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The Consequences of Recruitment Limitation: Reconciling Chance, History and Competitive Differences Between Plants

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Plant competition for space is studied using analytical and simulation models. Here, the interaction is viewed as a local competition between juveniles of different species for environmentally variable sites vacated by the random deaths of adults. Because plants are sedentary and have finite fecundity, often only a subset of species will compete for an available site. When a dominant species is recruitment limited, inferior competitors will win some sites by forfeit. It is shown that recruitment limitation allows "winning-by-forfeit" which lessens the effect of competitive asymmetries and slows population and community dynamics. Moreover, since recruitment limitation is likely to be most pronounced in highly diverse communities because of the rarity of many species, it is suggested that there is no conflict between the hypothesis that species-rich plant communities are more influenced by chance and history than regulated by competition, and observations of strong interspecific differences among plants.

Introduction

A disparity apparently exists between conclusions suggested by relatively small scale experiments and those suggested by population and community scale observations. On the one hand, a seemingly robust finding from relatively small scale field and greenhouse experiments is that interspecific competition between plants for space is prevalent, and generally dominated by different species under different homogeneous environmental conditions (Harper, 1977; Goldberg & Barton, 1992). This finding has formed the basis for the hypothesis that multiple competing plant species are maintained by habitat heterogeneity (Levin, 1974; Grubb, 1977; Tilman 1982; Comins & Noble, 1985; Chesson, 1986; Pacala & Tilman, 1993; and references therein).

On the other hand, observations on a relatively large scale of very diverse plant communities suggest that the relative abundances of species within guilds are more influenced by chance and history than tightly regulated by interspecific competition (Hubbell & Foster, 1986). This observation has added support to the alternative hypothesis of competitive equivalence for the multi-species coexistence among plants in highly diverse communities (Shmida & Wilson, 1985; Hubbell & Foster, 1986). According to this hypothesis, community dynamics are so slow that the relative abundances of species within guilds drift in a random walk. This allows historical and chance events in the dynamics of tree populations to have a lasting influence on the plant community.

Is the observation of the importance of chance and history in highly species-rich plant communities in conflict with the general finding of interspecific differences in competitive ability between plants? We use a simple model to suggest that the answer is no.

First, we assume that local scale habitat heterogeneity is critical to multi-species coexistence; we make the extreme assumption that every homogeneous habitat is clearly dominated by one species. However, we predict that highly diverse communities in heterogeneous habitats will be composed of populations that would recover only very slowly after perturbation from equilibrium. Following Sale (1977), the key to our hypothesis is recruitment limitation, which we define as the failure to have any viable juveniles at an available site. The effect of recruitment limitation is that it permits inferior species to win sites in the absence of dominant competitors—by forfeit.

Now, a variety of studies have documented or modeled "winning-by-forfeit" (Hutchinson, 1951; Skellam, 1951; Horn & MacArthur, 1972; Slatkin, 1974; Armstrong, 1976; Platt & Weiss, 1977; Atkinson & Shorrocks, 1981; Shmida & Ellner, 1984, Crawley & May, 1987; Caswell & Cohen, 1991*a*, *b*; Yeaton & Bond, 1991; Tilman, 1994 and others). This "fugitive species" literature demonstrates that a competitively inferior species may coexist with a dominant competitor if the fugitive is better able to colonize vacant space and if the vacant space is generated often enough. But these fugitives are competitively inferior under all conditions, and rely on a colonizing advantage over the dominant competitor.

In this paper, we analyze a model of a simple community in which every species is recruitment-limited, and where every species has a competitive advantage and disadvantage under some environmental condition. Thus, we consider a community in which every species sometimes wins by forfeit. We perform internal and boundary local stability analyses of the model community, and conduct experiments using computer simulation to extend our analytical work. We show that recruitment limitation allows winning-by-forfeit which lessens the effect of competitive asymmetries and slows population and community dynamics. Moreover, we demonstrate that recruitment limitation can prevent even extreme local determinism from strongly regulating the relative abundances of species at the community scale. Thus, since recruitment limitation is likely to be most common is highly species-rich communities because of the rarity of many species, we suggest that the importance chance and history in diverse plant communities is not in conflict with strong interspecific competitive differences between plants.

Methods

Our approach is to develop and analyze a simple model of multi-species plant dynamics that is governed by extreme species-specific determinism at the local scale of individual sites but which has sites coupled with stochastic dispersal between sites. In this section, we first describe the model, then we describe the analytical and computer simulation methods we use to analyze the model. Our analytical work consists of two tractable cases that depend on special symmetry assumptions. First, in the "internal stability analysis" we analyze the community dynamics near the internal equilibrium where each species is at equal abundance and there is no persistent unoccupied space. Then, in the "boundary stability analysis" we analyze invasibility of that same community. We use computer simulations to relax the special symmetry assumptions and to apply the model to finite habitats.

THE MODEL

We develop our model following Pacala & Tilman (1993), which is one of many such models explored to date (Skellam, 1951; Slatkin, 1974; Chesson & Warner, 1981; Shmida & Ellner, 1984; Yodzis, 1986; Comins & Noble, 1987; Armstrong 1989; Pacala 1989; Caswell & Cohen 1991*a*, *b*; and others). We imagine that within a habitat, space is partitioned into sites each of which can contain, at most, one adult plant at a time. Sites are vacated by the random death of adults. Vacant sites become occupied as the result of a competition between juveniles of different species present, and sites are coupled by the dispersal of juveniles produced by adults.

