Spatial Scale and the Determinants of Plant Species Richness

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Traditional ecological theory has stressed the importance of competitive interactions in regulating species richness. Recent research has transcended this viewpoint by considering the role of stochastic processes, mosaic phenomena and nonequilibrium conditions in the regulation of richness. This growing body of work indicates that the determinants of plant species richness may vary predictably over different spatial scales.

One of the great challenges to biologists is to explain the phenomenal geographical variation in the number of species on our planet. A complete answer must embody both the evolutionary processes which produce species in the first place and the ecological processes which secondarily regulate species richness. In this short review, we must forgo the issue of speciation, and simply take the wealth of organisms as given. Instead we focus on a central theme of modern ecology, the elucidation of determinants of species richness. We also limit our discussion to plants.

Traditional ecological theory offers two principal answers to the question of what determines the number of coexisting species at the local (community) level[1,2]: (1) species partition limiting resources so that each is limited by a different component of available resources (resource differentiation); and (2) species use different portions of available habitats or differ in the range of habitats in which they are competitively superior (habitat differentiation). Both explanations invoke the concept of a trophic niche – an organism's role in a community as defined by resource use and species interactions. Under both viewpoints interpretations of species coexistence were predicated on the competitive exclusion principle, which states that coexisting species must differ in their trophic niches[2].

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One need only glance at chapters in any of several new volumes on community ecology to appreciate that the issue of determination of species richness has been carefully re-examined over the last decade[3–5]. The deterministic, equilibrium explanations based on competition and niche theory have been superseded by models incorporating dynamic processes that influence species coexistence. Current research concentrates on three interrelated areas in particular: stochastic processes, patch dynamics, and equilibrium versus nonequilibrium states[6–8].

To illustrate this change in thinking, we examine in detail a familiar pattern of species richness, the species–area relationship. It has long been recognized that species number tends to increase with increasing sampling area[9] (Fig. 1). It is clear from Fig. 1 that the relative importance of various determinants of species richness varies with spatial scale. To account for scale and to categorize the myriad of possible determinants, we partition them into four groups: niche relations, habitat heterogeneity, mass effects, trophic equivalency[10]. This is by no means the only method of classification and space does not permit us to discuss all the suggested regulators of species richness. We present this example simply to illustrate some new avenues of research.

Niche relations

Plant species differ in their edaphic, climatic and biotic microhabit requirements and tolerances[2]; these niche relations, in combination with the size of source floras (available species pool), are important determinants of species richness over small spatial scales[10] (Fig. 1). Much of plant ecophysiology has focused on delineating the tolerances of plants to different abiotic regimes and elucidating the role of differential tolerance in limiting geographical distribution[11]. However, tolerance of environmental conditions alone is not sufficient for continued local existence because interspecific interactions, such as predation or allelopathy, may restrict niche dimensions. In fact, classic niche theory, which was developed largely by animal ecologists, viewed the impact of interspecific interactions (particularly competition) on niche dimensions as the principal determinant of local species richness[1,2].

Even though resource and habitat differentiation undoubtedly influence local species richness, it is difficult to envisage every plant species in a species-rich community occupying a different habitat niche (Box 1). Coexistence of species with similar habitat niches may be possible because of variation in other niche components[12]. For example, differences in size, productivity and architecture may permit coexistence, such as the co-occurrence of trees and herbs with similar resource requirements. In addition, differences in life form may enhance local richness because of dependent relationships, such as those between parasitic plants (or lianas, vines, etc.) and their hosts. Phenological differences between species that result in temporal division of resources may also increase local richness by mitigating competitive interactions[12].

One aspect of niche relations, the regeneration niche, may be particularly important in regulating local species richness[12,13] (Box 1). A species' regeneration niche encompasses the environmental conditions, biological attributes and biotic interactions required for perpetuation of a species in a community. Thus, germination requirements, mode and timing of seed dispersal, growth form, environmental tolerances of seeds and seedlings, characteristics of nearby vegetation, and interactions with pests and disease, are important elements of a species' regeneration niche.

