

# Limiting Similarity, Species Packing, and System Stability for Hierarchical Competition-Colonization Models

A. P. Kinzig,<sup>1,\*</sup> S. A. Levin,<sup>1,†</sup> J. Dushoff,<sup>2,‡</sup> and S. Pacala<sup>1,§</sup>

1. Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544;

2. Department of Physics, Academia Sinica, Nankang, Taipei, Taiwan

*Submitted March 17, 1998; Accepted October 31, 1998*

**abstract:** Hierarchical competition-colonization models have been used to explain limiting similarities among species, successional dynamics, and species loss under habitat destruction. This class of models assumes that there is an inverse relationship between competitive ability and colonization ability and that competitively superior species exclude competitively inferior species when both occupy the same site. This hierarchical model of performance trade-offs, however, exhibits some unusual behaviors in the high-diversity limit, including infinitesimally close species packing, pathologically slow dynamics, and fundamentally important regularities in trait-abundance relationships. In particular, under the condition of constant mortality across species, a  $3/2$ -power-law relationship emerges between abundance and fecundity under infinite packing (abundance of a species with fecundity  $f$  is inversely proportional to  $f$  to the  $3/2$  power). In this article, we explore the high-diversity limit of the hierarchical competition-colonization model, with particular emphasis on patterns of species packing, species-abundance relationships, and system stability. Because of the potential for pathologically slow dynamics following perturbations and infinitesimally close species packing in the high-diversity limit for this class of models, the models may need to be modified to include more realistic mechanisms governing the extent and timing of interspecific competitive exclusion in order to effectively capture the structure and dynamics of real-world ecosystems.

**Keywords:** competition-colonization trade-off, species packing, limiting similarity, ecosystem stability.

Understanding what controls species coexistence, species similarities or competitive differences, and maximum species diversity are fundamental issues in ecology. We know that continuous variations in traits do not occur across species; to some extent, it is the discontinuities that allow trait-based taxonomy to work (MacArthur 1971; May and MacArthur 1972). Along any niche dimension, there are characteristic differences that distinguish species (Hutchinson 1959). Researchers have invoked competitive trade-offs in an effort to explain the patterns seen (e.g., MacArthur and Levins 1967), although May and MacArthur (1972) showed that, in some simple competition models, environmental stochasticity alone sets a limit to how tightly species can be packed.

For species sharing space, such as intertidal invertebrates (Levin and Paine 1974; Paine and Levin 1981) or grassland or forest plants (Levin and Paine 1974; Tilman 1994), trade-offs between competition and colonization capabilities determine successional positions and permit coexistence. A hierarchical model of trade-offs between competition and colonization performance that permits coexistence of species has been discussed by Levins and Culver (1971), Horn and MacArthur (1972), Hastings (1980), and Nee and May (1992), among others. Tilman (1994) and May and Nowak (1994) have suggested that a model of this sort can be used to understand limiting similarity and finite species packing. These authors note that the model requires coexisting types or species to have discrete differences in competition-colonization traits. In addition, these hierarchical competition-colonization models have been used to explain the behavior of high-diversity systems. For instance, Tilman (1994) uses such a model to elucidate the successional dynamics and nutrient-allocation patterns in a prairie system containing approximately 40 species. May and Nowak (1994) examine patterns of species-strain abundances under loadings of several thousands of strains; such diversity might be found, for instance, among pathogens in a particular host. And Tilman et al. (1994) apply the competition-colonization model to understanding species loss under habitat destruc-

\* To whom correspondence should be addressed. Present address: Department of Biology, Arizona State University, Tempe, Arizona 85287-1501; e-mail: kinzig@asu.edu.

<sup>†</sup> E-mail: simon@eno.princeton.edu.

<sup>‡</sup> E-mail: jonathan@eno.princeton.edu.

<sup>§</sup> E-mail: pacala@princeton.edu.

tion in high-diversity tropical forest systems of tens to hundreds of species.

The hierarchical competition-colonization model, however, exhibits some interesting features and pathological dynamics in the high-diversity limit. In this article, we explore the high-diversity limit and examine the consequences for application of the hierarchical competition-colonization model to an understanding of limits to similarity, species packing, and successional dynamics in perturbed systems.

### Basic Features of the Model

Hierarchical competition-colonization models assume that species survivorship is determined by local intra- and interspecies interactions and that sites across the landscape are linked by dispersal and colonization. Species coexistence occurs because species that are the best competitors locally suffer fecundity (colonization) limitations relative to inferior competitors; thus, inferior competitors persist in sites not occupied by superior competitors.

The basic  $N$ -species model assumes that the landscape consists of sites that can be empty or occupied by any of a countable range of species that replace each other according to a strict competitive hierarchy. The species are ranked according to their competitive abilities, with species 1 being the best competitor and species  $N$  being the worst competitor. Superior competitors landing on sites occupied by inferior competitors "take over" these sites; inferior competitors cannot persist on sites at which there are superior competitors. There is an inverse relationship between competitive ability and colonization ability so that the fecundities ( $f_i$ ) per unit time increase with species rank; that is,  $f_i > f_j$  for  $i > j$ . These assumptions translate into the dynamic model

$$\begin{aligned} \frac{dp_i}{dt} = & f_i p_i \left(1 - \sum_{j=1}^N p_j\right) \\ & + f_i p_i \sum_{j=i+1}^N p_j - p_i \sum_{j=1}^{i-1} f_j p_j - m_i p_i, \end{aligned} \quad (1)$$

where  $p_i$  is the fraction of sites occupied by the  $i$ th species and  $m_i$  is the mortality rate of the  $i$ th species (Levins 1969; Hastings 1980; Tilman 1994). Each species produces propagules at a rate given by  $f_i p_i$ ; these propagules can fall on empty or occupied sites.

The first term in (1) represents colonization of empty sites, and the second gives the colonization of sites occupied by inferior competitors. Note that superior competitors always competitively exclude inferior competitors when both occupy the same site, and the loss of the inferior competitor is instantaneous on arrival of the propagule of

the superior competitor. The third term represents loss of sites due to arrival by superior competitors, and the final term gives mortality losses. Mortality is often taken to be constant across species in applications of this model; thus, we analyze the high-diversity limit under the constraint that  $m_i = m$  for all  $i$ . Such an assumption makes achieving the analytical results for the high-diversity limit more tractable and does not qualitatively affect the conclusions concerning limits to species packing in the high-diversity limit. Different equilibrium abundance-trait relationships, however, can emerge under different assumptions concerning mortality (see May and Nowak 1994).

In this model, all propagules are dispersed randomly throughout the landscape; a seed has an equal probability of falling on a neighboring site or anywhere else in the habitat. The model does not explicitly include resource competition, but the ranking of competitors from superior to inferior reproduces the qualitative features of competition for a single limiting resource (see Tilman 1994).

The first and second terms in (1) can be combined to yield

$$\frac{dp_i}{dt} = f_i p_i \left(1 - \sum_{j=1}^i p_j\right) - p_i \sum_{j=1}^{i-1} f_j p_j - m p_i. \quad (2)$$

Species "see" sites with superior competitors ( $j < i$ ) as being occupied; all other sites appear to be unoccupied and can be colonized. Thus, the dynamics of the  $i$ th species depends only on the superior competitors in the system; introduction of a species with  $j > i$  will not affect the abundance of the  $i$ th species.