More specifically, the local environmental conditions in the sites vary independently in time and space, and the relative competitive abilities of juveniles depend on the local environmental conditions. The juvenile that captures a vacant site is simply the strongest competitor present under the environmental conditions in the site at that time. Juveniles are dispersed randomly over the habitat, and immediately die unless they capture a vacant site. Thus, the model is spatial in the sense that environmental conditions vary locally and the sets of competitors for available sites are defined locally, but non-spatial in the sense that local environmental conditions vary independently in space and time and juveniles are dispersed randomly over the habitat. Generally, for Q species, the model is

$$\Delta X_i = -d_i X_i + \left[\sum_{j=1}^{Q} d_j X_j + 1 - \sum_{j=1}^{Q} X_j \right] R_i(X_i) W_i(\vec{X}), \qquad i = 1, 2, \ldots, Q \quad (1)$$

where X_i is the proportion of cells occupied by species i adults at time t, d_i is the adult death rate of species i, $R_i(X_i)$ is the probability that a juvenile of species i is present at a site, $W_i(\vec{X})$ is the probability that species i wins a vacant site given that it is present, and $\vec{X}$ is the vector $X_1, \ldots, X_Q$ not including X_i.

Death in species i

In this analysis, we restrict our attention to the simple special case where the adult death rate is constant and equal for all species ($d_i = d$, $i = 1, 2, \dots, Q$). Thus, proportion of species i that dies in each Δt is the death rate times the proportion of species i (the fraction dX_i).

Vacant space

Vacant space is the set of sites without an adult. We assume that adults do not modify sites in any lasting way. There are two sources of vacant space: sites vacated due to the death of an adult (the fraction $d\Sigma X_j$), and sites that were vacated previously but not yet recolonized (the fraction $1 - \Sigma X_j$).

Probability species i recruits to a site

We subsume all aspects of seed production, seed survivorship, and seed establishment into per capita fecundity. Like the adult death rate, here we restrict our attention to the simple case where the per plant fecundity is constant and equal for all species (F).

In addition, we assume that dispersal is random; the rain of juveniles on each cell is a Poisson random variable. The mean number of juveniles of species i landing on a cell in Δt is FX_i. Then, the probability that at least one individual of the ith species is present in a site at time t is one minus the probability that no juveniles are at the site

$$R_i(X_i) = 1 - \mathrm{e}^{-FX_i}. \qquad (2)$$

In Appendix B we relax the assumption of completely random dispersal by considering the simple case in which a fraction of seeds disperse into their mother's cell.

Probability species i wins a site given that it has recruited

We assume that species' competitive abilities depend on local environmental conditions. We define the competitive abilities so that environmental heterogeneity is required for multi-species coexistence; a single species will exclude all others in a homogeneous environment, but the identity of the dominant species is different under different environmental conditions.

Specifically, the environment varies independently in time and space along a single environmental axis (E) with a constant probability density ($P(E)$). On that axis, we define a species' "niche position" as the environmental condition where it is dominant over all potential competitors. We assume that a species will win an available site if the environment is closer to its niche position than to the niche position of any other species present. Pacala & Tilman (1993) show that this assumption is consistent with a wide range of mechanistic models of competition.

For convenience, we define a species "absolute niche" as the set environmental conditions in which a species is dominant over all potential competitors. A species is said to be "absolutely dominant" under environmental conditions within its absolute niche. A species is said to "win-by-forfeit" when it captures a site with an environment outside of its absolute niche, in the absence of a more dominant but recruitment limited competitor.

To compute the probability that a species captures a site with a particular environmental condition, given the species is present at the site, we take the niche positions of all of the potentially competing species and identify for each environmental condition E the set $S(E)$ of species that must be absent if the focal species is to capture a site with that environment. Note that this set will be empty for environments within a specie's absolute niche. We then derive the probability $V(S(E))$ that all the resident species in the set are indeed absent. Thus

$$W_i(\vec{X}) = \int V(S(E))P(E)\,\mathrm{d}E. \qquad (3)$$

INTERNAL STABILITY ANALYSIS

To begin, it is unreasonable to assume that in a community as diverse as a rain forest, every species places saplings in every gap. However, it is not unreasonable to assume that nearly every gap gets colonized by some species. Thus, we assume that the community as a whole is not recruitment limited (almost every gap is colonized by some species because the per plant fecundity is large), but individual species can be recruitment limited (not every species necessarily colonizes every gap because at least some species are rare).

Specifically we assume that the species have a sufficiently large per plant fecundity (F) such that almost no space remains vacant ($\exp(-F\Sigma X_j) \approx 0$). However, F will not generally be large enough for all species always to have juveniles at every site ($\exp(-FX_i) \gg 0$ for at least some species i).

Furthermore, we assume that the Q resident species have niche positions evenly spaced over the environmental axis and that the environmental axis is a closed loop (as in May & MacArthur, 1972; May, 1974). Thus, each species' absolute niche occupies $1/Q$ of the environmental axis. Finally, to simplify the presentation, we assume that the environment fluctuates uniformly along the environmental axis. These last three assumptions are merely for analytical convenience. In any case, we later relax these assumptions in computer simulations.

These assumptions allow us to specify the proportion of each species at equilibrium as

$$X_i^* = \frac{1}{Q}, \quad i = 1, 2, \ldots, Q. \tag{4}$$

In order to describe the dynamics of the populations in the community near equilibrium (4), we compute the $Q \times Q$ linearization matrix (Jacobian)

$$\mathbf{J} = \left(\left(\frac{\partial X_i(t+1)^*}{\partial X_j} \right)_{ij} \right), \tag{5}$$

and consider the magnitude of the rate limiting eigenvalue derived from it (May, 1974). The elements of the first row of the Jacobian are

$$c_0 = 1 - d + W_1^*[(d-1)(1 - \mathrm{e}^{-F/Q}) + dF\,\mathrm{e}^{-F/Q}] \tag{6}$$

and

$$c_k = (1 - \mathrm{e}^{-F/Q}) \left[(d-1) W_1^* + d \frac{\partial W_1^*}{\partial X_k} \right], \qquad k = 1, 2, \ldots, Q-1. \tag{7}$$

Recall that by definition W_1 is independent of X_1. In Appendix A, we compute W_1^* by applying eqn (3), where

$$W_1^* = \frac{1}{Q} \left[\frac{\mathrm{e}^{-F} - 1}{\mathrm{e}^{-F/Q} - 1} \right] \tag{8}$$

and by a similar method

$$\frac{\partial W_1^*}{\partial X_k} = -\frac{F}{2Q} \left[\frac{2\,\mathrm{e}^{-F} - \mathrm{e}^{-Fk/Q} - \mathrm{e}^{-F(Q-k)/Q}}{\mathrm{e}^{-F/Q} - 1} \right]. \tag{9}$$

Because of the symmetry assumptions, the Jacobian is symmetric and subsequent rows are cyclical permutations of the first row. Thus, the eigenvalues for perturbations near the equilibrium are

$$\lambda_k = \sum_{l=0}^{Q-1} c_l \cos\left(\frac{2\pi k l}{Q} \right) \qquad k = 0, 1, \ldots, Q-1 \tag{10}$$

(May, 1974). Value of the rate determining eigenvalue from eqn (10) are presented in the Results.

