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*Ecology*, Vol. 75, No. 1. (Jan., 1994), pp. 2-16.

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## COMPETITION AND BIODIVERSITY IN SPATIALLY STRUCTURED HABITATS<sup>1</sup>

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**Abstract.** All organisms, especially terrestrial plants and other sessile species, interact mainly with their neighbors, but neighborhoods can differ in composition because of dispersal and mortality. There is increasingly strong evidence that the spatial structure created by these forces profoundly influences the dynamics, composition, and biodiversity of communities.

Nonspatial models predict that no more consumer species can coexist at equilibrium than there are limiting resources. In contrast, a similar model that includes neighborhood competition and random dispersal among sites predicts stable coexistence of a potentially unlimited number of species on a single resource. Coexistence occurs because species with sufficiently high dispersal rates persist in sites not occupied by superior competitors. Coexistence requires limiting similarity and two-way or three-way interspecific trade-offs among competitive ability, colonization ability, and longevity.

This spatial competition hypothesis seems to explain the coexistence of the numerous plant species that compete for a single limiting resource in the grasslands of Cedar Creek Natural History Area. It provides a testable, alternative explanation for other high diversity communities, such as tropical forests. The model can be tested (1) by determining if coexisting species have the requisite trade-offs in colonization, competition, and longevity, (2) by addition of propagules to determine if local species abundances are limited by dispersal, and (3) by comparisons of the effects on biodiversity of high rates of propagule addition for species that differ in competitive ability.

*Key words:* biodiversity; coexistence; colonization limitation; competition; dispersal; metapopulations; spatial competition hypothesis; spatial subdivision.

### INTRODUCTION

Within any habitat, an individual organism is more likely to interact with neighboring organisms than with more distant ones. This is especially so for terrestrial plants, many marine invertebrates, corals, and other sessile organisms (Pacala 1986a, b, Goldberg 1987, Pacala and Silander 1990). Strong neighborhood interactions are also the rule for motile species that consume ephemeral and patchy resources (Hanski 1990, Shorrocks 1991). However, the dynamics and diversity of a community depend not only on neighborhood interactions, but on the dispersal of organisms among neighborhoods (e.g., Horn and MacArthur 1972, Rabenowitz and Rapp 1981, Gross and Werner 1982, Levin et al. 1984, Paine 1984, Howe et al. 1985, Cohen and Levin 1991, Hassell et al. 1991, and references cited in Shorrocks and Swingland 1990, Gilpin and Hanski 1991). For example, a species may be absent from a locality not because of local biotic interactions

but because none of its propagules has yet arrived at that site. Colonization limitation, which is also called recruitment or dispersal limitation, has been cited as an important factor determining successional dynamics, community diversity and composition, and long-term community dynamics following deglaciation (e.g., Horn 1971, Platt and Weis 1977, Hastings 1980, Davis 1981, 1986, Gross and Werner 1982, Connell 1985, Gaines and Roughgarden 1985, Huston and Smith 1987, Menge and Sutherland 1987, Cornell and Lawton 1992). In total, such studies suggest that sessile organisms often have strong interactions within neighborhoods, but that neighborhoods can differ in composition because of colonization limitation.

For mathematical and conceptual simplicity, most ecological models have assumed that all individuals of all species experience identical conditions, i.e., live in a well-mixed, homogeneous, nonspatial habitat in which all neighborhoods have identical compositions. However, because each individual organism exists at a discrete point in space, there are unavoidable site-to-site differences in the local biotic composition of a habitat

<sup>1</sup> For reprints of this Special Feature, see footnote 1, p. 1.

caused by random colonization and mortality. This occurs even though the underlying physical environment is homogeneous with no physical barriers to dispersal (e.g., Pacala and Silander 1990). Thus, the discreteness of individual organisms means that all organisms live in a spatially structured, subdivided habitat.

There have been numerous theoretical demonstrations that habitat subdivision can allow two species, a fugitive species and a superior competitor, to stably coexist as metapopulations (e.g., Skellam 1951, Levins and Culver 1971, Horn and MacArthur 1972, Armstrong 1976, Hastings 1980, Shmida and Ellner 1984). Spatial structure can also stabilize host-parasite and predator-prey interactions (Huffaker 1958, Kareiva 1987, Kareiva and Odell 1987, Pacala et al. 1990, Hassell et al. 1991), and influence the evolution of cooperative behavior (Nowak and May 1992). Despite its potential importance, spatial structure frequently has been ignored by field workers and theoreticians, myself included, because it greatly increases the types and amounts of data needed for field studies and complicates mathematical theory. However, there is increasingly strong evidence that spatial subdivision is an essential factor controlling the species dynamics and biodiversity of many communities.

My interest in spatial structure grew out of a decade of work regarding successional dynamics and biodiversity in grasslands. Our experiments have shown nitrogen to be the only limiting resource in the old fields and native prairie of Cedar Creek Natural History Area, Minnesota (Inouye et al. 1987, Tilman 1987, 1988, 1990). There is strong belowground competition among plants in these fields (Wilson and Tilman 1991a, b). Herbivory is of low intensity (Tilman 1990). Light is not limiting. Garden experiments have shown that little bluestem (*Schizachyrium scoparium*), a native bunchgrass, is the best nitrogen competitor (Tilman and Wedin 1991b, Wedin and Tilman 1993). Theory predicts that the best competitor for a single limiting resource should displace all other species from a habitat, independent of their initial densities (Tilman 1982). Long-term competition experiments performed in gardens have strongly supported this prediction (Tilman and Wedin 1991b, Wedin and Tilman 1993). Little bluestem did displace all other species from nitrogen-limited garden plots. Its monocultures were almost never invaded by other species, whereas monocultures of lesser competitors had to be weeded frequently. Why, then, do >100 species coexist with little bluestem in grasslands and native prairie in which nitrogen is the only limiting resource?

Explanations of diversity require an interspecific trade-off. A comparison of allocation patterns among 46 species common at Cedar Creek suggested strong

trade-offs between root and reproductive allocation (Gleeson and Tilman 1990). In addition, our five most abundant grass species differed greatly in their allocation to root vs. allocation to vegetative or sexual reproduction in long-term garden monocultures on low nitrogen soils (Tilman and Wedin 1991a). Species with greater allocation to root reduced the soil concentrations of dissolved ammonium and nitrate to significantly lower levels (Tilman and Wedin 1991a). The level to which an equilibrium monoculture of a species reduces the concentration of its limiting resource is called its " $R^*$ " (Tilman 1982). As predicted by theory, species with lower  $R^*$  values for nitrogen displaced other species from low-nitrogen garden competition plots, independent of the initial abundances of the competitors (Tilman and Wedin 1991b, Wedin and Tilman 1993). However, higher allocation to roots corresponded with lower allocation to reproduction, and with slower dispersal.

Our poorest nitrogen competitors, *Agrostis scabra* and *Agropyron repens*, invaded fields immediately after abandonment (Fig. 1A). In contrast, the two best nitrogen competitors, the native bunchgrasses, little bluestem and big bluestem, required 11–17 yr to invade abandoned fields (Fig. 1A), and 30–40 more years to spread across and dominate fields (Fig. 1B). Thus, inferior nitrogen competitors were displaced within 3 or 4 yr when colonization limitation was overcome by the addition of bunchgrass seed in our garden plots (Tilman and Wedin 1991b, Wedin and Tilman 1993), but displacement was extremely slow in nature when the bunchgrasses were self-recruiting. Moreover, these bunchgrasses were rarely more than 50% of plant mass in our grasslands. The species with which they coexisted in nature had higher allocation to reproduction (Gleeson and Tilman 1990, Tilman and Wedin 1991a), rapidly colonized fields, and dominated fields for decades, despite being poorer nitrogen competitors.

Could it be that superior competitors are prevented, by their poorer colonization abilities, from occupying the entire landscape, and that this provides sites in which numerous species of inferior competitors can persist? Might this be a general pattern in plant communities? The chalk grasslands of England and Europe are similar in having a matrix of tussock grasses within which numerous additional species persist (Grubb 1986). Grubb has suggested that differences in the dispersal and establishment abilities of these species are critical for the maintenance of diversity.