There are several other interesting relationships that derive from (2) that will be crucial to our subsequent discussions. If we define  $\theta_n$  as the number of empty sites remaining after species 1 through  $n$  have reached their equilibrium abundances ( $\hat{p}_j$ ) so that

$$\theta_n = 1 - \sum_{j=1}^n \hat{p}_j. \quad (3)$$

We can then rewrite (2), under equilibrium conditions ( $dp_j/dt = 0$  for all  $j$ ) such that

$$\frac{1}{\hat{p}_n} \frac{dp_n}{dt} = 0 = f_n \theta_n - \sum_{j=1}^{n-1} f_j \hat{p}_j - m \quad (4)$$

and

$$\frac{1}{\hat{p}_{n-1}} \frac{dp_{n-1}}{dt} = 0 = f_{n-1} \theta_{n-1} - \sum_{j=1}^{n-2} f_j \hat{p}_j - m. \quad (5)$$

Solving (5) for  $\sum f_j \hat{p}_j$  and substituting into (4) leads to the condition that

$$f_n = \frac{f_{n-1} \theta_{n-2}}{\theta_n}. \quad (6) \quad \text{and}$$

If we use (6), iteratively substitute for  $f_{n-1}$ ,  $f_{n-2}$ , and so on, and remember that  $\theta_1 = 1 - \hat{p}_1 = m/f_1$  (from [2]) and  $\theta_0 = 1$  (all sites free if no species present), we find that the species' fecundities must satisfy the relationship (Tilman 1994)

$$f_n = \frac{m}{\theta_n \theta_{n-1}}. \quad (7)$$

Further, from (3) the abundance of the  $n$ th species is

$$\hat{p}_n = \theta_{n-1} - \theta_n. \quad (8)$$

Since  $\theta_n < \theta_{n-1}$  (fewer free sites as more species are introduced to the system), we have

$$f_n = \frac{1}{\theta_n} \frac{m}{\theta_{n-1}} > \frac{1}{\theta_{n-1}} \frac{m}{\theta_{n-1}} \quad (9)$$

or

$$f_n > \frac{m}{\theta_{n-1}^2}. \quad (10)$$

This is the condition for invasion; in order to persist in the system with positive abundance, the  $n$ th species must have a high enough fecundity to satisfy (10). This condition and the implications are discussed further in the next section.

### Limits to Similarity and Species Packing

Consider the two-species version of this model. The equations governing the dynamics of the superior (species 1) and inferior (species 2) competitors are

$$\frac{dp_1}{dt} = f_1 p_1 (1 - p_1) - m p_1 \quad (11)$$

and

$$\frac{dp_2}{dt} = f_2 p_2 (1 - p_1 - p_2) - f_1 p_1 p_2 - m p_2, \quad (12)$$

with equilibrium abundances given by

$$\hat{p}_1 = 1 - \frac{m}{f_1} \quad (13)$$

$$\hat{p}_2 = 1 - \frac{m}{f_2} - \left(1 + \frac{f_1}{f_2}\right) \hat{p}_1. \quad (14)$$

Species must have positive abundances at equilibrium so that  $\hat{p}_1, \hat{p}_2 > 0$ . Using these constraints in equations (13) and (14) gives the necessary and sufficient conditions

$$f_1 > m \quad (15)$$

and

$$f_2 > f_1^2/m \quad (16)$$

(see Durrett and Swindle 1991). Assuming (15) holds, set

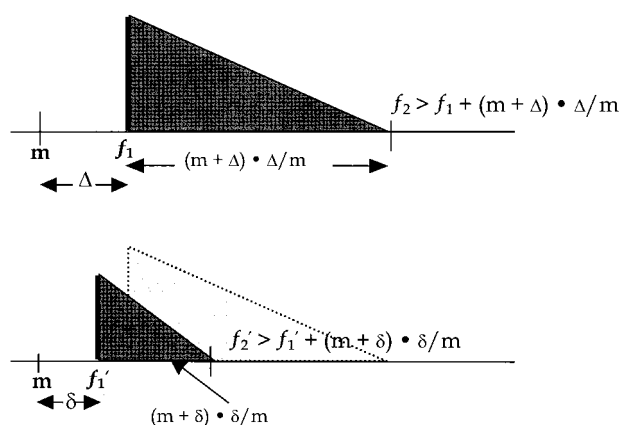
$$\Delta = f_1 - m > 0. \quad (17)$$

Equation (16) is then equivalent to the condition

$$f_2 - f_1 > (m + \Delta)(\Delta/m). \quad (18)$$

In other words, if a superior competitor is present in the system with fecundity  $f_1$ , there is a region in fecundity space in which an inferior competitor cannot exist; in particular, the next best competitor must have a fecundity greater than  $f_1 + (m + \Delta)(\Delta/m)$ . Figure 1 displays this effect graphically along a fecundity axis, with the low fecundity (superior competitor) to the left and the high fecundity (inferior competitor) to the right. Note that the superior competitor, with  $f_1$ , casts a "shadow" along the fecundity axis, of length  $(m + \Delta)\Delta/m$ , within which the inferior competitor cannot exist. As  $\Delta$  decreases, the abundance of the superior competitor decreases (by [13]), leaving more free space available and, thus, increasing the probability of successful colonization of an empty site by the inferior competitor. (Remember that the inferior competitor, by definition, cannot colonize a site occupied by the superior competitor.) In this case, the niche shadow cast by the superior competitor becomes shorter; in other words, the smaller the offset between the fecundity and mortality of the superior competitor, the lesser the niche differentiation required between the top two competitors and the greater the density of species in the region of low fecundity (see fig. 1).

Although species cannot invade in the shadow cast to the right of the superior competitor on the  $f$ -axis, there is nothing in the model system to prevent species invasion



**Figure 1:** The niche shadow cast by the superior competitor in the hierarchical competition-colonization model as described by (2). The superior competitor is labeled type 1 and has a fecundity  $f_1$ . Other types cannot invade or persist within the niche shadow (shown in gray). The length of the niche shadow depends on the abundance of the superior competitor, which in turn depends on the distance between  $f_1$  and  $m$  (mortality) on the fecundity axis (shown by  $\Delta$  and  $\delta$  in the figure). The vertical bar at  $f_1$  is proportional to the abundance of type 1. The greater the offset between  $f_1$  and  $m$ , the greater the abundance of type 1, the longer the niche shadow, and the greater the potential difference between the superior competitor and the next type that can appear in the system. Inferior competitors also cast niche shadows; their abundance, and the length of the niche shadows they cast, will depend on the distance between their fecundities  $f$  and the edge of the preceding niche shadow on the fecundity axis.