BOUNDARY STABILITY ANALYSIS

Using the assumptions from the previous section, we explore the conditions necessary for invasion of a resident community at equilibrium. To summarize, we assume that the "resident species" are at the internal equilibrium ($X_i^* = 1/Q$, $i = 1, 2, \ldots Q$) with sufficiently large F such that approximately no space remains uncolonized ($\exp(-F\Sigma X_i) = 0$, $i = 1, 2, \ldots, Q$). We then introduce a rare "invading species"—labeled "I"—with a niche position intermediate between two resident species. This invading species is both the most recruitment limited, and has the smallest absolute niche. This latter assumption is conservative for exploring limits to diversity and is relaxed in the computer simulations that follow.

Assuming that the resident community internal equilibrium is locally stable, invasion depends on the eigenvalue associated with the invading species which is

$$\lambda_I = 1 - d + dFW_I^*, \tag{11}$$

where, by applying eqn (3) using a method similar to that in Appendix A,

$$W_I^* = \frac{1}{Q} \left[\frac{1}{2} + \frac{\mathrm{e}^{-F} - \mathrm{e}^{-F/Q}}{\mathrm{e}^{-F/Q} - 1} \right]. \tag{12}$$

Invasion succeeds if

$$\frac{1}{Q} \left[\frac{1}{2} + \frac{\mathrm{e}^{-F} - \mathrm{e}^{-F/Q}}{\mathrm{e}^{-F/Q} - 1} \right] > \frac{1}{F}. \tag{13}$$

SIMULATION

We developed a computer simulation of the model primarily to verify that the symmetry assumptions in the analytical work are not too restrictive and to extend the analytical work with simulated experiments. In the large habitat-limit, our simulator is identical to the analytical model. Simulated habitats, however, are necessarily finite, and finite habitats introduce sampling error. The sampling error occurs in assigning patch states, which include both the environmental condition and the local assemblage of competitors, to only a finite number of patches. Just as genetic drift arises from taking a finite sample of an assumed infinite allele pool, "ecological drift" arises here from taking a finite sample of an assumed infinite patch pool.

To test whether the symmetry assumptions in the analytical work of even niche position spacing and a closed environmental axis are overly restrictive, we simulated cases with even and random spacing of niche positions on both closed and linear resource axes. We explored both the assembly of diverse communities through continual immigration of new species, and the long term persistence of diverse communities. To explore the consequences of ecological drift, we simulated habitats ranging from 900 to 20,000 sites with 1 to 500 species.

To illustrate the affect of ecological drift on limiting similarity, which we define as the minimum spacing between the strategies of species that must be exceeded for the species to coexist (Pacala & Tilman, 1993), we compared the average absolute niche width of species that went extinct in simulations with the expected "null distributions" of extinctions. In each of these simulations, we initialized the model by filling the habitat with equal abundances of 75 species with random niche positions on a closed environmental axis. We then ran the model for 100 time steps and recorded the absolute niche widths of species that went extinct, as determined at the moment they went extinct. To produce the null distributions, we reinitialized the model with the same 75 species, then randomly eliminated the number of species that had gone extinct in the simulation, and repeated this process 200 times. We computed the average absolute niche width of extinct species each time and thus produced a null distribution with 200 average widths. We then compared this distribution to the average absolute niche width of species from the simulation.

Results

To begin, we draw on both the internal and boundary local stability analyses. Using these methods, we show that in the special case with symmetry assumptions, the model permits enormous richness of species, and that as we increase recruitment limitation either by increasing species richness or by decreasing per plant fecundity, there is more winning-by-forfeit which in turn slows population and community dynamics. We then present the results of computer simulation experiments. We first illustrate that the symmetry assumptions made for analytical convenience are not too restrictive. We then illustrate some of the consequences of slow dynamics in finite habitats. In particular, we show that ecological drift both caps species richness and establishes an effective limiting similarity despite the extreme determinism assumed in the local competitive interactions.

THE CAP ON SPECIES RICHNESS IS ENORMOUS

We explored the limits to species richness by exploring the limit given by the invasion condition (13) for a range of values of the per plant fecundity (F). Figure 1 illustrates the cap on species richness as a function of (F). In this model, the deterministic cap on species richness is enormous.

WINNING-BY-FORFEIT INCREASES WITH INCREASED RECRUITMENT LIMITATION

Why is the deterministic cap on species richness so large? We begin by noting from eqn (12) that the probability that an invading species captures a randomly chosen vacant site by absolute dominance, given that it is present, is