Similar questions arise for animal communities. Hanski (1990) studied the fly community that consumes carrion in southern Finland. Although all 14 fly species persist in nature, only 3 of 14 species persisted when confined to cages provisioned with liver each week of the growing season. One of these species was

the best competitor. The persistence of the other two depended on liver being provided as numerous small pieces scattered across the cage. Hanski (1990) suggested that natural diversity was maintained by interspecific differences in competition and dispersal abilities. Shorrocks (1991) studied competition for ephemeral resources by two species of *Drosophila*. The superior competitor, *D. melanogaster*, displaced *D. immigrans* from undivided habitats, but the species coexisted in spatially subdivided habitats. Thus, spatial subdivision allowed global coexistence of competitors despite one species being a superior competitor in any food patch.

Such results raise a number of questions that are addressed in this paper. Can spatial subdivision allow the stable coexistence of a large number of competing species that could not coexist in a well-mixed habitat? If so, what traits must organisms have to stably coexist? Are such traits likely? What are the dynamics of such communities? Are there deterministic limits to the similarity of coexisting competitors? Can coexistence occur when the only source of "disturbance" is the death of individual organisms?

Aspects of these questions have been addressed in models of competition and dispersal in subdivided habitats (e.g., Levins 1969, Levin 1974, 1976, Yodzis 1978, Hastings 1980, Hanski 1982, 1983, 1989, Shmida and Ellner 1984, Harrison et al. 1988, Gotelli 1991, Nee and May 1992), and in papers that treat space as if it were just another essential resource (Platt and Weis 1977, Tilman 1982). In this paper, I first summarize the original model of Levins (1969) and the extensions by Hastings (1980) and by Nee and May (1992). A modified version of their models is then used to explore interactions in a subdivided habitat among a potentially unlimited number of species. This demonstrates that spatial subdivision can explain the stable coexistence of an unlimited number of competing species in a physically homogeneous habitat.

#### THEORY OF COMPETITION IN A SUBDIVIDED HABITAT

##### *Levins' model of the dynamics of a single species*

Consider a single sessile species living in a habitat composed of distinct sites, where each site is the size of the area occupied by one adult. The death of an adult would provide an opening for colonists. The dynamics of site occupancy would depend on the difference between the rate at which empty sites were colonized and the rate at which sites became vacant because of mortality. The dynamics of the entire habitat are the sum of the individual-by-individual processes of

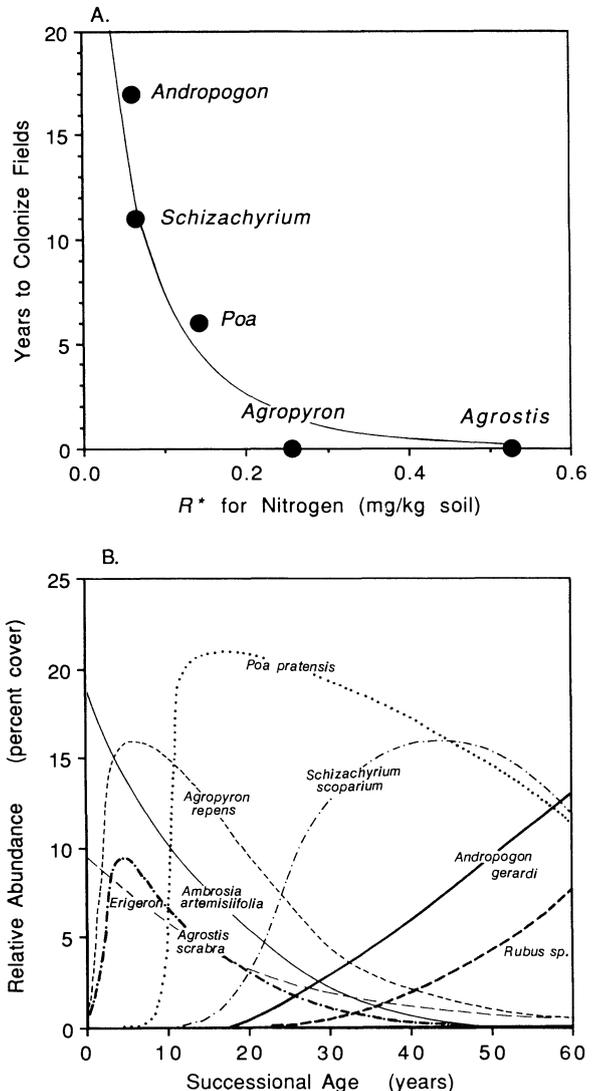


FIG. 1. (A) The observed interspecific trade-off between the years required for a dominant grass species to invade old fields and the competitive ability of the species for soil nitrogen (from Tilman 1990). Competitive ability is expressed as the observed  $R^*$  of each species for soil nitrogen, as determined in long-term monocultures of each species on a low nitrogen soil (Tilman and Wedin 1991a). Species with lower  $R^*$  values are superior nitrogen competitors in a long-term garden study (Tilman and Wedin 1991b, Wedin and Tilman 1993), but are much slower to colonize abandoned fields at Cedar Creek Natural History Area. (B) The approximate dynamics of succession at this site, based on a chronosequence of old fields (from Tilman 1988).

death (mortality) and replacement (colonization) in each site.

Let  $p$  be the fraction of sites occupied by a species, which will be called its abundance. Levins (1969) proposed a simple, general model for the dynamics of site

occupancy in such a system:

$$\frac{dp}{dt} = cp(1 - p) - mp, \quad (1)$$

where  $c$  is the colonization rate and  $m$  is the mortality (local extinction) rate. Propagules disperse randomly among all sites. The rate of propagule production by the occupied sites,  $cp$ , is multiplied by the proportion of sites that are not yet occupied,  $1 - p$ , to give the rate of production of newly colonized sites. The mortality rate,  $m$ , is multiplied by the proportion of occupied sites,  $p$ , to give the density-independent rate at which occupied sites become vacant. A site becomes vacant when the individual occupying that site dies.

This model, which is directly analogous to the classical logistic growth equation, has a globally stable equilibrium point (Hastings 1980), as does the logistic. Global stability means that the abundance of a species eventually approaches its equilibrium value,  $\hat{p}$ , for all possible initial abundances (except  $p = 0$ ), and returns to this equilibrium after any size perturbation away from equilibrium (except one that gives  $p = 0$ ). Equilibrium occurs when  $dp/dt = 0$ , i.e., when there is no change in the abundance of the species. Thus, when Eq. 1 is set equal to zero, it is seen that the proportion of the habitat occupied at equilibrium,  $\hat{p}$ , is

$$\hat{p} = 1 - \frac{m}{c}. \quad (2)$$

This shows that a species can persist in a habitat only if its colonization rate,  $c$ , is greater than its mortality rate,  $m$ . Greater colonization rates or lower mortality rates lead to greater abundance.

The most interesting feature of Eq. 2 is that a sessile species can never fill a habitat (i.e., have  $\hat{p} = 1$ ). For a species to completely fill a spatially structured habitat, the species would have to be immortal ( $m = 0$ ) or have infinite dispersal abilities ( $c \rightarrow \infty$ ), both of which are biologically unrealistic. The remainder of this paper assumes that  $m_i > 0$  and  $c_i$  is finite for all species  $i$ . Such values mean that a species must leave a portion,  $\hat{s}$ , of the sites open, where  $\hat{s} = 1 - \hat{p} = m/c$ .

In the purest interpretation of this mathematics, each site should be the size of a single adult individual. This is the interpretation that I use throughout this paper. However, this model can approximate the dynamics of a series of local populations that are linked via dispersal, which Levins (1969) called a metapopulation (see Gilpin and Hanski 1991). When this model is used for a metapopulation, it must be assumed that each site is either empty or has attained its carrying capacity, and that the transition to a filled site occurs rapidly compared to colonization (Hanski and Gilpin 1991).