to the left of the superior competitor. The new top competitor may displace the previous top competitor, but the length of the niche shadow cast by the top competitor decreases as the top competitor moves to the left on the fecundity axis. Thus, an inferior competitor may appear in a region that was previously uninhabitable. In figure 1, the previously shaded (uninhabitable) portion of the fecundity axis emerges from the niche shadow when a new superior competitor enters the system. Because stochastic effects are ignored, this process can continue until  $f_1$  comes infinitesimally close to  $m$  (and the abundance of the first type approaches 0), the shadow becomes infinitesimally small, and  $f_2$  and  $f_1$  both approach  $m$ . Similarly, species 2 (with fecundity  $f_2$ ) also casts a shadow in niche space within which an inferior competitor cannot persist (and so on for all subsequent competitors; see app. A). As  $f_2$  approaches  $f_1$ , however, this niche shadow also declines in length, and subsequent invaders can approach  $f_2$  in fecundity niche space. Thus, as long as invasion is permitted by other species or mutation is allowed, limits to similarity can erode and the system can approach one in which there

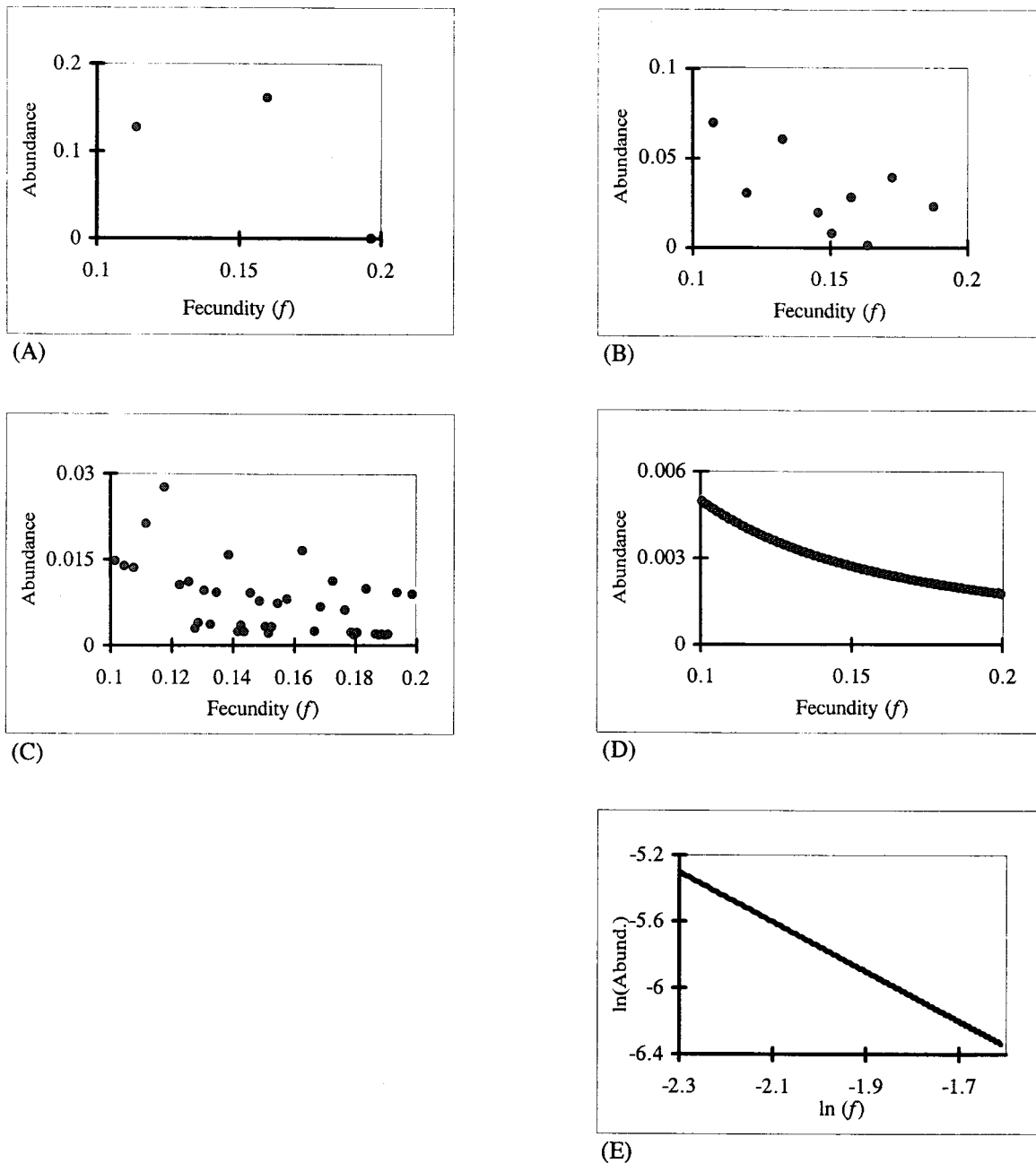
is a continuous distribution of types in niche space, each with vanishingly small abundance.

This process of invasions and subsequent increases in species packing is shown in figure 2A–D. Species are introduced randomly in the system from an external pool of  $N = 100$  possible species and permitted to achieve their equilibrium abundances (provided that they are able to invade at all, given the niche shadows cast by other species present in the system). The mortality  $m$  (eq. [2]) is 0.1 for all species. (Other values for mortality could have been used, with fecundities scaled accordingly.) The species in the external pool have fecundities that are determined by evenly dividing the fecundity axis into  $N$  bins (where the fecundity axis stretches from  $m$  to  $f_{\max}$ ) and assigning the  $i$ th type a fecundity corresponding to the center of the  $i$ th fecundity bin. In our example,  $f_{\max} = 0.2$  and  $N = 100$ ; thus, for instance, species 1 has a fecundity of 0.1005, species 2 has a fecundity of 0.1015, and species 100 has a fecundity of 0.1995. Some species that are able to persist initially disappear in the niche shadows of invading superior competitors; these disappearing species are able to reinvade later as superior competitors begin to “crowd” the region of the fecundity axis close to the limits of mortality, reducing the niche shadows cast and increasing the regions of the fecundity axis available for invasion. Finally, each of the 100 species is able to persist, and there is a smooth relationship between abundance and fecundity. Each species still casts a niche shadow, but the shadow lengths become small relative to the spacing between species as more species invade. Thus, all 100 species are eventually able to coexist with no competitive exclusion. The relationship between abundance and fecundity in figure 2D is given by  $p(f) \propto f^{-3/2}$  (as shown in fig. 2E), a powerful scaling law that calls for closer examination.

