentiation. New adaptive zones often provide opportunities for range expansions of species which enter them. Range expansions, in turn, offer increased opportunities for reproductive isolation and geographic speciation arising from stationary geographic barriers, tectonic activity, or isolation-by-distance (Mitter *et al.* 1988; Slowinsky & Guyer 1989). The generation of new species from such reproductive isolates does not require a heterogeneous niche space, only that the isolate be genetically segregated from the parental population. Similarly, new adaptive zones are often free of potential competitors so that species proliferation may also occur via decreased rates of competitive extinctions of new reproductive isolates. Again, such isolates can generate new species simply by genetic segregation from other populations with no requirement for niche differentiation (Mitter, Farrell & Wiegmann 1988).

Moreover, there are at least two alternatives to the adaptive zone hypothesis which do not require open niche space as a prerequisite to diversification (Mitter, Farrell & Wiegmann 1988).

1. Rapid speciation is promoted by stenotopy which fosters isolation and differential selection.
2. Rapid speciation is promoted by particular breeding systems or population structures, e.g. sexual selection and founder effects in the Hawaiian drosophilids, or other genetic processes.

Finally, there seem to be numerous cases where there is open niche space and no adaptive diversification. Developmental constraints on taxa may act as channels for change, and only those groups capable of developing appropriate innovations will be able to move into a given adaptive zone. For example, the interesting question about the Hawaiian drosophilid radiation may not be the actual radiation, but why the drosophilids and not something else?

These arguments suggest that open niche space is neither necessary nor sufficient for species diversification. Instead, the tendency to proliferate may be an intrinsic property of specific taxa, based on genetic and biogeographic attributes, and may be effectively independent of local ecology and niche complexity. Local ecological opportunity may thus have little impact on regional richness and ultimately, on richness levels in local assemblages over both ecological and evolutionary time.

Concluding remarks

The origins of species richness at different spatial scales are obviously linked, but are a chicken and egg problem in that it is unclear whether local richness derives mainly from regional richness or vice versa. In this short review we argue that many ecological communities should not be saturated, and hesitantly offer some mechanisms to account for limits on regional, and ultimately, local richness which do not rely on local process in the traditional sense. Our speculations inevitably suggest that the principal direction of control is from regional to local, but the correctness of this conclusion will rely on a combination of evidence on saturation and the role (or lack thereof) of niche diversification in the proliferation of regional biotas. Presently, such data are sorely lacking.

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