### Competition between two species

Because individuals of a single species cannot occupy all the sites in a habitat, a species that is an inferior competitor may be able to invade into and survive in the open portion of a habitat. This, in essence, is the basis for stable coexistence of two competitors in the cases discussed by Levins and Culver (1971), Horn and MacArthur (1972), Hastings (1980), Nee and May (1992), and others. In reviewing their work, I will use Hastings's formulation, because it is the simplest, but will increase its generality by having mortality be a species-specific parameter. Hastings (1980) assumed that all species experienced the same mortality (disturbance) rate. Consider two competing species whose interactions are structured to give a competitive hierarchy. Let the superior competitor be species 1 and the inferior competitor be species 2. Subscripts refer to species. Let us assume that the superior competitor always displaces the inferior competitor when both species co-occur in a site, but that the inferior competitor can neither invade into nor displace the superior competitor from a site. This leads to two equations:

$$\frac{dp_1}{dt} = c_1 p_1 (1 - p_1) - m_1 p_1 \quad (3.1)$$

$$\frac{dp_2}{dt} = c_2 p_2 (1 - p_1 - p_2) - m_2 p_2 - c_1 p_1 p_2. \quad (3.2)$$

The superior competitor (Eq. 3.1) has the same equation as would a species living by itself, and thus is totally unaffected by the inferior competitor. The inferior competitor, species 2, can colonize only sites in which both it and species 1 are absent (the term  $1 - p_1 - p_2$  in Eq. 2). However, species 1 can invade into and displace species 2 (the term  $-c_1 p_1 p_2$  in Eq. 3.2). If the species have identical mortality rates, any two-species equilibrium point is globally stable (Hastings 1980). Global stability occurs because the first species grows logistically, and approaches its equilibrium abundance. Once the first species is at (or very near to) equilibrium, species 2 grows logistically to its equilibrium.

The superior competitor must have a colonization rate of  $c_1 = m_1 / (1 - \hat{p}_1)$  to attain an equilibrium abundance of  $\hat{p}_1$ . The inferior competitor can invade only if  $dp_2/dt > 0$  for  $p_1 = \hat{p}_1$ . When the value of  $c_1$  (above) is substituted into Eq. 3.2 with  $dp_2/dt > 0$ , it is seen that species 2, the inferior competitor, can invade only when

$$c_2 > c_1 \left( \frac{\hat{p}_1}{1 - \hat{p}_1} + \frac{m_2}{m_1} \right). \quad (4.1)$$

Any two-species equilibrium point ( $\hat{p}_1, \hat{p}_2 > 0$ ) that results from the inferior competitor having a coloni-

zation rate that obeys this inequality is locally stable (Appendix). By substituting in the equilibrium abundance of species 1, this can be expressed as

$$c_1 > m_1 \quad (4.2)$$

and

$$c_2 > \frac{c_1(c_1 + m_2 - m_1)}{m_1} \quad (4.3)$$

These are the necessary and sufficient conditions for the stable coexistence of a superior and an inferior competitor in a subdivided habitat. When mortality rates are equal, with  $m_1 = m_2 = m$ , Eq. 4.3 simplifies to  $c_2 > c_1^2/m$ , which is the relationship derived by Hastings (1980). In this case  $c_2$  must be greater than  $c_1$  because  $c_1 > m$ , and  $c_1/m$  is thus  $> 1$ .

If the mortality rate of the inferior competitor ( $m_2$ ) is greater than or equal to the mortality rate of the superior competitor ( $m_1$ ), then the inferior competitor can only exist ( $\hat{p}_2 > 0$ ) if it also has a greater colonization rate (Eqs. 4.2 and 4.3). However, as shown by Nee and May (1992), if the inferior competitor has a lower mortality rate than the superior competitor, it may stably coexist even if it has a lower colonization rate than the superior competitor. The inferior competitor-colonist coexists with the superior competitor-colonist because its lower mortality rate reduces the amount of open space that it needs to survive. When its mortality rate is sufficiently low, it may be able to survive in the space left open by the superior competitor-colonist. However, this occurs only if at least half of the habitat is left open by the superior competitor-colonist species. If there is less open space than this, an inferior competitor must have greater colonization ability in order to coexist, no matter how low its mortality rate might be. Eq. 4.1 shows this because, when  $\hat{p}_1 = 0.5$ , it simplifies to  $c_2 > c_1(1 + m_2/m_1)$ , and this means that  $c_2$  must be greater than  $c_1$  no matter how small  $m_2$  might be.

At equilibrium (Eqs. 3.1 and 3.2 set equal to 0),  $\hat{s}_2$ , the proportion of sites not occupied by the two species, is

$$\hat{s}_2 = 1 - \hat{p}_1 - \hat{p}_2 = \frac{m_2}{c_2} + \frac{c_1}{c_2} \left( 1 - \frac{m_1}{c_1} \right). \quad (5)$$

Because  $c_1$  must be greater than  $m_1$  for species 1 to exist, the term  $(1 - m_1/c_1)$  is always positive, as are the other terms in this equation. Thus  $c_2$  has to approach  $\infty$  for the amount of open space,  $\hat{s}_2$ , to approach 0. It is impossible for species 1 and 2 to fill the entire habitat if each experiences some mortality and each has a finite colonization rate. A portion of the habitat remains open and potentially can be invaded by other species.

#### *Additional results of Hastings and of Nee and May*

Hastings (1980) and Nee and May (1992) used competition models similar to that given above. Hastings focused on the effects of disturbance on species richness, and thus had all species experience the same mortality rate. He derived the interesting result that species richness should be maximal at intermediate disturbance rates, but that this need not be a unimodal relationship. Indeed, it is possible for species richness to rise and fall several times as disturbance rate increases in a system in which the presence or absence of one species affects the ability of another species to invade.

Nee and May (1992) addressed the important question of the effects of habitat destruction on two-species competition. Their model included the proportion of the habitat made inhospitable to both species by habitat destruction. They showed that increased habitat destruction led to increased abundance of a weedy, fugitive species in the portion of the habitat that was undisturbed. Thus, habitat loss can lead to significant changes in the composition of the remaining, undisturbed patches, even though disturbed patches are not serving as sources of weedy propagules.

#### *Multispecies competition*

Previously published work has clearly demonstrated that spatial subdivision may allow the stable coexistence of two species that are incapable of coexisting in any single site. This stable coexistence does not depend on any underlying physical heterogeneity or barriers in the habitat. Rather, all that it requires is for each individual to compete only within its neighborhood, for neighborhoods to be joined by dispersal, and for species to have appropriate trade-offs.

To generalize this to any number of species, rank the species from the best competitor (species 1) to the poorest. The equation for the dynamics of the  $i^{\text{th}}$  species is

$$\frac{dp_i}{dt} = c_i p_i \left( 1 - \sum_{j=1}^i p_j \right) - m_i p_i - \left( \sum_{j=1}^{i-1} c_j p_j p_i \right). \quad (6)$$

There are  $n$  such equations for  $n$  species. The dynamics of each species depend on colonization (the first term), on mortality (the term  $-m_i p_i$ ), and on competitive displacement (the last term). A species is only affected by species that are superior competitors.

Before analyzing this model, let us consider its assumptions. The model does not include the mechanisms of resource competition (e.g., O'Brien 1974, Tilman 1976, 1982, Hsu et al. 1977). Rather, it summarizes the essential qualitative features of competition for a single limiting resource. The model assumes that a single species is the best competitor (i.e., would have the lowest " $R^*$  value" in a model of competition for

a single resource; Tilman 1982), and would displace and exclude all other species from a site. All species are arranged in a simple competitive hierarchy, comparable to a ranking from the lowest to highest  $R^*$ . A better competitor can invade a site containing a poorer competitor and displace it, but a poorer competitor can neither invade nor displace a better competitor. The habitat is spatially subdivided but, for any given species composition, the outcome of competition is identical in all localities. However, localities may differ in species composition as a result of local biotic displacement, local mortality, and colonization. All recruitment is internal. Once a species has gone extinct throughout the habitat, there is no possibility of re-establishment. Organisms reproduce, colonize, and die continuously. Thus, the model deals with the internal dynamics of recruitment, biotic interaction, and mortality in a spatially subdivided, but infinitely large habitat. The model does not include local dispersal, but rather assumes that propagules are scattered, at random, over the entire habitat.