$$W^*_{\mathrm{Ia}} = \frac{1}{2Q} \tag{14}$$

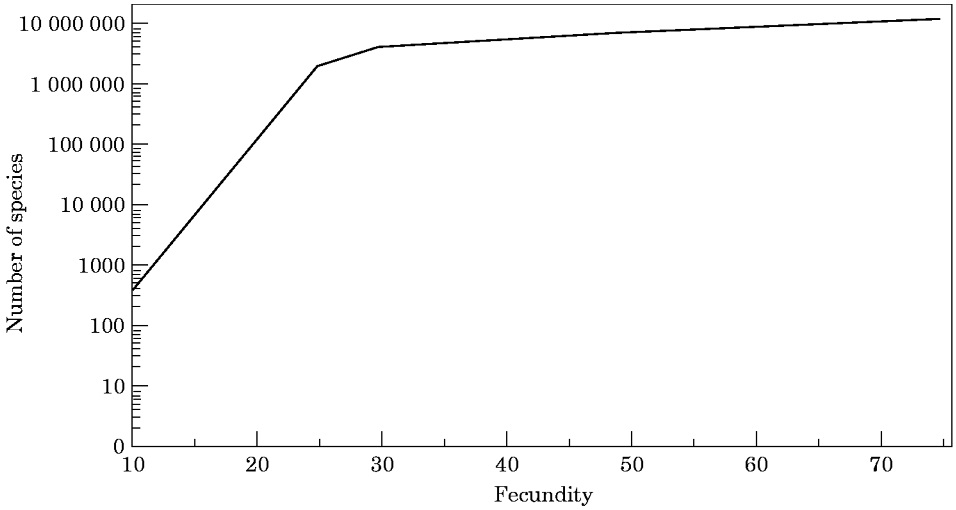

FIG. 1. The cap on species richness as a function of per plant fecundity (F). This curve illustrates the numerical solution to condition (13). Note that in this model, the cap on species richness is enormous.

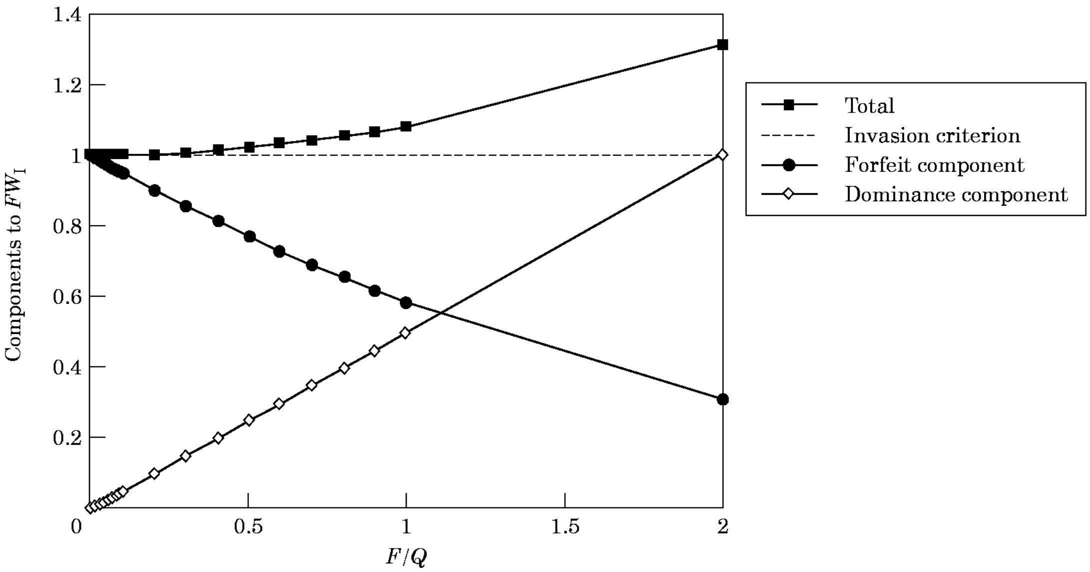

FIG. 2. The win-by-absolute-dominance (FW_{Ia}) and win-by-forfeit (FW_{If}) components to the critical term FW_I^* of an invading species' eigenvalue as a function of F/Q. F/Q is a measure of the recruitment limitation in the community, with small F/Q corresponding to high recruitment limitation. At small F/Q (high diversity relative to fecundity), the invading species win sites primarily by forfeit and is thus frequently found outside of its absolute niche. At large F/Q (low diversity relative to fecundity), the invading species wins sites primarily by absolute dominance and is thus rarely found outside of its absolute niche.

Then also using eqn (12), we approximate the probability that an invading species captures a randomly chosen available site by forfeit, given that is present, as

$$W_{If}^* \approx \frac{1}{Q}\left[\frac{e^{-F/Q}}{1-e^{-F/Q}}\right]. \tag{15}$$

Approximation (15) is consistent with our previous assumption that terms of order $\exp(-F)$ are negligible. The approximation is important because it allows us to simplify the invading species eigenvalue [eqn (11)] by combining F and Q into a single variable F/Q. The approximation is used only for the illustrative purposes of Fig. 2.

Figure 2 shows the contributions of the absolute dominance component [F multiplied by eqn (14)] and the win-by-forfeit component [F multiplied by eqn (15)] of the invader's niche to the invader's eigenvalue as a function of F/Q. Note from eqn (2) that the probability that each resident species colonizes a randomly chosen site when at equilibrium is $1-\exp(-F/Q)$. Thus, F/Q is a measure of the recruitment limitation of each species in the community, with small F/Q corresponding to high recruitment limitation. As we explore the limits to species richness and increase the number of species in the community (decrease F/Q for a given F), or as we reduce per plant fecundity (decrease F/Q for a given Q), each species becomes more recruitment limited, and the invading species' dynamics depend less on absolute dominance, and more on winning-by-forfeit. Moreover, as species capture more sites by forfeit they are found increasingly outside their absolute niche. Because of the relatively large contribution of the winning-by-forfeit component at small F/Q, the cap on diversity in this model would collapse without winning-by-forfeit for reasonable values of F.

THE PACE OF POPULATION DYNAMICS DECREASE WITH INCREASED WINNING-BY-FORFEIT

What is the consequence of winning-by-forfeit for the pace of population and community dynamics? We first examined how the rate of invasion depends on F and Q. Each curve in Fig. 3 corresponds to a different rate of invasion (value of the invader's eigenvalue) for a given death rate. To produce the lowest curves in the Fig. 3 we substituted $\lambda_I = 1.1$ into eqn (11) and then numerically solved for Q as a function of F. Thus, the lowest curves show, for each value F, the divesity at which rate of invasion is $\lambda_I = 1.1$. The remaining curves correspond to slower rates of invasion (eigenvalues closer to zero, see legend). Figure 3 illustrates that in this model the rates of invasion are extremely slow at high diversity (eigenvalues near one), and that the rates of invasion decrease with increased species richness or decreased per plant fecundity.