To see where this 3/2-power law comes from, it is easier to manipulate a continuous approximation to (2). Indeed, the collapse into a smooth distribution of closely spaced species (as shown in fig. 2) suggests that one can move to a continuous version of (2) to generate solutions to equilibrium abundances in the high-diversity case. The simplest continuous limit of (2) is given by replacing the summations by integrals, such that

$$\frac{1}{p(f)} \frac{dp(f)}{dt} = f \left[ 1 - \int_{f_0}^f p(x) dx \right] - \int_{f_0}^f x p(x) dx - m, \quad (19)$$

where  $f_0$  indicates the fecundity of the superior competitor in the continuous version (equivalent to  $f_1$  in the discrete version). It remains to be proven formally that the solutions to the process given above converge to solutions of this equation in the limit of infinitesimal packing. The more appropriate limit, found by multiplying (19) by



**Figure 2:** Patterns of abundance for a system in which species are randomly chosen for invasion from a pool of 100 possible species and allowed to reach their equilibrium abundances. The system is described by (2), and equilibrium abundances are determined by (3)–(5). All types are given a mortality  $m$  of 0.1, and the fecundities of the 100 types are evenly spaced between 0.1 and 0.2, with the fecundity of the best competitor (type 1) being 0.1005 and the fecundity of the worst competitor (type 100) given by 0.1995. The four graphs show equilibrium abundances when community size first reaches three species (A), nine species (B), 36 species (C), and 100 species (D). Initially, when species packing is low and abundances are high, niche shadows are relatively long and many species either die out or fail to successfully invade when selected for invasion (i.e., equilibrium abundances are found to be 0 or negative). As the invasions proceed, however, species appear close to the edges of preceding niche shadows (not shown), abundances decline, niche shadows become shorter, and more species can be packed into the system, until finally all 100 are able to persist in the system with positive abundances (D). (Note the change in the scale on the Y-axis and the decline in abundances as more species are packed into the system.) Graph D conforms to a  $-3/2$ -power law for abundance as a function of fecundity (see text); this is demonstrated by replotting the data from graph D on an  $\ln$ - $\ln$  plot scale in graph E.

$p(f)$ , admits regions where  $\hat{p}(f) = 0$ , as might be caused by shadowing.

Let us consider only equilibrium distributions for (19) ( $dp(f)/dt = 0$ ), implicitly assuming that there are no intervals where  $p(f) = 0$  (as for fig. 2D). We can then set the right-hand side of (19) equal to 0. If we assume the density function  $p(x)$  is differentiable, then we can differentiate the right-hand side of (19) twice with respect to  $f$ . The first differentiation gives

$$1 - \int_{f_0}^f p(x) dx - 2fp(f) = 0, \quad (20)$$

and the second,

$$-3p(f) - 2fp'(f) = 0 \quad (21)$$

or

$$\hat{p}(f) = \frac{K}{f^{3/2}}. \quad (22)$$

The function  $p(f)$  is a probability distribution; in other words, if one surveys a particular site, the probability that one will find a species with fecundity between  $x$  and  $x + \epsilon$  is given by integrating  $p(f)$  from  $x$  to  $x + \epsilon$ . If we allow an infinite range of types in the system, and allow the most inferior competitor to have infinite fecundity, then all sites will be occupied. Moreover, in the case of infinitesimally close packing, the superior competitor will crowd the lower limits on fecundity imposed by mortality; in other words,  $f_0$  will approach  $m$ . Thus, the integral of  $p(f)$  from  $f_0(=m)$  to  $f_{\max}(=\infty)$  must yield a value of 1. Carrying out the integration gives  $K = 1/2 \times m^{1/2}$ . Thus, we have

$$\hat{p}(f) = \frac{\sqrt{m}}{2f^{3/2}}. \quad (23)$$

Equation (23) provides a fit to the 3/2-power law in figure 2D, but the validity of (19) as a substitute for (1) or (2) can be questioned. In particular, if figure 2D were replaced by one generated by a stochastic simulation of competition, in which  $f_i$  and  $m$  were transformed into probabilities per unit time for birth and death, discontinuities would have been admitted, and Lebesgue integration would have to replace the Riemann integral (Riesz-Nagy 1952).

An alternative approach to determining the validity of (19) and its solutions is to return to the discrete model

and to bound its solutions. Using (7) and recognizing that  $\theta_n < \theta_{n-1}$ , we can write

$$\sqrt{\frac{m}{f_{n+1}}} < \theta_n < \sqrt{\frac{m}{f_n}}. \quad (24)$$

If, as  $f_n$  becomes large relative to  $m$ , the species are closely spaced in the weak sense that  $f_{n+1} \approx f_n$ , then these boundaries converge, implying that cumulative abundance varies as  $f^{-1/2}$ , as would be expected from a continuous distribution of types in fecundity space such that  $\hat{p}(f)$  is proportional to  $f^{-3/2}$ . The actual distribution of the  $\theta_n$  remains discontinuous but tends in the limit to the approximating curve.

The 3/2 law represented in figure 2 is generated assuming  $m$  is constant across types and that the types are confined to one per "bin" along the fecundity axis, where the bins are of constant (but small) width. Both assumptions can be relaxed. In particular, if  $m$  is a function of  $f$ , and we again differentiate (19) twice with respect to  $f$ , the equilibrium distribution (if it exists) is given by

$$3p(f) + 2fp'(f) + m''(f) = 0. \quad (25)$$

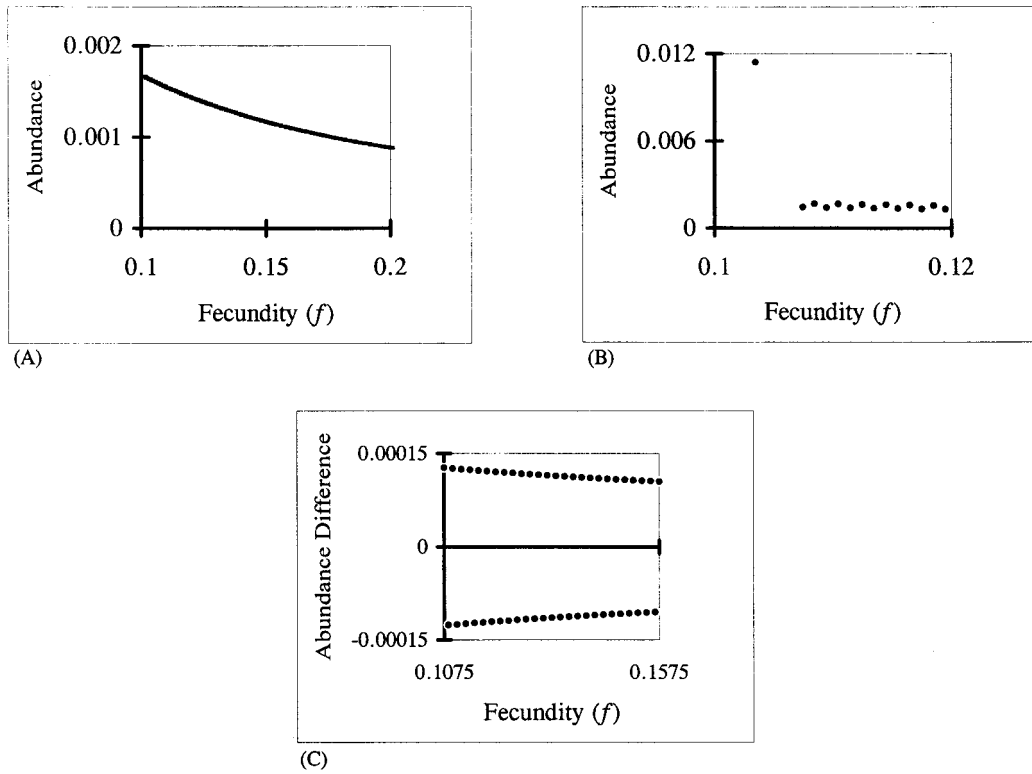
Whether equilibria will now exist will depend on the convexity of  $m(f)$ ; if  $m''(f)$  is too great, for example, only the lowest fecundity type can survive.