At equilibrium (Eq. 6 set to 0), the  $n^{\text{th}}$  species occupies a proportion,  $\hat{p}_n$ , of the habitat, where

$$\hat{p}_n = 1 - \frac{m_n}{c_n} - \sum_{j=1}^{n-1} \left[ \hat{p}_j \left( 1 + \frac{c_j}{c_n} \right) \right]. \quad (7)$$

This is similar to the equation for the abundance of a single species ( $\hat{p} = 1 - m/c$ , Eq. 2), except that the abundance of the  $n^{\text{th}}$  species also is reduced by the summed abundances of all its superior competitors and by the summed ratio of the rate at which it is displaced by superior competitors to its dispersal rate.

It is possible to sequentially calculate, starting with species 1, the colonization rate required for each species to attain its equilibrium abundance (Appendix). The required colonization rate of the  $n^{\text{th}}$  species is

$$c_n = \frac{\sum_{i=1}^{n-1} (\hat{p}_i m_i) + \left( 1 - \sum_{i=1}^{n-1} \hat{p}_i \right) m_n}{\left( 1 - \sum_{i=1}^{n-1} \hat{p}_i \right) \left( 1 - \sum_{i=1}^n \hat{p}_i \right)}. \quad (8)$$

All multispecies equilibria resulting from such colonization and mortality rates are locally stable (Appendix).

Eq. 8 can be rearranged to show that it is impossible for a chain of  $n$  species, no matter how long, to occupy all sites in a habitat. A portion of the sites,  $\hat{s}_n$ , remains open at equilibrium:

$$\hat{s}_n = 1 - \sum_{j=1}^n \hat{p}_j = \frac{m_n \hat{s}_{n-1} + \sum_{j=1}^{n-1} \hat{p}_j m_j}{c_n \hat{s}_{n-1}} > 0. \quad (9)$$

It has already been shown that neither the first nor the

first and second species (Eq. 5) can occupy the entire habitat. Clearly, this is also true for three species ( $n = 3$  in Eq. 9). Given this, it is also true for  $n = 4$ , and so on, as long as  $c_n$  is finite and  $m_i > 0$  for all  $i$ . Thus, by induction, Eq. 9 demonstrates that it is impossible for a string of any number of species to occupy all sites in a habitat at equilibrium.

This means that it is theoretically possible to find colonization rates and mortality rates that allow an additional species, species  $n + 1$ , to invade and stably coexist with any number of superior competitor species. No matter what the colonization and mortality rates of superior competitors might be, an inferior competitor with appropriate traits can always invade and persist. Thus, within the framework of this model, there is no limit to the number of species that can coexist stably in a spatially subdivided habitat, even though the best competitor would displace all other species from a habitat that was not spatially subdivided. This may be called the spatial competition hypothesis of diversity.

If all species have identical mortality rates,  $m$ , Eq. 8 becomes the simple relationship that species  $n$  will be able to invade and persist only if its colonization rate is

$$c_n > \frac{m}{\hat{s}_{n-1}^2}. \quad (10)$$

An inferior competitor must have a colonization rate that is greater than the universal mortality rate divided by the square of the proportion of the habitat left open by its superior competitors. Thus, the requisite colonization rate rises quite steeply as the amount of open space declines.

#### Multispecies dynamics

In this model (Eq. 6), interactions that start away from equilibrium lead to damped oscillations (Figs. 2–4). The dynamics of two species are simple. The superior competitor is unaffected by the inferior species and displays logistic (sigmoid) growth. Because of its higher colonization (Fig. 2A) and/or lower mortality rate (Fig. 2B), the inferior competitor can more rapidly fill an empty habitat, but is brought to equilibrium as the superior competitor approaches equilibrium.

For four species that have identical colonization rates but differ in mortality rates, the superior competitor (species 1) and the next best competitor have dynamics much as illustrated in Fig. 2, but the two next poorer competitors have more complex dynamics (Fig. 3A). A similar pattern occurs for four species with identical mortality rates but different colonization rates (Fig. 3B). There need be no relationship between the equilibrium abundances of species and their competitive abilities. The poorest competitor can have the highest

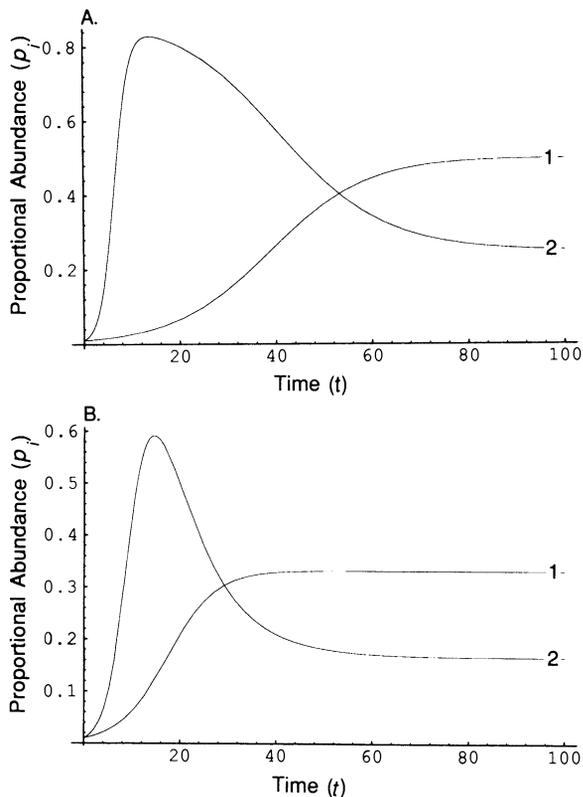


FIG. 2. Dynamics of competition among two species, with species 1 being the better competitor. (A) Species 1 had colonization rate  $c_1 = 0.2$  and mortality rate  $m_1 = 0.1 \text{ yr}^{-1}$ . Species 2 had  $c_2 = 0.8$  and  $m_2 = 0.1 \text{ yr}^{-1}$ . Both species had initial proportional abundances of 0.01. (B) Here, species 1 had  $c_1 = 0.6$  and  $m_1 = 0.4 \text{ yr}^{-1}$ . Species 2 had  $c_2 = 0.6$  and  $m_2 = 0.1 \text{ yr}^{-1}$ . Both species had initial proportional abundances of 0.01. These, and all other simulations in this paper, represent iterative solutions to Eq. 5, using the NDSolve routine in Mathematica (Wolfram 1991).

equilibril abundance (Fig. 3C). In these and other numerical solutions of the model (Eq. 6), all species attained their predicted equilibria, independent of initial abundances, suggesting that multispecies equilibria are globally stable. Once the best competitor attains its globally stable equilibrium, the equation for the next best competitor takes on the form of the equation for the first species, and the second species goes to equilibrium. This should propagate down through any number of species, leading to global stability for the multispecies equilibrium point. Mathematical global stability, however, does not mean that perturbations would not cause the loss of biodiversity in a real ecosystem. Ecosystems have a finite size. Forces not included in this simple model, such as demographic stochasticity (May 1973) and random walks to extinction, can prevail during the periods of low abundance that follow a perturbation.

Consider, also, the dynamics of competition among 40 species (Fig. 4A–C). For these cases, species were chosen to have colonization and mortality rates such that their equilibril abundances formed a geometric series, i.e.,  $\hat{p}_i = z(1 - z)^{i-1}$ , where  $i$  refers to species, with species 1 being the best competitor. For this case,