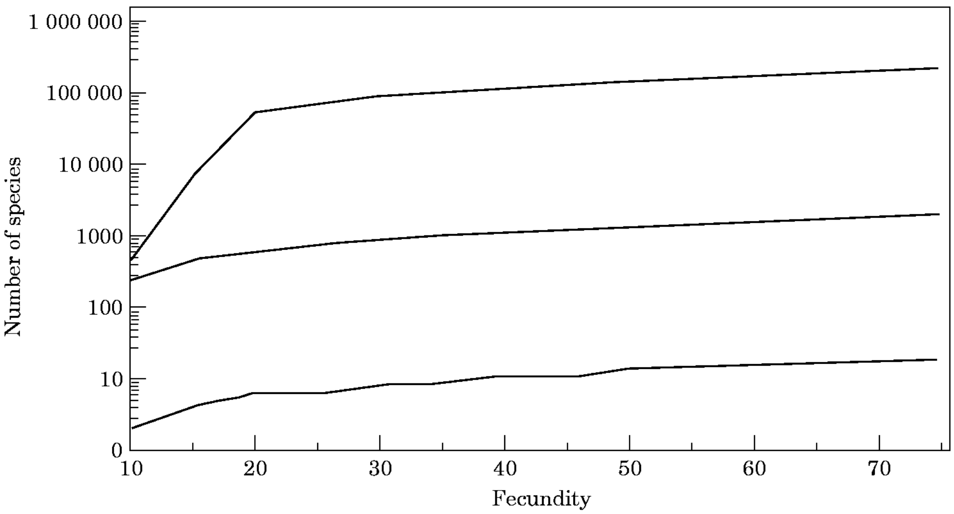

FIG. 3. These curves illustrate the numerical solution of eqn (11) with eqn (12) for the number of species (Q) as a function of the per plant fecundity (F) and a variety of different values of the eigenvalue governing invasion. From top to bottom, the curves corresponds to eigenvalues of, 1.000000001, 1.00001, and 1.1. To produce these curves,the death rate (d) was set to 0.1.

Using the internal local stability analysis, we can extend these results to the community dynamics in general. Figure 4 shows how the rate of return to the community internal equilibrium decreases as species richness increases and as per plant fecundity decreases. To produce Fig. 4, we computed the rate determining eigenvalue for local community dynamics given by eqn (10) as a function of species richness for two values of per-plant fecundity (F) and for a given death rate (d). For the top curve, we set $F=10$ and for the bottom curve we set $F=100$. In both cases, the rate determining eigenvalue for local community dynamics approaches one as the number of species increases. Decreased per plant fecundity causes increased recruitment limitation and winning-by-forfeit which slows dynamics (eigenvalue near one); in the top curve, there is more recruitment limitation and slower dynamics for a given

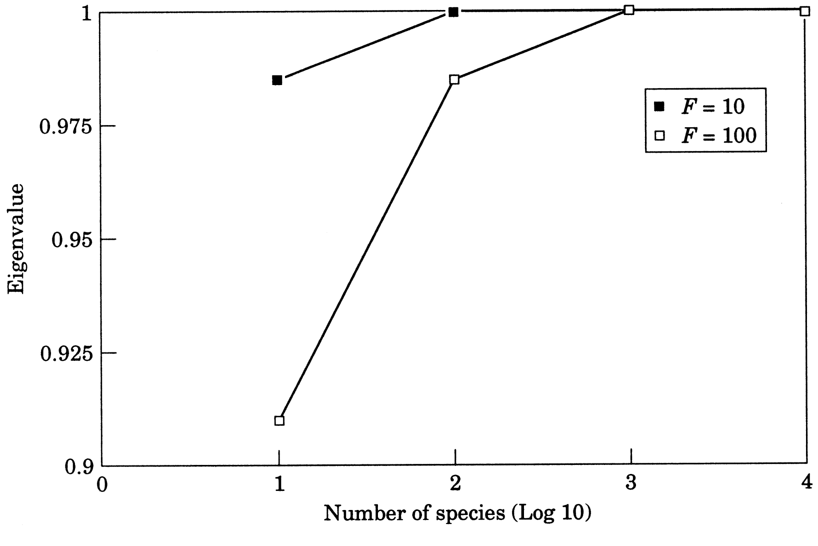

FIG. 4. These curves illustrate the numerical solution of the rate determining eigenvalue for the community dynamics near equilibrium as a function of per plant fecundity (F) and species richness (Q) from eqn (10). For both curves $d=0.1$. In the top curve, $F=10$. In the bottom curve, $F=100$. For a given species richness, the top curve represents lower per plant fecundity, more recruitment limitation, and slower dynamics. As species richness increases, each species is rarer thus more recruitment-limited, resulting in slower community dynamics (eigenvalues near 1). Note that over the range of Q presented, neither of these curves actually intersects 1, though they get very close to 1.