For cases in which  $m = kf^n$  ( $n \neq 1/2$ ,  $n < 1$ ), a general solution for (25) is

$$p(f) = \left[ \frac{f_0^{1/2}}{2} - \frac{kn}{(4n-2)} f_0^{n-1/2} \right] \times f^{-3/2} + \frac{kn(1-n)}{(2n-1)} f^{n-2} \quad (26)$$

(see app. B). Note that for  $n = 0$ , we recover (23) (as expected). If mortality increases faster than linearly with fecundity ( $n > 1$ ), no equilibrium is possible, in part because the increased cost of mortality cannot be compensated by increased reproduction (fecundity) if mortality grows too quickly. (See app. A for the conditions required for invasion when mortality varies with fecundity in the case of discrete types.) Note also that we have not been able to determine the stability of the general equilibrium solutions to (25).

For specificity, consider the case where  $m$  increases as  $f^{2/3}$ . Figure 3A shows a distribution for this situation where 100 types are evenly spaced along the fecundity axis (and so  $\hat{p}_i(f)$  is generated using [2]). A smooth relationship between fecundity and abundance emerges, and species are closely packed, as we would expect; furthermore, a continuous curve can be fitted to the  $\hat{p}_i(f)$ , where abun-



**Figure 3:** Species packing and equilibrium abundances when there is a fecundity-mortality trade-off such that  $m(f) \propto f^{2/3}$ . Thus, equilibrium abundances are found by setting the left-hand side of (2) equal to 0 and replacing  $m$  with  $m(f)$ . There are 100 possible types in the system, with fecundities evenly spaced between 0.1 and 0.2 ( $m = 0.1$ ); the fecundity of the best competitor is 0.1005, and the fecundity of the worst competitor is 0.1995. *A*, All 100 types are present; moreover, the  $p_i(f)$  distribution can be fit with a curve where  $p(f) = 2.3 \times 10^{-7} - 0.00016f^{-3/2} + 0.00031f^{-4/3}$ . (Note that we did not force the constant to be 0 in the fit, though we would have expected the constant to be 0 from [26]. The resulting fit, however, has a constant impressively close to 0.) *B*, Type 1 ( $f = 0.1005$ ), type 2 ( $f = 0.1015$ ), and type 3 ( $f = 0.1025$ ) are removed from the system. This increases the abundance of the fourth type, increases the length of the niche shadow cast by the fourth type, and eliminates the next three types. After the gap caused by the niche shadow, all types are once again present, but with a “seesaw” pattern in abundances. *C*, Comparison between the seesaw pattern from *B* with the equilibrium abundances from *A* (abundance difference equals the abundance from *A* minus the abundance from *B*); abundances from *B* are alternately higher or lower than abundances of the same type in *A*. This seesaw pattern occurs because the equilibrium abundance of each type depends on its distance from the edge of the niche shadow cast by its nearest superior competitor. Thus, if we compare *A* and *B*, the best competitor in *B* is able to enter with relatively high abundance (because the three best competitors found in *A* are removed and their niche shadows eliminated). The niche shadow cast by this new best competitor eliminates the next three types (present in *A* but not *B*) and also depresses the abundance of the next inferior competitor relative to what it was in *A*. This lower abundance means a shorter niche shadow (recall fig. 1), and, thus, the next type is able to invade with a higher abundance, casting a relatively longer niche shadow and thus depressing the abundance of the next type. This process continues, with every other type having low or high abundance relative to the abundances found in *A*, though the impact of the removal of the top competitors declines as we move toward inferior types.

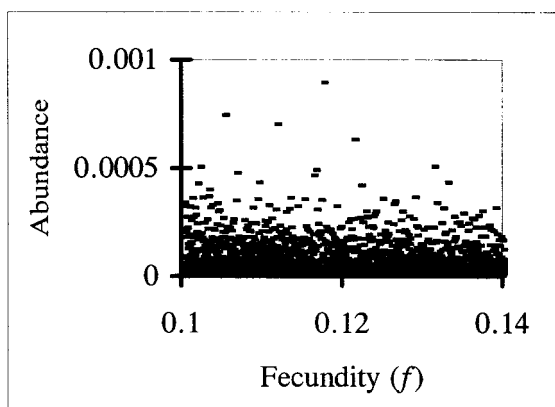
dance varies as the sum of two powers,  $f^{-3/2}$  and  $f^{-4/3}$  (as expected from [26]).

Other interesting continuous distributions can be generated. Figure 3*B* shows equilibrium abundances for a situation in which  $f_0$  is forced to be offset from  $m$ . This offset would occur, for instance, if physiological constraints prevented a plant from allocating so much photosynthate to root that its fecundity approached  $m$ . The possible types

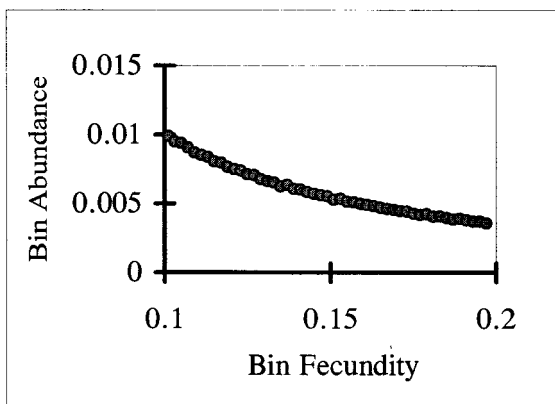
are still assumed to be evenly spaced along the fecundity axis, with mortalities as given in figure 3*A*; after a gap caused by the shadow the  $f_0$  type casts in niche space, continuous packing once again ensues, with all types present from the edge of the niche shadow to  $f_{\max}$ . (See fig. 3*C* for a comparison of equilibrium abundances for the two cases shown in figs. 3*A*, *B*.)

The assumption that possible species or mutants are

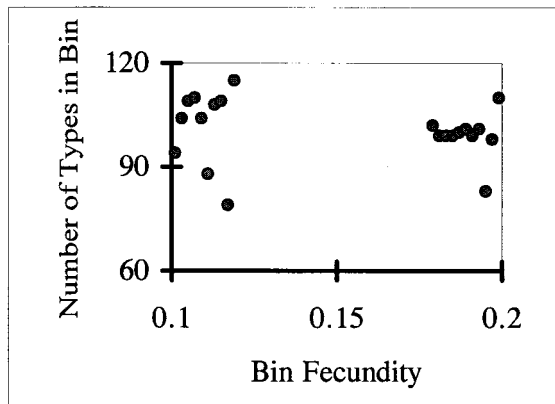
evenly spaced along the fecundity axis is relaxed in figure 4A, where 10,000 species are introduced with randomly generated fecundities falling between 0.1 and 0.2 ( $m = 0.1$ ). Five thousand species were able to occupy the system (the other half had zero or negative equilibrium abundances). There is only a weak inverse correlation between fecundity and abundance. If, on the other hand, the fe-



(A)



(B)



(C)

cundity axis is divided into 100 "bins" (in order to allow comparison with the 100 types used in generating fig. 2), with each bin having a width of 0.001, and the abundances of all types falling within each bin are summed, we again recover a  $3/2$  law for bin abundance versus bin fecundity (fig. 4B). Thus, if types can be divided into regularly spaced guilds in character space, the smooth relationship between fecundity and abundance again results. Finally, figure 4C demonstrates that this decline in bin abundance with increasing bin fecundity is not due to a decline in the number of types falling within each bin.