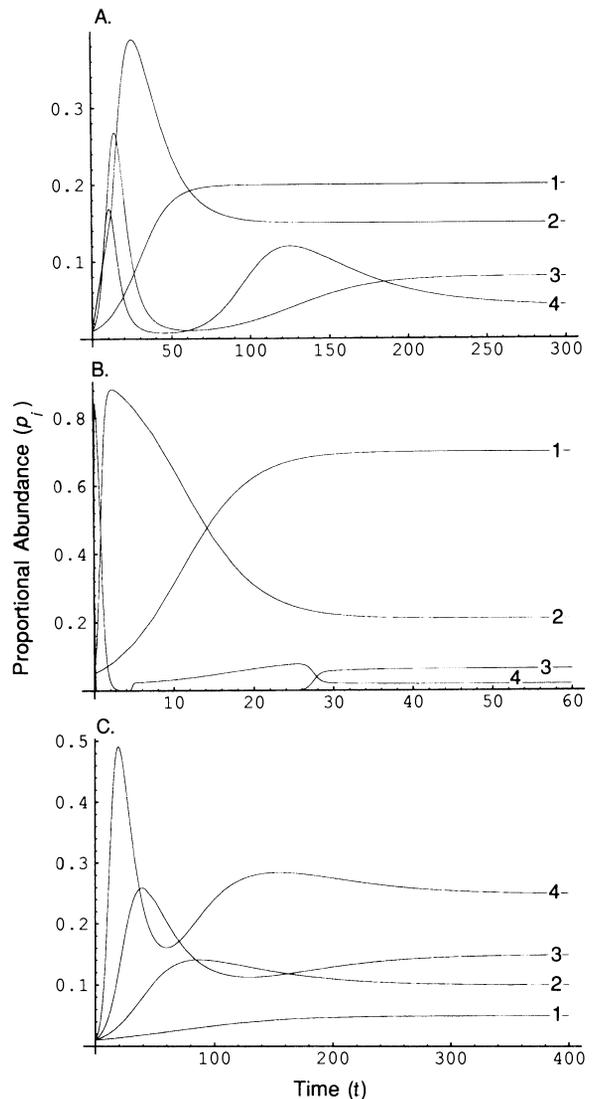


FIG. 3. Dynamics of competition among four species, with species 1 being the best competitor and species 4 the poorest. (A) In this case, all species have identical colonization rates ( $c_i = 0.5$  for  $i = 1, 4$ ), but different mortality rates ( $m_1 = 0.4$ ,  $m_2 = 0.225$ ,  $m_3 = 0.11$ ,  $m_4 = 0.05 \text{ yr}^{-1}$ ). All species had initial abundances of 0.01. (B) Species have identical mortality rates (0.1  $\text{yr}^{-1}$ ), but different colonization rates ( $c_1 = 0.333$ ,  $c_2 = 3.7$ ,  $c_3 = 41.15$ ,  $c_4 = 457.2$ ). All species had initial abundances of 0.05. (C) Colonization rates ( $c_1 = 0.421$ ,  $c_2 = 0.377$ ,  $c_3 = 0.369$ ,  $c_4 = 0.476$ ) and mortality rates ( $m_1 = 0.4$ ,  $m_2 = 0.3$ ,  $m_3 = 0.2$ ,  $m_4 = 0.1 \text{ yr}^{-1}$ ) give an equilibrium in which the best competitor is the rarest.

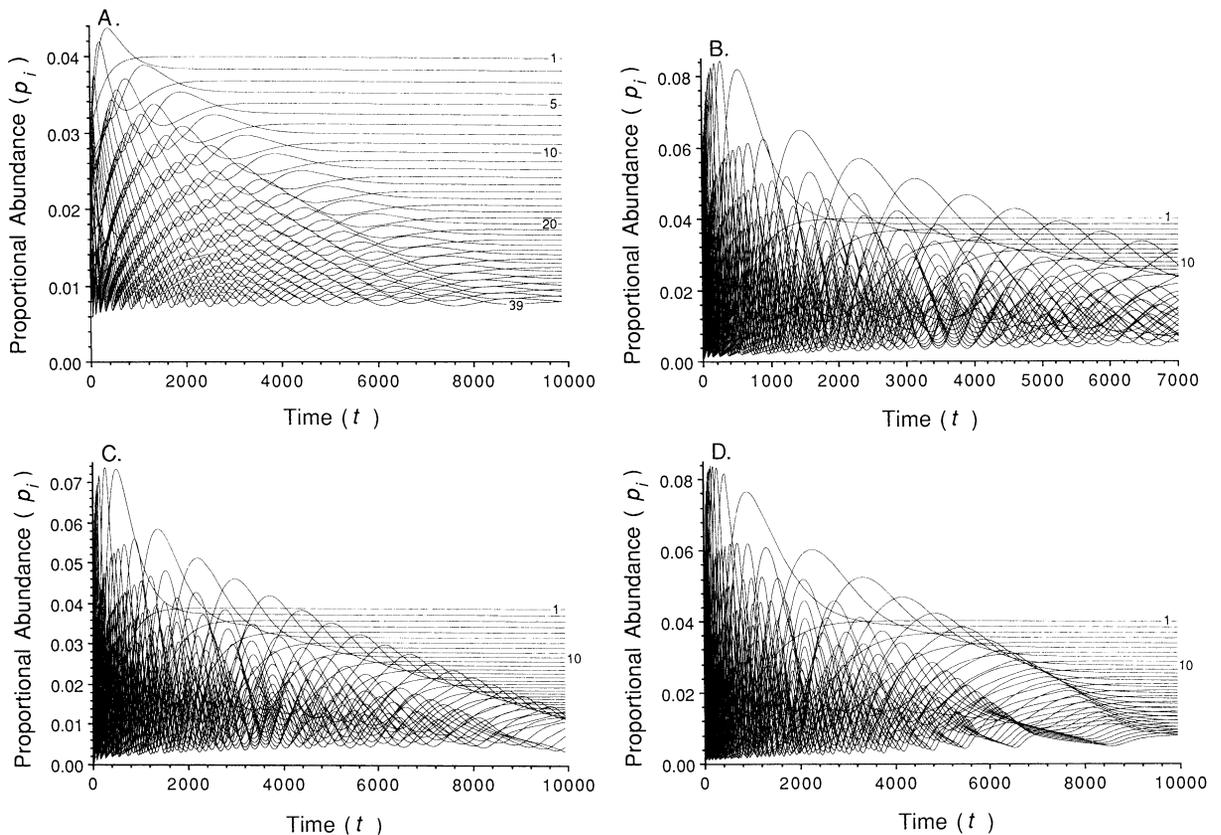


FIG. 4. Dynamics of competition among 40 species, as determined by numerical solutions of Eq. 5, with species 1 the best competitor and species 40 the worst. (A) Species had traits shown in Fig. 5A, with  $m = 0.1 \text{ yr}^{-1}$  for all species. Each species had an initial proportional abundance equal to 75% of its predicted equilibrium abundance. (B) Species traits identical to those of part (A), except initial abundances depended on their colonization rates. The initial abundance of species  $i$  was  $c_i/31$ , for  $i = 1, 40$ . This meant that 99.5% of sites were filled initially, and that better colonists occupied more sites, initially, than did poorer colonists. (C) Species traits identical to those of part (A), except all species were initially equally rare (each had a proportional abundance of 0.005). (D) Species had the traits shown in Fig. 5B. Species differed in both colonization and mortality rates. The best competitor, species 1, had the lowest mortality rate. The mortality rate of species  $i$  was  $m_i = 0.04 + 0.01i$ . The colonization rates required, for species with these mortality rates and competitive abilities, to attain the equilibrium abundances shown in Fig. 5B were calculated with Eq. 8.

the best competitor is rare ( $z = \hat{p}_1 = 0.04$ ), poorer competitors are progressively rarer, and all species have identical mortality rates ( $m = 0.1 \text{ yr}^{-1}$ ). Eq. 8 gives the colonization rate each species must have to obtain its equilibrium abundance (Fig. 4B). The dynamics of competition among the 40 best competitor species are illustrated for cases in which all species started either close to their equilibrium abundances (Fig. 4A), or at an initial density that was greater the greater their colonization rate (Fig. 4B), or at identical but rare abundances (Fig. 4C).

In all cases, all 40 species persisted for the entire simulation. Initially they displayed complex dynamics, but were kept from extinction by the stabilizing effect of spatial subdivision and by the infinite habitat that the model assumed. The best competitor approached

equilibrium first, followed by the next best competitor, and so on (Fig. 4A–C). All species that reached equilibrium by the end of the simulations had attained their predicted abundances. However, many species had not reached equilibrium after 100 generations (assuming a generation time of 100 yr). Another case, in which species differed in both mortality and colonization rates, gave qualitatively similar dynamics (Fig. 4D). If species are rarer, or have lower mortality rates, the approach to equilibrium is even slower.

#### Limiting similarity

An interesting feature of this model of spatial competition is its analytical limit to the similarity of adjacent species in the competitive hierarchy. This limiting similarity means that it is not sufficient for an

inferior competitor to have a lower mortality rate and/or a higher colonization rate than its next best competitor. Rather, its traits must differ from those of its superior competitor by a finite amount that depends, mainly, on the abundance of its superior competitor. Although this can be shown for the general case in which species differ in both mortality rate and colonization rate (by solving Eq. 8 for  $p_n = 0$ ), it is most easily understood for the two special cases below.