The concept of regeneration niches emphasizes the importance of investigating habitat requirements of all life-history stages of a plant, rather than just those of adults, since they may shift over a species life cycle[14]. For example, common short-lived forbs of chalk grasslands exhibit different microsite preferences in seedling and in vegetative and reproductive stages[15]. Age-specific changes in niche relations suggest that species may not always be able to colonize an open microsite produced by death of a mature conspecific.

Despite the many ways in which differentiation in various niche components may facilitate coexistence, some researchers have suggested that there need not be any significant differences in the niches of some co-occurring species[16], particularly sparse ones[13,17] (see below).

Habitat heterogeneity

As sampling area begins to exceed the size of individual organisms, habitat heterogeneity becomes a determinant of richness. The influence of habitat diversity on species richness is apparent over many spatial scales from local pattern of microsites to regional spatial heterogeneity[10]. Traditionally, habitat heterogeneity was interpreted to influence richness through the niche-based processes of interspecific competition, habitat differentiation and resource partitioning[2]. Obviously, an increase in local habitat diversity provides a more varied backdrop for differentiation and specialization. Recent research, however, suggests numerous other ways in which heterogeneity, particularly microsite pattern, can influence richness.

Better understanding of the impact of microsite pattern on richness has emerged from greater appreciation of the causes of microsite heterogeneity, the regeneration process, and the nature of plant competition. Over the last decade, plant communities, including non-seral ones, have increasingly been viewed as mosaics of microsites that differ in environmental attributes and successional status[7,8]. Some of this within-community heterogeneity is relatively static and predictable, such as local variation in topography or edaphic factors. However, habitat mosaics are frequently created by a variety of stochastic disturbances. Within-community patches result from small-scale disturbances, such as the death of a tree which opens a new microsite for colonization. Larger disturbances, such as fires, hurricanes or other extrinsic factors, are usually invoked to account for intercommunity mosaics[8].

The importance of disturbance and patch dynamics in regulating community richness is an extremely active area of ecological research. Virtually every type of plant association has been re-interpreted in the context of disturbance and habitat mosaics[8,18]. A major theme emerging from this research is that not all disturbances are catastrophic ones that reduce richness. Instead, the predictability, frequency and intensity of disturbance will determine which of the existing species may be expected to withstand the perturbation.

Within-habitat heterogeneity in resource quality and availability can influence richness substantially through its impact on the regeneration process. As mentioned above, age-specific differences among and within species in their microsite requirements can, if a mosaic of such microhabitats exists, provide a basis for specialization, and thereby promote richness[19]. However, regeneration depends upon successful colonization of such suitable habitats, the location of which may be unpredictable in space or time. Which propagules reach a microsite depends on species composition of the source pool of potential colonists and the dispersal ability, reproductive biology and phenology of these species[8,18,20].

The dynamic aspect of regeneration is reflected in the population dynamics and life histories of many plants. For example, local extinction of biennials is common in many habitats because conditions suitable for germination and seedling establishment are transient[21]. For these species to persist, they must repeatedly colonize new habitat patches. One finds myriad adaptations among plant species to the unpredictability in time and space of safe sites, including seed dormancy, delayed flowering and variable dispersal propensities[6,22]. Considerations of regeneration processes have frequently led to suggestions that in many plant communities preemptive competition (competition to reach and occupy a suitable microsite first) is more intense than interactive competition among established individuals[22,23].

Dissatisfaction with two basic tenets of niche theory has paralleled appreciation of the importance of preemptive competition and regeneration in determining local richness. Unlike most of traditional niche theory, much of the research in the last decade neither assumes equilibrium assemblages, nor ignores stochastic environmental variation[23–26]. By considering patchy distribution of resources and small-scale spatial and temporal disturbances, recent empirical and theoretical research suggests that in many communities more than one species can occupy the same (or at least a very similar) trophic niche[6,16,23]. We refer to these species as trophic equivalents, stressing the notion that despite similar patterns of resource use and habitat preferences, these species may differ in ecologically significant traits such as reproductive behaviour or seed dispersal mechanism.