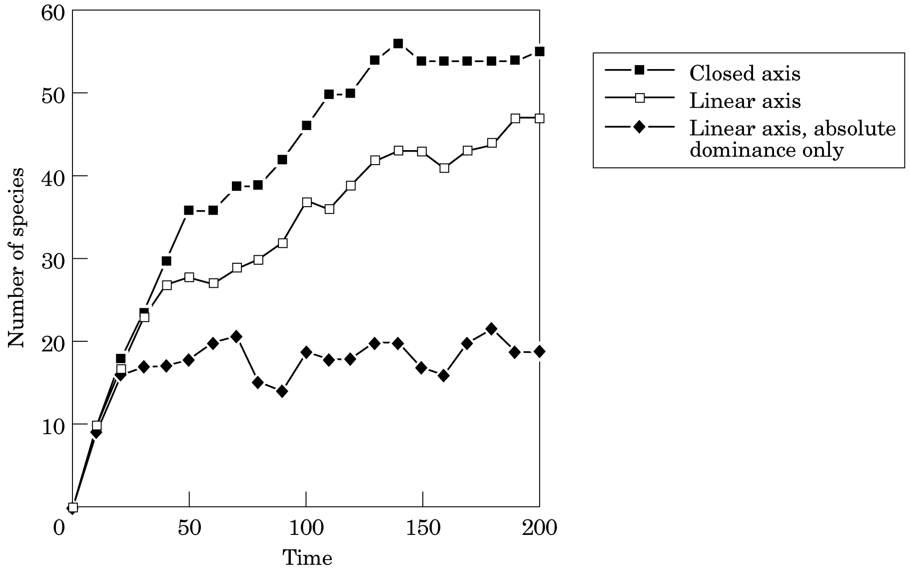

FIG. 5. The species richness of communities over time as they are assembled by adding a single individual of a new species with a random niche position each iteration. In this simulation, $F = 25$, $d = 1.0$, and we used habitats of 1000 and 10 000 cells. The results from the closed axis and linear axis runs are similar—suggesting that the closed axis assumption in the analytical work is not too restrictive. The lowest curve illustrates that excluding winning-by-forfeit places a relatively low cap on maximum diversity, as suggested by the analytical work.

specie richness than in the bottom curve because the per plant fecundity is lower in the top curve.

THE SPECIAL CASE IS NOT TOO RESTRICTIVE

Figure 5 demonstrates that the symmetry assumptions in the analytical work (even niche spacing and closed environmental axis) are not too restrictive of the analytical results. This figure illustrates the diversity of communities over time as they were assembled by the continual immigration of single individuals of new species with random niche positions in our simulation. Since invading species have random niche positions, the species do not have equal abundance at equilibrium and the invading species do not necessarily have the smallest absolute niches, as in the case we treated analytically. To produce the lowest curve, we did not allow winning-by-forfeit and used a linear axis. In this case, available sites without an absolutely dominant competitor remained empty. The lowest curve shows that species richness is capped at a relatively low level without winning-by-forfeit, just as the analytical results suggest. To produce the remaining two curves, we allowed winning-by-forfeit and compared linear and closed environmental axes. With winning-by-forfeit, there can be much higher species richness, also as the analytical work predicts. Moreover, the two upper curves show that there is little difference between simulations with linear and closed environmental axes which suggests that the closed environmental axis assumed for the analytical work may not be too restrictive; the species richness in the community with the linear environmental axis is perhaps slightly lower due to edge effects of the linear environmental axis.

A CAP ON DIVERSITY EXISTS DUE TO ECOLOGICAL DRIFT

Slow population dynamics (eigenvalues close to one) make the consequences of ecological drift potentially severe. Since, in the analytical work, we found only enormous limits to diversity, and since the rate of invasion decreases with increased diversity, the limit to

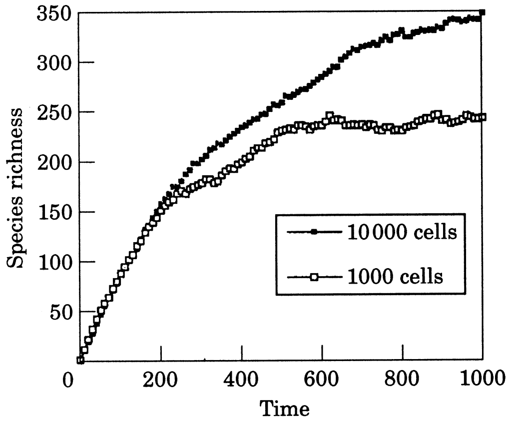

FIG. 6. The effect of finite habitat size on the species richness trajectories of communities being assembled by repeated colonization of new species. In this simulation, $d = 0.01$, and we used habitats of 1000 and 10 000 cells. In each case, we ran the model for 1000 time steps. In all cases, one individual of a new species with a random niche position on a linear environmental axis was introduced in each time step. The smaller habitat supports fewer species because drift is more severe there.

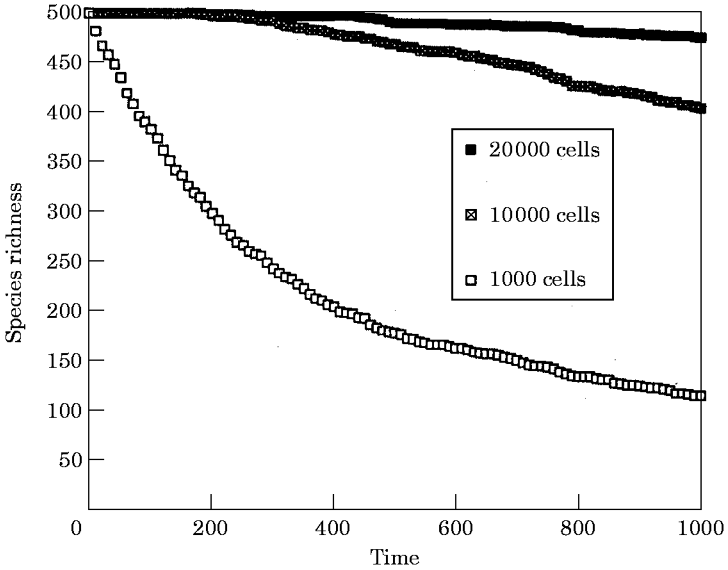

FIG. 7. The effect of finite habitat size on the species richness trajectories of communities assembled in an initial colonization event. In all cases, the habitat was initially colonized with one individual of each of 500 species with random niche positions on a linear environmental axis. Then the model was run with $F=25$ and $d=0.01$ for 1000 time steps.The smaller habitats support fewer species because drift is more severe there.

diversity in finite populations should be set by ecological drift.