*Identical mortality rates.*—If all species have identical mortality rates, Eq. 8 can be used to show that the minimal colonization rate of species  $n$  (i.e., the rate that gives  $p_n > 0$ ) must be greater than the colonization rate of species  $n - 1$  by an amount that depends on the amount of open space left by the superior competitors:

$$c_n > c_{n-1} \left( \frac{\hat{s}_{n-2}}{\hat{s}_{n-1}} \right). \quad (11)$$

Having  $c_n > c_{n-1} > \dots > c_1$  is not sufficient to assure that all  $n$  species can coexist. Rather, there is an analytical limit to similarity. For example, if the amount of open space left by species 1 to  $n - 2$  was 0.1 and if the amount of open space left by species 1 to  $n - 1$  was 0.02, then for species  $n$  to exist ( $\hat{p}_n > 0$ ), it must have a colonization rate more than  $c_{n-1}(0.1)/(0.02)$ , or  $5c_{n-1}$ . This means that an inferior competitor that had a colonization rate  $< 5$  times  $c_{n-1}$  would not persist. The difference between  $\hat{s}_{n-2}$  and  $\hat{s}_{n-1}$  is just  $p_{n-1}$ . Thus, it is mainly the abundance of the next best competitor,  $\hat{p}_{n-1}$ , that determines the limit to similarity. For instance, if  $\hat{s}_{n-2} = 0.1$ , and if species  $n - 1$  were rare, e.g.,  $\hat{p}_{n-1} = 0.01$ , then  $c_n$  would just have to be 1.11 times  $c_{n-1}$  ( $1.11 = 0.1/0.09$ ). Or, if  $\hat{p}_{n-1} = 0.001$ , then  $c_n$  would only have to be 1.01 times  $c_{n-1}$ . When superior competitors are rarer, species may be more similar in their colonization abilities and still coexist, assuming that all species experience the same mortality rate. This limit to similarity need not limit species diversity. An inferior competitor with a sufficiently greater colonization rate can always invade and coexist, no matter how abundant its superior competitor might be.

*Identical colonization rates.*—There is a comparable limit to similarity in mortality rates if species have identical colonization rates,  $c$ . For species 1 to attain an equilibrium abundance of  $p_1$ , it must have a mortality rate of  $m_1 = c(1 - \hat{p}_1)$ . For species 2 to have an abundance of  $\hat{p}_2$ , its mortality rate must be  $m_2 = c(1 - 2\hat{p}_1 - \hat{p}_2)$ . In general, for the  $n^{\text{th}}$  species to have an equilibrium abundance of  $\hat{p}_n$ , Eq. 7 can be used to show that its mortality rate must be

$$m_n = c(\hat{s}_{n-1} + \hat{s}_n - 1). \quad (12)$$

The less open space there is in a habitat, the lower must

be the mortality rate of an inferior competitor if it is to coexist with a group of species that have identical colonization rates. However, all mortality rates must be  $> 0$ . If Eq. 12 is constrained to have  $m_n > 0$ , species  $n$  can only exist (i.e., have  $\hat{p}_n > 0$  in Eq. 12) if

$$\hat{s}_{n-1} > \frac{1}{2}. \quad (13)$$

Thus, this model leads to a surprising prediction. Once superior competitors fill at least a habitat, it is impossible for an inferior competitor to coexist, even if it were immortal, if all species have identical colonization rates. However, until this limit is reached, it is possible for a series of species to stably coexist if inferior competitors have sufficiently lower mortality rates than their next better competitors.

Assuming that Eq. 13 holds, Eq. 12 can be used to derive the analytical limit to similarity in mortality rates for competitively adjacent species with identical colonization rates:

$$m_n < m_{n-1} \left( \frac{2\hat{s}_{n-1} - 1}{\hat{s}_{n-1} + \hat{s}_{n-2} - 1} \right). \quad (14)$$

For instance, if the amount of open space left by species 1 to  $n - 1$  were 0.55, and that left by species 1 to  $n - 2$  were 0.65, then  $m_n$  must be less than  $m_{n-1}/2$ . Values of  $m_n$  lower than this would lead to a greater equilibrium abundance,  $\hat{p}_n$ , for species  $n$ . If  $m_n$  were greater than this, species  $n$  would go extinct.

These analyses have shown that competitively adjacent species can coexist only if the colonization and/or mortality rates of the inferior competitor are sufficiently different from those of its next best competitor. However, interspecific differentiation in longevity is only possible if less than half of the sites in a habitat are filled with superior competitors, whereas differentiation in colonization can occur for any abundances of superior competitors.

## DISCUSSION

### *Interspecific trade-offs and stable coexistence*

As Pacala (1986a, b), Ives (1988), and Hanski and Cambefort (1991) have shown, neighborhood interactions and local dispersal increase intraspecific competition relative to interspecific, and thus encourage stable coexistence. Hassell et al. (1991) have shown that spatial subdivision and local dispersal can cause intriguing spatial dynamics and stabilize predator-prey dynamics. Nisbet and Gurney (1982) demonstrated that the persistence time of a population with a metapopulation structure increases exponentially with the number of habitat sites. The multispecies model developed here demonstrates that spatial subdivision has similar

effects on competitors, allowing a potentially unlimited number of species to stably coexist in a physically homogeneous, equilibrium habitat.

This model, which I call the spatial competition hypothesis, provides an alternative explanation for the high species richness of many communities of sessile organisms. It demonstrates that the concept of stable coexistence of a competitor and a fugitive (e.g., MacArthur and Wilson 1967, Horn and MacArthur 1972) can be extended to an unlimited number of species. Coexistence occurs even though a single species would displace all others from any given site. Diversity does not require large-scale disturbances, but can occur through plant-by-plant replacement in a subdivided habitat in which all species are limited by and compete for a single resource. Spatial subdivision, which is an unavoidable result of the sessile life-style, thus may be a major factor favoring high local diversity in communities of sessile organisms. Moreover, even in motile species, neighboring individuals are more likely to interact than are more distant individuals. Thus, the spatial competition hypothesis may also explain coexistence of motile competitors.

Species that coexist by the mechanisms assumed by the spatial competition hypothesis must have the appropriate two- or three-way interspecific trade-offs among competitive ability, colonization ability, and longevity. Allocation differences may cause unavoidable trade-offs between competitive and colonization abilities (e.g., Werner and Platt 1976). Biomass and nutrients allocated to competitive structures (root for nutrient-limited plants or leaf and stem for light-limited plants) cannot be allocated to dispersal structures (seed, fruit, pappus, rhizome, etc.). This is the major axis of interspecific differentiation among plants at Cedar Creek (Gleason and Tilman 1990).

However, it is uncertain if there must be a trade-off between longevity and competitive ability. Many species that are good nutrient competitors are nutrient-conserving evergreens (Chapin 1980). Because nutrient conservation is often accomplished via increased tissue longevity, better competitors may be more long lived. Similarly, better competitive ability for light requires greater allocation to stems, and such plants are only successful if they survive long enough to reach the canopy. Thus, differentiation between dispersal and competitive ability may be more important than differentiation between longevity and competitive ability in allowing multispecies coexistence, but this question merits additional study.

#### *Limits to diversity*

These results indicate that there need be no limit to species richness in a spatially subdivided habitat with a single limiting resource, assuming that species have

the appropriate two-way or three-way trade-offs among competitive ability, colonization ability, and longevity. What might limit diversity in such a system?

The spatial competition model assumed that a habitat was infinitely large. For instance, species  $n$  was assumed to be able to invade and stably persist if  $\hat{p}_n > 0$ . In a finite habitat, there are a finite number of sites, and a species will be present only if it always occurs in at least one site. This means that a species would go extinct if its abundance fell below some minimum value,  $p_{\min}$ , which should be inversely dependent on area. This would restrict species richness to a finite value. There would be an absolute upper bound on species richness of  $1/p_{\min}$ , and species richness would be lower than this by an amount that depended on the actual abundances of the more abundant species.