Tilman (1994) and May and Nowak (1994) have noted that this hierarchical competition-colonization model (or similar versions) has the attractive feature that, even when an infinite number of species exists in the system (an infinite grid, no limits to fecundity), an analytical limit to the similarity of adjacent species in the competitive hierarchy still emerges from the model. It is true that a given community configuration will indeed prevent invasions or mutations in certain regions of the competitive hierarchy. But the maintenance of fixed limits to similarity over time depends on other mechanisms not contained in the model, such as finite habitat size or the effects of demographic or environmental stochasticity (see, e.g., May and MacArthur 1972). (Tilman [1994] invokes the mechanisms of finite habitat and stochasticity to explain the finite number of species present in systems but does not conclude that these mechanisms are also required to explain the maintenance of limits to similarity.)

May and Nowak (1994) extended the model by assuming that there is enough time for the system to reach dynamic equilibrium after each invader and showed that in this case limits to similarity persist in the infinite system, even without demographic stochasticity. (May and Nowak are dealing with a hierarchical competition-virulence model rather than competition-colonization model, but the general structure of their model is the same as the one presented here.) Further they showed that, as time goes on, there is an increasingly fine division of niche space

Figure 4: A, Patterns of abundance when 10,000 species are introduced in the system, with fecundities randomly selected to fall between 0.1 and 0.2 ( $m = 0.1$ ); 5,000 species are able to persist, but there is only a weak correlation between competitive ranking (fecundity) and abundance. The system is described by (2), and equilibrium abundances are determined by (3)–(5). B, Cumulative abundances when the 5,000 species are grouped into 100 bins, each of width 0.001. Thus, bin 1 extends from  $f = 0.1$  to  $f = 0.101$ ; the individual abundances of any type falling within that bin are summed and the sum assigned to the "bin abundance." In this case, a  $3/2$  law once again emerges. C, The number of types found in each bin for the 10 lowest-fecundity bins ( $f = 0.1$  to  $f = 0.11$ ) and the 10 highest-fecundity bins ( $f = 0.19$  to  $f = 0.2$ ).



among the superior competitors (increasingly close packing as the superior competitor approaches the theoretical limit). This result should be contrasted with our own simulations in figure 4. We took the opposite extreme assumption by assuming all of our random species were introduced before any had time to go extinct. In this case, there is no fixed limit to similarity; as the number of species goes up, the similarity between neighbors increases without bound. Furthermore, there was no difference in species packing along the fecundity axis from low to high values (see fig. 4C).

Reality is likely to lie somewhere between these two extremes. May and Nowak's assumption of dynamic equilibrium between invaders corresponds to the classical conceptualization of slow evolutionary change. In fact, however, ecological dynamics in this model may be extremely slow (as we discuss below), calling the assumption into question. The assumption of no extinctions between invasions in figure 4 does not fit the classical framework of slow evolution but may be relevant to populations that are relatively frequently invaded from outside or communities where extinction is very slow compared with other processes, for example, soil bacteria, where many types are assumed to be present but dormant, "waiting" for favorable conditions to appear. Thus, limiting similarity may or may not emerge from the hierarchical competition model, and this emergence will have as much to do with the rules governing the appearance of mutants or invaders as with any characteristic behavior of the model.

### Species Packing and System Stability

If the competition-colonization model given in (2) effectively captures the essential features of performance trade-offs and system dynamics in real-world systems, then the model can be used to predict or interpret the results of experimental manipulations or other perturbations in those systems. In this section, we examine the dynamics of the competition-colonization model as a tool for understanding system dynamics by analyzing the eigenvalues and stability of the discrete system (eq. [2]) in the high-diversity limit.

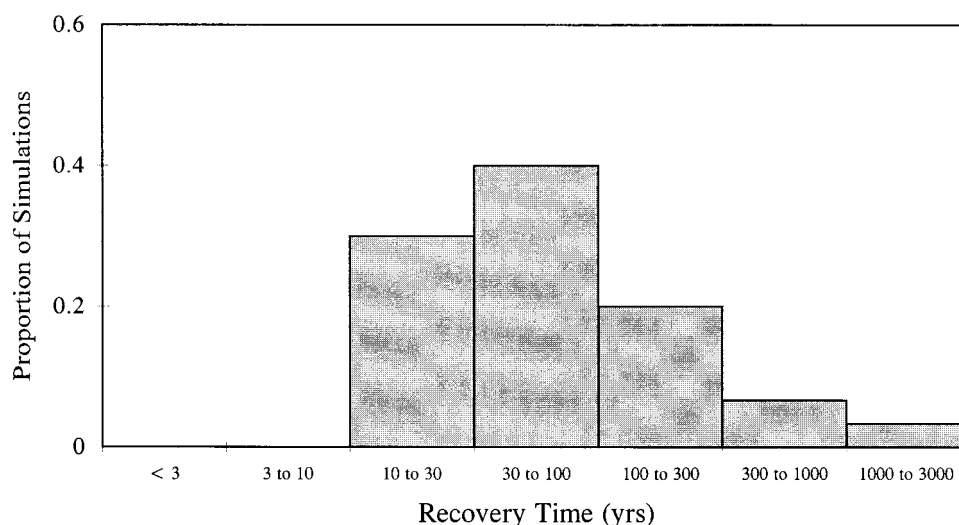
For an  $N$ -species system, the most rapid rate of return to equilibrium following a perturbation (given by the most negative real part of the dominant eigenvalue of the Jacobian matrix; see app. C) is achieved when species have equilibrium abundances inversely proportional to their fecundities ( $\hat{p}(f) \propto 1/f$ ). In this case, the return time is given by

$$\tau_{\min} \approx \frac{N}{\sqrt{f_N m}}, \quad (27)$$

where  $m$  is the mortality,  $N$  is the number of species, and  $f_N$  is the maximum fecundity (i.e., the fecundity of the most inferior competitor) (app. C). Note that this fecundity-abundance relationship ( $\hat{p}(f) \propto 1/f$ ) is different than the 3/2-power law derived above. If we allow  $N$  to approach infinity and constrain fecundities such that they are only permitted to appear at certain equally spaced positions on the fecundity axis, as in figure 2D, we recover  $\hat{p}(f)$  inversely proportional to  $f^{3/2}$ . The system with the fastest return time, with  $\hat{p}(f)$  inversely proportional to  $f$ , can be constructed with finite species packing and with a particular spacing of species along the fecundity axis, as derived in appendix C. Note also that there is nothing to suggest that the system with the fastest return time will evolve or appear under natural conditions; we examine this condition here only to determine a lower bound for return times following a perturbation.