Figure 6 shows the trajectories of species richness with repeated colonization of a habitat by species with random niche positions on a linear environmental axis. As expected, habitat size limits the number of species that can coexist in the simulation; fewer species coexist in the smaller habitat than in the larger habitat.

Figure 7 illustrates species richness trajectories through time for small and large habitats ranging from 1000 to 20 000 cells. Ecological drift, exacerbated by small patch size, explains the difference in the extinction of species between the two runs.

LIMITING SIMILARITY IS SET BY ECOLOGICAL DRIFT

Figures 8(a) and 8(b) show the results of two experiments which compare the average absolute niche width of species to go extinct with the model simulation, to null distributions made by repeatedly forcing species extinct at random. In both the large [Fig. 8(a)] and small [Fig. 8(b)] habitat, the average absolute niche width of species that went extinct in the model was significantly less than any average in the null distribution. Limiting similarity structures the community non-randomly in each simulation. However, when ecological drift is more severe, the effects of limiting similarity are more pronounced: the average absolute niche width of extinct species in the small habitat is three times larger than in the large habitat.

Discussion

We find that highly species-rich communities of extreme competitors may be only slowly regulated by competition because of a positive feedback between richness, winning-by-forfeit, and a decrease in the pace of population dynamics. This feedback works as follows. The probability that dispersing propagules of a species colonize a vacant site decreases with a decrease in the abundance of that species. In other words, increased species richness causes each species to become proportionally rarer, which in turn causes each species to become more recruitment limited. Recruitment limitation allows winning-by-forfeit, which lessens the effect of competitive asymmetries among species and decreases the pace of population and community dynamics. Under the cases considered here, even with reasonable per plant fecundity the deterministic cap to species richness is enormous because of the winning-by-forfeit that recruitment limitation allows.

In finite communities, however, the effective limiting similarity in our model is set by ecological drift. This is because, as diversity increases, the pace of population dynamics slows (eigenvalues near one), and species with the slowest dynamics are also the rarest and the least bounded away from extinction. With pronounced recruitment limitation, the limiting similarity imposed by drift replaces the deterministic limit. Recruitment limitation acts to reduce the effect of competition between species, but simultaneously

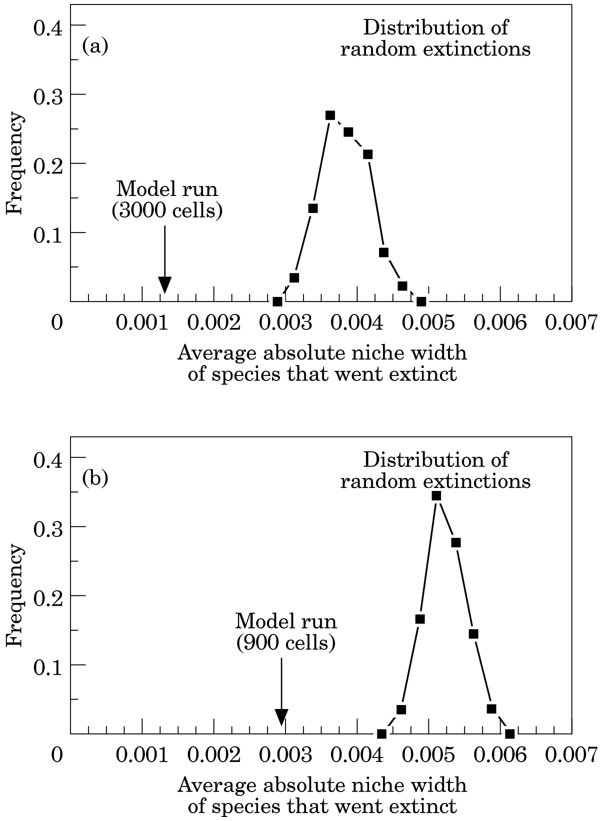

FIG. 8. In these figures, we compare the average niche width of species that went extinct in simulations to null distributions (see text). In simulations, we initialized the model with equal abundances of 300 species with random niche position on a closed environmental axis, then ran the model for 100 time steps with $F=25$ and $d=1$. In Fig. 8(a), the habitat had 3000 cells and 75 species went extinct. In Fig. 8(b), the habitat had 900 cells and 188 species went extinct. Ecological drift imposes a limiting similarity here that non-randomly structures the community and caps diversity.

slows population dynamics, causing ecological drift to create non-random structure in communities. The concept of ecological drift is of course not new (May, 1974; Chesson & Case, 1986; and others), but we have illustrated that with recruitment limitation and winning-by-forfeit, ecological drift can arise even in communities with extreme local determinism. In Appendix B, we illustrate that a simple case of local dispersal does not jeopardize these results, but instead tends to amplify them.

Hubbell & Foster (1986) suggested that the tree species comprising the highly diverse forest on Barro Colorado Island, Panama are organized into guilds, in which the relative abundances of species are not tightly regulated by competition, but most influenced by chance and history. They explained this hypothesis by suggesting that species within guilds are competitively equivalent. They hypothesized that competitive equivalence was an *evolutionary consequence* of "neighborhood-biotic-uncertainty", in which the unpredictability of the local assemblage of competitors around each individual plant prevents directional selection for specialization. How could their "chance and history" hypothesis be tested? One approach might be to perform a series of pot-type experiments to test if the species are in fact competitively equivalent—the key to their explanation. However, we have shown that, because of an *ecological consequence* of neighborhood biotic uncertainty—individuals capturing sites by forfeit of recruitment limited competitors—the chance and history hypothesis is not rejected even if pot-type experiments reveal extreme competitive differences among species.