Spatial or temporal habitat heterogeneity can promote trophic equivalency[6]. First, consider temporal environmental variation. As noted above, predictable seasonal events may permit phenological

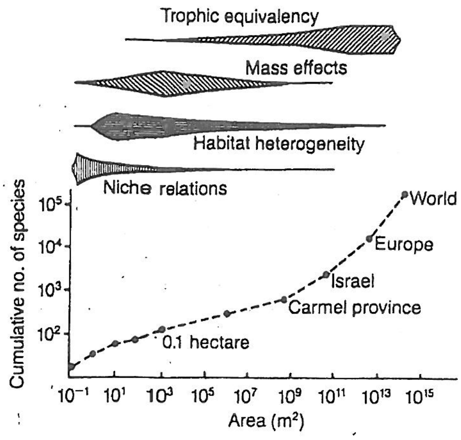

Fig. 1. Species–area curve extending over several scales, from samples in the mattoral (chaparral) in Israel to the entire world. The depth of each hatched area shows the postulated contribution of each factor to species richness at different spatial scales. *Redrawn, with permission, from Ref. 10.*

Box 1. Components of a plant niche

To account for the diverse aspects that define a plant's niche, Grubb[12] has subdivided the niche into four components: habitat, life-form, phenological and regeneration niches. Habitat niches are defined by the physical and chemical limits tolerated by mature plants. Life-form niches are related to growth form and productivity. Seasonal patterns of development delimit phenological niches. Regeneration niches encompass all conditions required for perpetuation of a species in a community.

separation of potential competitors. Alternatively, the suitability of a microsite for a given species may depend on stochastic environmental variation. For instance, three codominant grasses co-occur in parts of central Texas[27]. Although the relative favorability of different microsite types varies little among the species, differences do exist in the effect of soil moisture on germination. Codominance of these species appears to result from differential year-to-year success among species as a result of fluctuations in timing of rainfall and temperature[27].

Numerous mathematical models have also demonstrated the possibility of coexistence of trophically equivalent species provided there is environmental fluctuation. Prominent among these are 'lottery' models which assume that competition among recruits is for space and that space is allocated randomly to propagules of different species[6,26]. Although there are many variations on the basic model, two criteria for coexistence generally must be met. First, environmental variation is necessary so that each species has periods of strong recruitment at low densities. Second, generations must be overlapping. This criterion need not be met only by adult cohort persistence; annual plants with a seed bank may also be considered to have overlapping generations. Long-term coexistence results when each species has positive average population growth because of occasional periods of strong recruitment[26].

Spatial variation in recruitment based upon habitat patchiness can likewise produce coexistence of trophically equivalent species, provided there is non-uniform seed dispersal between patches[26]. In this case dispersal takes the place of overlapping generations. One may infer from models of spatial heterogeneity that species with alternative life histories, such as a superior competitor and a superior disperser, can coexist[6]. Frequently, spatial and temporal heterogeneity coincide, suggesting a multiplicity of ways in which variation in colonization strategy can promote coexistence. Weedy plants, for example, exhibit a suite of highly correlated adaptations ranging from an annual growth form with limited dispersal ability but long seed dormancy to perennial, vegetatively-reproducing species with long range seed dispersal but limited seed dormancy[22].