Demographic stochasticity would further reduce species richness. Demographic stochasticity is the temporal variance in population density caused by randomness in the reproduction and mortality of individuals (May 1973). The lower the average density of a species, the greater, on a percentage basis, is the fluctuation around the mean caused by demographic stochasticity (May 1973). These fluctuations could cause species to go extinct even though their  $\hat{p}$  was greater than  $p_{\min}$ .

Evolutionary limits to dispersal ability or longevity would also limit diversity. For inferior competitors to invade and coexist, their dispersal abilities must increase as one over the square of the amount of space unoccupied by superior competitors (Eq. 10). If there were a maximal possible dispersal rate,  $c_{\max}$ , and a minimal possible mortality rate,  $m_{\min}$ , then, for any given distribution of relative species abundances, there would be a limit to diversity even in an infinitely large habitat.

Dispersal limitation might also explain latitudinal diversity gradients. Glaciations and associated climatic changes are greater toward the poles. Species that presently occupy more poleward habitats have had to migrate great distances in response to climatic change (Davis 1981, 1986) and have experienced major range contractions. These would have increased the chance of extinction of temperate or arctic species, especially less well-dispersed species. If historical climatic changes led to shorter migration distances per unit time in subtropical or tropical habitats than in temperate and arctic habitats, the more equatorial habitats would have experienced lower extinction rates and thus have greater species richness.

#### *Comparisons with Hubbell and Foster*

The spatial competition model analyzed here differs significantly from the model of Hubbell (1979) and Hubbell and Foster (1986), even though both models

consider colonization and mortality in spatial habitats. Hubbell (1979) and Hubbell and Foster (1986) suggested that there were a few major guilds of tropical tree species, including gap specialists. However, they felt that many more species coexisted within a guild than could be explained by interspecific differentiation. They hypothesized that each guild contained large numbers of functionally identical species for which competitive displacement would not occur. Rather, the abundances of such species would be determined by random local mortality and colonization. This leads to random drift in abundances, with the ultimate outcome being random walks to extinction of all but one species. They suggested that the rate of such extinctions is slowed by spatial subdivision in large habitats, and that the extinction rate may be as low as the rate of evolution of new species. Thus, they hypothesized that rain forest diversity may be maintained by a loose balance between speciation and the slow extinction of functionally identical species.

The spatial competition hypothesis provides an alternative explanation for species-rich plant communities. Tree species differ in dispersal and longevity (e.g., Howe et al. 1985, Lieberman and Lieberman 1993). If there are the requisite interspecific trade-offs among dispersal, longevity, and competitive ability, the spatial competition model demonstrates that these could allow stable persistence of numerous species competing for a single resource. Although this coexistence requires limiting similarity, most rain forest trees are rare. The model predicts that rare species can be quite similar and still stably coexist (Eqs. 10 and 13).

For instance, of the 40 species that stably coexisted in Fig. 4, the 10 best competitors (numbered 1 to 10) have sufficiently similar colonization rates (Fig. 5A, B) that it might be tempting to classify them as a guild of superior competitors. The 10 best dispersers (numbered 31 to 40) might similarly be lumped as a guild of gap specialists. However, the trade-offs associated with their small interspecific differences in colonization and competitive abilities allow their long-term, stable coexistence. Subtle interspecific trade-offs, which are ignored when species are grouped as guilds, may allow the long-term coexistence of numerous species. Clearly, further data and analyses are needed to test among the spatial competition hypotheses, the hypothesis of functionally identical plant species guilds, and other hypotheses (e.g., Janzen 1970, Huston 1979, Tilman 1982) of the maintenance of highly diverse plant communities. Because species in the spatial competition model can persist during long periods of wide-amplitude oscillations in abundances (Fig. 4), the existence of "nonequilibrium communities" does not refute the spatial competition hypothesis. It is also possible that

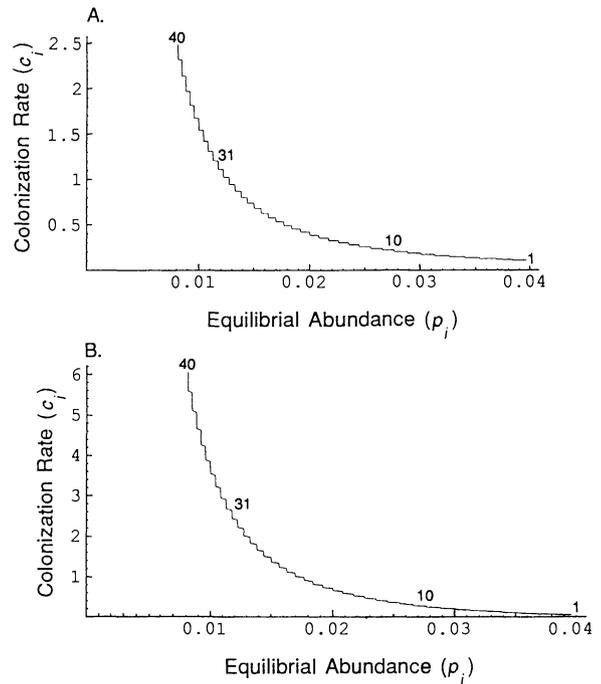


FIG. 5. (A) The relationship between colonization ability and equilibrium abundance for the 40 species used in the simulations of Fig. 4A, B, and C. (B) This same relationship, but for the 40 species used for the simulation of Fig. 4D.

several diversity-promoting mechanisms are operating simultaneously in tropical rain forests. For instance, seed and seedling predation may keep dominant competitors rare (Janzen 1970), and this rarity may allow many more species to coexist by the mechanisms assumed by the spatial competition hypothesis.

The random drift hypothesis (Hubbell and Foster 1986) and the spatial competition hypothesis may operate simultaneously. As Hubbell and Foster (1986) noted, the more similar two competitors are, the slower should be the rate of competitive displacement. However, the spatial competition hypothesis assumes that the rate of competitive displacement is constant, independent of the similarity of the competing species. I have performed simulations with a model similar to the spatial competition model, but in which the rate of competitive displacement within each site was slower when competitive abilities were more similar. This modification often led to a several fold increase in the species richness of a finite habitat.

This paper has focused on interactions within a physically homogeneous habitat. An alternative explanation for species diversity is that habitats are spatially heterogeneous, and that such heterogeneity allows coexistence (e.g., Tilman 1982). Soils have considerable heterogeneity in nutrient content, and sites differ in

slope, elevation, aspect, and microclimate. Plant species can be differentiated with respect to each of these factors, and such differentiation may be a major cause of the changes in life-form and species composition along environmental gradients, including geographic gradients (Tilman 1988). However, within any small and fairly homogeneous region, such differentiation may be a less important determinant of diversity than the effects of competition in a spatially subdivided habitat.

#### *Testing theory*

There are a variety of observational and experimental tests for determining if the diversity of a community is explained by the spatial competition hypothesis. This theory requires a two-way or three-way trade-off among colonization ability, competitive ability, and longevity. This information would be determined best by direct studies of these processes. Comparisons of allocation patterns might provide a reasonable approximation. For instance, because we know that Cedar Creek prairie is nitrogen limited, and because we know that allocation to root is a good predictor of competitive ability for nitrogen, we can test for the requisite trade-off by comparing allocation patterns to root vs. reproductive structures. Such a comparison (Gleeson and Tilman 1990) was the first to show that the major trade-off among our species was between colonization and competition. For light-limited communities, the comparable trade-off would be between proportional allocation to stem (and height) vs. proportional allocation to seed. If the organisms living in a community do not have appropriate trade-offs among competition, dispersal, and longevity, the spatial competition hypothesis cannot explain the biodiversity of that community.

Experimental tests are preferable, but will require more time. If species have similar longevities, species abundances should be limited by their dispersal abilities, and this limitation should be greater for species that are better competitors. Thus, if the rate of arrival of propagules of a species were experimentally increased, its abundance should increase. The best competitors should have the greatest increases in abundance following propagule addition.