Recall that the fecundity  $f_j$  is the number of seeds that would survive and germinate in a year if only one individual from the  $j$ th species were present in the system. Consider a 40-species prairie system. A reasonable, order-of-magnitude value for  $f_N$  would be 100 per year; if we take  $m = 0.1$  per year, the best competitor can be expected to have individual lifetimes of about a decade. With these numbers ( $N = 40$ ,  $f_{\max} = 100$ ,  $m = 0.1$ ), the fastest return time for an  $N = 40$ -species system would be about 12 yr, by (27). On the other hand, a tropical forest system with 500 tree species,  $m = 0.005$  (individual lifetime  $\approx 200$  yr for the late successional species) and  $f_N$ , again taken as 100 per year, would give, at best (i.e., most rapid), a return time of 700 yr following perturbation ([27] with  $N = 500$ ,  $m = 0.005$ , and  $f_{\max} = 100$ ).

These recovery times apply only to communities in which the plants happen to have the specific fecundities that minimize the return time following a perturbation; for all other communities, recovery times would be slower. For instance, we simulated communities in which 10 species were randomly generated, such that any fecundity between 0.1 ( $=m$ ) and 100 was permitted, with the constraint that all 10 species have abundances of at least 0.001 (the most rare species occupies at least 0.1% of the sites). Seventy percent of 30 such randomly constructed communities thus "generated" had minimum recovery times of greater than 30 yr (as measured by  $1/\text{smallest negative eigenvalue}$ ), and no communities had recovery times less than 10 yr (see fig. 5). These recovery times are far from the lower bound of 3 yr found by using the same parameters for  $f_{\max}$  and  $m$  and assuming that the specific structure of the community is such that return time following a



**Figure 5:** Recovery times (based on the dominant eigenvalue of the Jacobian matrix given in app. C) for 30 different 10-species communities. In each of the 30 communities, 10 species were randomly assigned fecundities between 0.1 ( $=m$ ) and 100, subject to the constraint that no species has an equilibrium abundance below 0.001. The system is described by (2), and equilibrium abundances were determined by (3)–(5).

perturbation is minimized (as in [27]). Moreover, the model assumes instantaneous replacement of an inferior competitor by a superior one arriving at the same site. More realistically, allowing competitive displacement to occur over some finite time determined by nutrient dynamics or plant lifetimes would likely decrease eigenvalues, further slowing recovery times. These calculations call into question our ability to correctly infer the dynamics of systems over the time scales of typical field experiments if systems are really characterized by the competition-colonization trade-off as it is described in (2).

Moreover, (27) suggests that, when species become infinitely tightly packed, the return time of the system following a perturbation approaches infinity. Thus, the equilibrium solutions to (19) would be pathological in that it would take an infinite amount of time to reach them. Nonetheless, there is nothing in the discrete version of the competition-colonization model ([1] and [2]) that prevents infinitely high species packing and infinitely slow dynamics; if one were to permit invasions of new types for long time periods, species packing would continue to increase and system dynamics would continue to slow.

### Conclusions

We have analyzed a competition-colonization model that has played an important role in the literature since Levins

and Culver (1971) first proposed it. The model has been used by several authors to explain the equilibrium distribution of competing types and dynamics of succession and species loss in high-diversity communities when competition and colonization trade-offs are the major axes of differentiation of species. A  $3/2$  law emerges in the limit (with abundance of a type with fecundity  $f$  inversely proportional to  $f^{3/2}$ ); it remains to be seen whether this law describes actual abundance distributions in high-diversity communities.

This hierarchical competition-colonization model has been used to explain limiting similarity in biological systems. For a given configuration of species, there are indeed regions where mutations and invasions cannot be successful. If mutations and invasions occur over infinite time, however, and population dynamics are slow relative to the dynamics of invasion and mutation, species may become infinitely tightly packed and trait differentiation will be lost. Return times to equilibrium following perturbations do become increasingly slow as species diversity increases, suggesting that ecological dynamics may become slow relative to invasion dynamics in the high-diversity limit. These return times, however, approach unrealistic values given what we know about the dynamics of real-world systems, calling into question the relevance of these simple, deterministic hierarchical competition-colonization models for understanding the emergence of limits to similarity. The model, however, is only a first approximation, in-

volving an unrealistic absolute and instantaneous hierarchical competitive exclusion, and this gives rise to some of the pathologies observed in the high-diversity limit. Incorporation of finite habitat size and explicit space in later work may shed some light on these issues and increase our understanding of the patterns of species packing and competitive exclusion in systems governed by hierarchical competitive trade-offs.

### Acknowledgments

We are grateful to R. Durrett, L. Stone, and an anonymous reviewer for comments on an earlier version of this manuscript and B. Bolker for useful discussions. This work was supported by grants from the Alfred P. Sloan Foundation (grant 97-3-5), from the Andrew W. Mellon Foundation, and the National Aeronautic and Space Administration (NASA), grants NAGW-4688 and NAG5-6422.

## APPENDIX A

### Conditions for Invasion

In general, it is easy to compute from (10) and (7) that the conditions for invasion for each type are such that

$$f_{2n} > \frac{1}{m} \left[ \frac{f_1 \times f_3 \dots f_{2n-1}}{f_2 \times f_4 \dots f_{2n-2}} \right]^2 \quad (\text{A1})$$

and

$$f_{2n+1} > m \left[ \frac{f_2 \times f_4 \dots f_{2n}}{f_1 \times f_3 \dots f_{2n-1}} \right]^2, \quad (\text{A2})$$

when mortality is the same for all types. If mortality is not constant, then (10) becomes

$$f_n > \frac{m_1}{\theta_{n-1}^2} + \frac{1}{\theta_{n-1}^2} \sum_{j=1}^{n-1} \theta_j [m_{j+1} - m_j]. \quad (\text{A3})$$

In the case of constant mortality ([A1] and [A2]), the length of the niche shadow (quantity on the right-hand side) depends only on the characteristics of the superior competitors. In the case of mortality varying by type, the characteristics of the invading type in part determine the length of the niche shadow (i.e., the niche shadow for  $f_m$  given by the right-hand side of [A3], depends on  $m_n$ ).