Disturbances *per se* may also maintain local species richness by altering competitive interactions among adults. For example, shifts in competitive dominance resulting from differential response to spring versus autumn droughts appear to be one of the mechanisms promoting coexistence of two species of *Erodium*[28]. In addition, any disturbance that reduces or maintains population sizes of resident species below a point at which competitive exclusion is possible (or rapid), but not intense enough to result in local extinctions, may permit trophically similar or equivalent species to coexist[6,13]. The extent to which this occurs may depend on the intensity of competition and degree of dominance found within a community. Variability in competitive ability and dominance of species in different communities may in turn be associated with differences in productivity. Grime[20] suggests that intermediate productivity allows interactions among niche differentiation, disturbance and habitat heterogeneity which together maintain high richness. This hypothesis, that productivity influences the impact of disturbance on biotic interactions, and consequently richness, is supported by studies of subalpine meadow vegetation[29].

Either biotic or abiotic 'disturbances' may be involved in maintaining species richness. For instance, disturbance from wave action and fluctuating water levels appears more important in regulating coexistence of lakeshore vegetation than does specialization along a water-depth gradient[30]. Similarly, predation or pathogen attack focused upon more vigorous species (compensatory mortality) can reduce dominance and prevent exclusion of inferior competitors[31,32]. By altering dominance patterns, disturbances may be extremely important in maintaining the sparse and patchily distributed species that comprise a large proportion of the total richness of many communities[13,17]. The low population sizes and spatial arrangement of these species suggests that they may be more suppressed by dominant species than by each other.

Many interpretations of within-community mosaics and patch dynamics assume an overall dynamic equilibrium state at the community level, despite disequilibria at the patch level[28]. However, other hypotheses suggest that in some communities disturbance is frequent enough that steady-state conditions are never attained. Prominent among these is the 'intermediate disturbance hypothesis' which predicts that the highest richness should be maintained when disturbance is intermediate in frequency and intensity[25]. If disturbance is too frequent, low richness will result from insufficient time or inappropriate conditions for recolonization. If disturbance is very infrequent, richness will decrease because of competitive elimination of some species.

Despite its prominence in current ecological literature, the generality of the intermediate disturbance hypothesis is questionable. As noted above, disturbance can maintain richness through its influence on niche differentiation, regeneration or dominance expression. The impact of disturbance, therefore, should depend on the type of competitive interactions found within a community, and the extent to which species, especially dominant ones, are affected selectively. Yodzis[23] distinguishes three types of competitive structure: (1) niche control, in which consumptive competition is paramount; (2) dominance control, in which spatial (preemptive) competition predominates and functional dominants occur; and (3) founder control, in which spatial competition operates through colonization because dominants are lacking. The relationship between disturbance intensity and richness varies among these community types.

Unlike niche-dependent theory, non-equilibrium models emphasize the importance of chance and history in determining species richness. For instance, the phenomenally high local diversity of tropical rain forests is frequently discussed in terms of non-equilibrium conditions resulting from stochastic disturbance[24,25].

Hubbell and Foster[16] argue that a history of disturbance has produced guilds of functionally equivalent generalist tree species, in part because neighbors, and hence inter-tree interactions, are temporally and spatially unpredictable. High local richness results from the slow dynamics of competitive elimination under these conditions.

These mechanisms demonstrate how habitat heterogeneity and the processes producing heterogeneity can influence species richness at the community level. The stochastic nature of many of these mechanisms also explains much of the variability among community samples. As sampling area exceeds the size of a community, habitat heterogeneity will continue to contribute to an increase in richness because of the inclusion of new habitat types[10].

Mass effects

Mass effect is the transient dispersal and establishment of species from nearby habitats into sites where they are not self-maintaining[10] (Fig. 2). Since natural communities are not closed systems, some propagules arriving at any site may belong to species established in nearby communities. A subset of these species may be able to survive but not reproduce in the new habitat. Persistence of these species in less favorable areas depends on copious seed production in, and continued dispersal from, their source habitats.