It should be possible to increase the species richness of a habitat by addition of low densities of propagules of species that can live in that region but that are absent from that habitat. If the propagules of any species were repeatedly added in high density, that species should displace and exclude all species that were poorer competitors than it. Thus, constant addition of numerous propagules of the best competitor should lead to the competitive exclusion of all other species. The displaced species should not be able to invade back into the habitat until propagule addition ceased and mortality caused the density of the superior competitor to

thin back toward its equilibrium density. In contrast, repeated addition of numerous propagules of a poorer competitor should have no effect on its superior competitors, and only a minor effect on diversity.

Propagule addition experiments could also be performed with a single time of propagule addition. In this case, there should be a short-term decrease in diversity caused by addition of a superior competitor, but diversity should return to its former level as the abundance of the superior competitor returned toward equilibrium. Thus, in testing this theory, it is important to distinguish between short-term and long-term predictions.

We have begun experiments at Cedar Creek to test the applicability of the spatial competition hypothesis to our site. Preliminary results have shown dispersal limitation of species abundances. Many prairie species that were absent from a site, but present in a field or in nearby fields, germinated and grew when their seeds were added, i.e., when dispersal limitation was overcome. Addition of numerous seed or seedlings of a superior nitrogen competitor, little bluestem, is causing the displacement of other species from multispecies communities. However, it will be several more years before the long-term effects of such species additions are clear.

#### *Caveats*

The model presented here is an extreme simplification of the complexity of nature. It abstracts many essential features of competition among sessile organisms in a physically homogeneous habitat. More complex and realistic variations on this model are possible, and should give additional insights. For instance, resource concentrations and resource competition could be modeled, as could the allocation basis of interspecific trade-offs among colonization, competition, and possibly longevity. An explicit model of resource competition would likely lead to slower rates of competitive displacement among competitively similar species, and thus increase diversity in a finite habitat. Random dispersal could be replaced with neighborhood dispersal. However, numerous simulations (Pacala and Tilman 1993) suggest that such modifications do not change the major qualitative predictions of the spatial competition model.

Spatial structure is an unavoidable result of the discrete nature of individual organisms. It may allow an almost unlimited number of competing species to stably coexist in a physically homogeneous habitat, even though a single species is the superior competitor in any given site. The spatial competition hypothesis thus must be added to the list of hypotheses that may explain the existence of highly diverse communities (reviewed in Tilman and Pacala 1993). With few excep-

tions, all that is required to explain the stable coexistence of a large number of species are interspecific trade-offs in traits that determine responses to major environmental limiting factors. Tests of these alternative hypotheses are clearly needed. The wise management of nature and the preservation of its biodiversity depend on knowledge of the actual forces that maintain biodiversity in particular ecosystems. For plants and other sessile organisms, one of the major forces may well be embodied in the spatial competition hypothesis.

#### ACKNOWLEDGMENTS

I thank Jim Clark, Peter Abrams, Stephen Pacala, Clarence Lehman, David Wedin, Tania Vincent, Erik Wardenaar, Evan Siemann, Amy Rovellstad, Karen Jones, Walter Carson, Colleen Rasmussen, Deborah Lawrence, Kirsten Fondren, Yavor Parashkevov, Cristin Corless, Lionel Sanchez, Brian Inouye, and three anonymous reviewers for their comments on this manuscript, and NSF (BSR-8811884) and the Andrew Mellon Foundation for support.

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APPENDIX

STABILITY OF MULTISPECIES EQUILIBRIUM POINTS

The local stability of a multispecies equilibrium point is determined by the eigenvalues of the Jacobian matrix, where the element in the  $i^{\text{th}}$  row and the  $j^{\text{th}}$  column of the matrix,  $q_{i,j}$ , is

$$q_{i,j} = \left. \frac{\partial f_i}{\partial p_j} \right|_*$$

and where  $f_i = dp_i/dt$  (as in Eq. 5), and where  $|*$  means the expression is evaluated at equilibrium.

Because the dynamics of a superior competitor are unaffected by the presence of an inferior competitor,  $q_{i,i} = 0$  for  $j > i$ . This means that the Jacobian matrix is triangular, i.e., has a triangular wedge of zeros above the principal diagonal (where the principal diagonal is composed of the elements  $q_{i,i}$ , with  $i = j$ ). The eigenvalues of such a triangular matrix are just the elements of the principal diagonal (e.g., Noble 1969), i.e., they are the terms  $q_{i,i}$ , for  $i = 1, n$ . There are as many eigenvalues as there are species. Because the addition of an inferior competitor (but better colonist/survivor) does not influence the dynamics of superior competitors, the addition of such species does not change the eigenvalues associated with the superior competitors. Thus, each species has a particular eigenvalue associated with it. This value depends on the traits of this species and of all species that are superior competitors compared to it. As before, assume that the equilibrium proportional abundances of the species are  $\hat{p}_1, \hat{p}_2, \dots, \hat{p}_n$ . Then the partial derivative of  $f_i$  with respect to  $p_i$  is:

$$\frac{\partial f_i}{\partial p_i} = c_i - m_i - 2c_i p_i - \sum_{j=1}^{n-1} [p_j(c_j + c_i)]. \quad (\text{A.1})$$

To evaluate this at equilibrium, it is necessary to substitute in, for each species  $i$ , the value of  $c_i$  that allows that species to attain its equilibrium abundance,  $\hat{p}_i$ . These values are derivable by setting  $dp_i/dt = 0$  in Eq. 8, and solving for  $c_i$ . To obtain the value for  $c_i$  expressed in terms of the equilibrium abundances of all species,  $(\hat{p}_1, \hat{p}_2, \dots, \hat{p}_i)$ , but not in terms of the colonization rates of the other species, it is necessary to first solve for the colonization rate of species 1,  $c_1$ . Thus,

$$c_1 = \frac{m_1}{(1 - \hat{p}_1)}$$

This value is then substituted into the equation for  $c_2$  to give

$$c_2 = \frac{[\hat{p}_1 m_1 + (1 - \hat{p}_1) m_2]}{(1 - \hat{p}_1)(1 - \hat{p}_1 - \hat{p}_2)}$$

The process can be continued, giving a value for the  $i^{\text{th}}$  species:

$$c_i = \frac{\sum_{j=1}^{i-1} (\hat{p}_j m_j) + \left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) m_i}{\left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) \left(1 - \sum_{j=1}^i \hat{p}_j\right)}. \quad (\text{A.2})$$

In order to obtain the eigenvalues of the Jacobian matrix, it is necessary to substitute the values of  $c_i$  into Eq. A.1. After rearrangement of terms, this yields the equation for the eigenvalue associated with the  $i^{\text{th}}$  species,  $\lambda_i$ , where

$$\lambda_i = - \frac{\hat{p}_i \left[ m_i \left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) + \sum_{j=1}^{i-1} m_j \hat{p}_j \right]}{\left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) \left(1 - \sum_{j=1}^i \hat{p}_j\right)}. \quad (\text{A.3})$$

If a habitat contained a single species, the only eigenvalue would be  $\lambda_1 = -m_1 \hat{p}_1 / (1 - \hat{p}_1)$ , which is always negative because  $m_1$  and  $\hat{p}_1$  are greater than 0, and  $\hat{p}_1$  is less than 1. Thus, as long as the species exists in the habitat ( $0 < \hat{p}_1 < 1$ ), its equilibrium point is stable. By substituting in the equilibrium requirement that  $\hat{p}_1 = 1 - m_1/c_1$ , it can be seen that  $\lambda_1 = m_1 - c_1$ . For a habitat with two species, there are two eigenvalues,

$$\lambda_1 = \frac{-m_1 \hat{p}_1}{(1 - \hat{p}_1)},$$

and

$$\lambda_2 = - \frac{\hat{p}_2 [m_1 \hat{p}_1 + m_2 (1 - \hat{p}_1)]}{(1 - \hat{p}_1)(1 - \hat{p}_1 - \hat{p}_2)}$$

Both of these are always negative for any biologically possible values of parameters (i.e.,  $0 < m_1, m_2; 0 < \hat{p}_1, \hat{p}_2 < 1; \hat{p}_1 + \hat{p}_2 < 1$ ), and thus the two-species equilibrium point is locally stable. Indeed, as indicated in Eq. A.3, all eigenvalues are always negative, indicating that all multispecies equilibrium points defined by the model are always locally stable, as long as  $\hat{p}_1, \dots, \hat{p}_n > 0$  and  $\sum \hat{p}_j < 1$ .