## APPENDIX B

### General Equilibrium Solution for the Continuous Version

Equation (26) can be generated by assuming (25) holds and noting that

$$\begin{aligned} [p(f)f^{3/2}]' &= p'(f)f^{3/2} + \frac{3}{2}p(f)f^{1/2} \\ &= \frac{f^{1/2}}{2} [2p'(f) + 3p(f)] \\ &= -\frac{f^{1/2}}{2} m''(f). \end{aligned} \quad (\text{B1})$$

Integrating gives

$$p(f)f^{3/2} = -\frac{1}{2} \int_{f_0}^f x^{1/2} m''(x) dx + \text{constant}. \quad (\text{B2})$$

For  $m = kf^n$ , we get ( $n \neq 1/2$ )

$$p(f) = -\frac{kn(n-1)}{(2n-1)} f^{n-2} + \text{constant} \times f^{-3/2}. \quad (\text{B3})$$

The constraint

$$\int_{f_0}^{\infty} p(x) dx = 1, \quad (\text{B4})$$

where  $f_0$  = the fecundity of the best competitor, requires that  $n < 1$  and further more that

$$\begin{aligned} p(f) &= \left[ \frac{f_0^{1/2}}{2} - \frac{kn}{(4n-2)} f_0^{n-1/2} \right] \\ &\times f^{-3/2} + \frac{kn(1-n)}{(2n-1)} f^{n-2}. \end{aligned} \quad (\text{B5})$$

For the special case of  $n = 1/2$ , integrating (B2) and multiplying both sides by  $f^{-3/2}$  gives

$$p(f) = K_1 \ln(f) f^{-3/2} + K_2 f^{-3/2} + K_3. \quad (\text{B6})$$

## APPENDIX C

## Stability and Return Times Following Perturbations

For small perturbations from equilibrium, system response can be captured with the eigenvalues of the Jacobian matrix (Bulmer 1994); for an  $N$ -species system governed by (2), the Jacobian is given by

$$J = \begin{bmatrix} -f_1\hat{p}_1 & 0 & \cdots & 0 \\ -f_1\hat{p}_1 - f_2\hat{p}_2 & -f_2\hat{p}_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ -f_1\hat{p}_1 - f_N\hat{p}_N & -f_2\hat{p}_2 - f_N\hat{p}_N & \cdots & -f_N\hat{p}_N \end{bmatrix}, \quad (C1)$$

with eigenvalues  $\lambda_j = -f_j\hat{p}_j$ . Since all eigenvalues are negative (for all  $\hat{p}_j > 0$ ), the competition-colonization equilibrium is locally stable. The return time to equilibrium in this case is then given by the inverse of the dominant eigenvalue (the negative of the smallest value of  $f_j\hat{p}_j$ ).

Since  $\hat{p}_j = \theta_{j-1} - \theta_j$  and  $f_j = m/(\theta_j - \theta_{j-1})$ , we have

$$\lambda_j = -m\left(\frac{1}{\theta_j} - \frac{1}{\theta_{j-1}}\right), \quad (C2)$$

where, again,  $\theta_j$  gives the proportion of sites that are unoccupied when the top  $j$  competitors achieve their equilibrium abundance. The value of  $|\lambda_j|$  is small, that is, there is a long return time to equilibrium—when  $\theta_j \approx \theta_{j-1}$  or when the  $j$ th species is just able to invade with small abundance because its fecundity is close to the edge of the niche shadow cast by its nearest superior competitor. (Since we have returned to the discrete case without forcing even distribution of types along the fecundity axis, equilibrium abundances may or may not follow a pattern like the 3/2 law given in figure 2. In particular, some superior competitors may have very low abundances while inferior competitors have very high abundances, and any  $\lambda_j$  could be the dominant eigenvalue.)

If species are randomly introduced to the system, we would expect an increasing probability of a species invading close to the edge of a niche shadow with increasing number of species. Thus, system stability should in general decrease with increasing number of species. More rigorously, we note that, for any  $N$ -species system governed by (2),

$$\sum_{j=1}^N |\lambda_j| = m\left(\frac{1}{\theta_N} - 1\right) \quad (C3)$$

(since  $\lambda_1 = -m(1/\theta_1 - 1)$ ). The  $N$ -species competition-colonization systems can be generated with many different combinations of types; types can be equally spaced (as in fig. 2D) or randomly spaced along the fecundity axis, and each of these systems would have, in general, different patterns of abundance, different least-negative negative eigenvalues, and different return times to equilibrium following perturbation. For a given  $\theta_N$ , however (i.e., for a given level of “free space” left in the system after all types have reached their equilibrium abundances), the fastest return time will be achieved when all the eigenvalues are equal; that is, when  $\hat{p}_j$  is inversely proportional to  $f_j$ . (Since the sum of all eigenvalues equals a constant, the least negative eigenvalue can always be made more negative by making another eigenvalue less negative until all eigenvalues are equal.) Thus, the dominant eigenvalue corresponding to the fastest possible return time following a perturbation is given by

$$|\lambda_{\min}|_{\max} = \frac{m}{N}\left(\frac{1}{\theta_N} - 1\right), \quad (C4)$$

where  $\lambda_{\min}$  denotes the dominant eigenvalue for any system, and max indicates the largest possible absolute value for this dominant eigenvalue. Using  $\lambda_N = m/N(1/\theta_N - 1) = m(1/\theta_N - 1/\theta_{N-1})$  (for the special case of fastest return time and from [C4] and [C2], respectively) and  $\theta_{N-1} = m/(\theta_N f_N)$ , we find, in the high-diversity limit ( $N \gg 1$ ,  $\theta_N \ll 1$ ), under the condition that all eigenvalues are equal (i.e., [C4] holds), that

$$\theta_N \approx \sqrt{\frac{m}{f_N}} \quad (C5)$$

and

$$|\lambda_{\min}|_{\max} \approx \frac{\sqrt{f_N m}}{N}, \quad (C6)$$

where  $m$  is the mortality,  $N$  is the number of species, and  $f_N$  is the maximum fecundity (i.e., the fecundity of the most inferior competitor). Remembering that the return time following a perturbation is proportional to  $1/\lambda$  gives

$$\tau_{\min} \approx \frac{N}{\sqrt{mf_N}}. \quad (C7)$$

Applying this result to the other (equal) eigenvalues and solving for  $\theta_j$  and, thus,  $\hat{p}_j$  gives

$$f_j = \frac{j(j-1)f_N}{N^2} \quad (\text{C8})$$

for  $j \gg 1$ , all eigenvalues equal, and

$$\hat{p}_j = \frac{\sqrt{mf_N}}{N} \frac{1}{f_j}, \quad (\text{C9})$$

all eigenvalues equal.

Thus, the fastest return time following a perturbation occurs when  $p(f)$  is proportional to  $1/f$  and the  $j$ th type has a fecundity given by (C8).

#### Literature Cited

- Bulmer, M. 1994. Theoretical evolutionary ecology. Sinauer, Sunderland, Mass.
- Durrett, R., and G. Swindle. 1991. Are there bushes in a forest? *Stochastic Processes and Their Applications* 37: 19–31.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* 18:363–373.
- Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749–752.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why there are so many kinds of species. *American Naturalist* 93:145–159.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the USA* 71: 2744–2747.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the USA* 68:1246–1248.
- MacArthur, R. H. 1971. Patterns of terrestrial bird communities. Pages 189–221 in D. S. Farner and J. King, eds. *Avian biology*. Vol. 1. Academic Press, New York.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences of the USA* 69: 1109–1113.
- May, R. M., and M. A. Nowak. 1994. Superinfection, metapopulation dynamics, and the evolution of diversity. *Journal of Theoretical Biology* 170:95–114.
- Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37–40.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* 51:145–178.
- Riesz-Nagy, F. 1952. *Functional analysis*. Ungar, New York.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature (London)* 371:65–66.

Associate Editor: Nicholas J. Gotelli