The contribution of mass effects to species richness depends on the amount of dispersal of species from their regions of self-maintenance, size and environmental complexity of the region of invasion, and the richness of nearby biotas[10]. Generally, mass effects are most important at meso-spatial scales (Fig. 1). In small areas, limited target area will constrain the invasion of species. Similarly, at scales that exceed the dispersal distances of most species mass effects will be minimized. Mass effects should be most pronounced in areas of transition between distinct floras[10].

Trophic equivalency

Although trophic equivalency can contribute to species richness at small to medium spatial scales through habitat heterogeneity (discussed above), its greatest effect is probably at larger (regional to continental) scales. At such scales, topographic and geographical barriers to dispersal restrict the possibility of mingling. Geographically isolated species may, in fact, have not only similar trophic niches but also similar reproductive and dispersal syndromes[10] (ecological equivalency).

Conclusions

In summary, a multitude of factors may regulate species richness, and the relative importance of any given factor varies with spatial scale[33]. We have emphasized the influence of habitat heterogeneity, because recent research on stochastic processes and patch dynamics has greatly enhanced understanding of richness determination. This research also demonstrates that different determinants do not function associatively, but rather interact in diverse ways to govern richness.

Further understanding of the determinants of richness and their interactions should help reconcile some current debates in community ecology. For example, the idea of community convergence extends the concept of ecological equivalency to the community level, suggesting that communities in geographically isolated but environmentally similar regions should converge in growth form or species richness[34,35]. Convergence would imply that contemporary climate and edaphic conditions are paramount in determining richness, whereas non-convergence would suggest differences in phytogeography, floristic history and disturbance[33]. Current empirical evidence on convergence in richness is equivocal, due in part to inadequate sampling procedures, but also to differences in the scale of comparisons[34]. For instance, comparisons made over small spatial scales where niche relations are a primary richness determinant are probably more likely to show convergence than are ones made over large scales where the impact of disturbance and history is more pronounced. Resolution of the issue of convergence, as well as many others in community ecology,

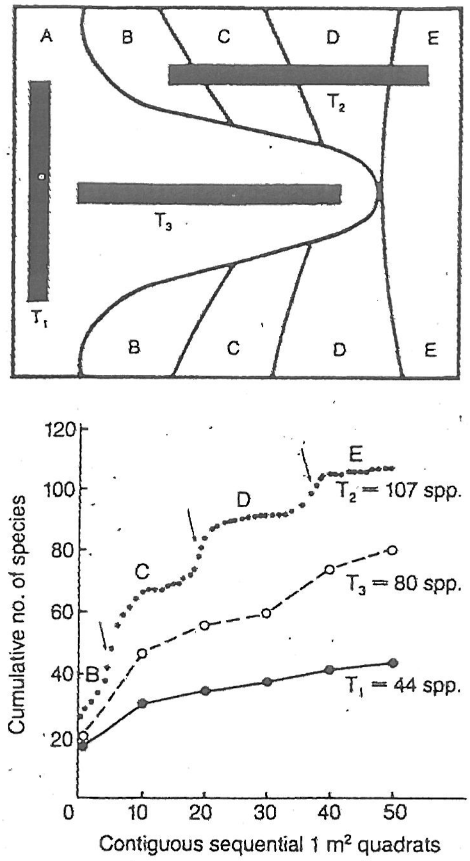

Fig. 2. The influence of mass effect on species richness. The upper diagram shows three transects in the Judean Desert, Israel: T_1, across a homogeneous valley habitat (A); T_2, across foothills encompassing four habitat types (B–E); and T_3, along the same homogeneous valley except adjacent to the foothills. The lower diagram shows the relationship between richness and sampling area over the three transects described above; the arrows indicate the positions of the habitat boundaries crossed by T_2. Transect T_3 has 36 more species than transect T_1; the presence of 29 of these can be attributed to mass effects. More rapid increases in species richness along transect T_3 coincide with habitat transitions along transect T_2. *Redrawn, with permission, from Ref.* 10.

awaits greater understanding of the extent to which local and regional determinants of diversity interact.

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