We believe that recruitment limitation is a neglected and perhaps underestimated topic in plant community ecology (Eriksson & Ehrlen, 1992; Ribbens *et al.*, 1994). Attempts have only recently been made to assess the role that recruitment limitation actually plays in forest dynamics by empirically calibrating relevant multi-species models (Ribbens *et al.*, 1994). Our assumption here of extreme competitive differences between species tends to exaggerate the role that recruitment limitation plays, as there are certainly other sources of stochasticity in the outcome of local competitions. On the other hand, we have intentionally not included the tradeoffs in fecundity, or dispersal that have previously been shown to facilitate coexistence because of the winning-by-forfeit that recruitment limitation allows. We make these assumptions not to argue that competition is in fact this severe, nor that differences in life history are unimportant, but to make our argument conservative (by showing that recruitment limitation can result in slow community dynamics even with extremely deterministic local competition) and relatively simple (by omitting life-history tradeoffs that promote winning-by-forfeit by completitively disadvantaged species). From this point of view, slow community dynamics may be a general characteristic of highly diverse plant communities in which recruitment limitation is likely to be especially pronounced—regardless of the degree of determinism in the outcomes between locally competing species.

In addition, in this model the realized niche of species is strongly affected by the degree of recruitment limitation in the community. With no recruitment limitation, plants are found only inside of their absolute niche (a small realized niche). With recruitment limitation, plants are also found outside of their absolute niche (a larger realized niche) because of winning sites by forfeit in the absence of more dominant but recruitment limited competitors. This should serve as an added warning to attempts to infer the fundamental requirements of plant species from the characteristics of their realized niches (Pacala & Hurtt, 1993).

Finally, our goal in this paper has been to illustrate that even extreme local determinism can be reasonably contained within a system that has slow dynamics on the community scale. The work presented here offers a mechanism—recruitment limitation—that may in part reconcile the importance of chance and history in species-rich plant communities with findings of interspecific competitive differences between plants.

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REFERENCES

Armstrong, R. A. (1976). Fugitive species: experiments with fungi and some theoretical considerations. *Ecology* **57,** 953–963.

Armstrong, R. A. (1989). Competition, seed predation, and species coexistence. *J. theor. Biol.* **141,** 191–195.

Atkinson, W. D. & Shorricks, B. (1981). Competition on a divided and ephemeral resource: a simulation model. *J. Anim. Ecol.* **50,** 461–471.

Caswell, H. & Cohen, J. E. (1991*a*). Communities in patchy environments: a model of disturbance, competition, and heterogeneity. In: *Ecological Heterogeneity* (Kolasa, J. & Pickett, S., eds) pp. 97–122. New York: Springer Verlag.

Caswell, H. & Cohen, J. E. (1991*b*). Disturbance, interspecific interaction and diversity in metapopulations. *Biol. J. Linn Soc.* **42,** 193–218.

Chesson, P. L. & Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* **117,** 923–943.

Chesson, P. L. (1986). Environmental variation and the coexistence of species. In: *Community Ecology* (Diamond, J. & Case, T. J., eds) pp. 240–256. New York: Harper & Row.

Chesson, P. L. & Case, T. J. (1986). Overview: nonequilibrium community theories: chance, variability, history, and coexistence. In: *Community Ecology* (Diamond, J. & Case, T. J., eds) pp. 229–239. New York: Harper & Row.

Comins, H. N. & Noble, I. R. (1985). Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *Am. Nat.* **126,** 706–723.

Crawley, M. J. & May, R. M. (1987). Population dynamics and plant community structure: competition between annuals and perennials. *J. theor. Biol.* **125,** 475–489.

Eriksson, O. & Ehrlen, J. (1992). Seed and microsite limitation of recruitment in plant populations. *Oecologia* **91,** 360–364.

Goldberg, D. E. & Barton, A. M. (1992). Patterns and consequences of interspecific competition in natural communities; a review of field experiments with plants. *Am. Nat.* **139,** 771–801.

Grubb, P. J. (1977). The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52,** 107–145.

Harper, J. L. (1977). *Population Biology of Plants*. London: Academic Press.

Horn, H. S. & MacArthur, R. H. (1972). Competition among fugitive species in a harlequin environment. *Ecology* **53,** 749–752.

Hubbell, S. P. & Foster, R. B. (1986). Biology, chance, and history and the structure of tropical rain forest tree communities. In: *Community Ecology* (Diamond, J. & Case, T. J., eds) pp. 314–329. New York: Harper & Row.

Hutchinson, G. E. (1951). Copepodology for the ornithologist. *Ecology* **32,** 571–577.

Levin, S. A. (1974). Dispersion and population interactions. *Am. Nat.* **108,** 207–228.

May, R. M. (1974). *Stability and Complexity in Model Ecosystems*, 2nd edn. Princeton, NJ: Princeton University Press.

May, R. M. & MacArthur, R. H. (1972). Niche overlap as a function of environmental variability. *Proc. Nat. Acad. Sci. U.S.A.* **69,** 1109–1113.

Pacala, S. W. (1989). Plant population dynamic theory. In: *Perspectives in Ecological Theory* (Roughgarden, J., May, R. M. & Levin, S. A., eds) pp. 54–67. Princeton, NJ: Princeton University Press.

Pacala, S. W. & Hurtt, G. C. (1993). Terrestrial vegetation and climate change: integrating models and experiments. In: *Biotic Interactions and Global Change* (Kingsolver, J., Kareiva, P. & Huey, R., eds) pp. 57–74. Sunderland, MA: Sinauer.

Pacala, S. W. & Tilman, D. (1993). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.* **143,** 222–257.

Platt, W. J. & Weis, I. M. (1977). Resource partitioning and competition within a guild of fugitive prairie plants. *Am. Nat.* **111,** 479–513.

Ribbens, E., Silander, J. A. & Pacala, S. W. (1994). Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75,** 1794–1806.

Sale, P. F. (1977). Maintenance of high diversity in coral reef fish communities. *Am. Nat.* **111,** 337–359.

Shmida, A. & Ellner, S. (1984). Coexistence of plant species with similar niches. *Vegetatio* **58,** 29–55.

Shmida, A. & Wilson, M. V. (1985). Biological determinants of species diversity. *J. Biogeog.* **12,** 1–20.

Skellam, J. G. (1951). Random dispersion in theoretical populations. *Biometrika* **38,** 196–218.

Slatkin, M. (1974). Competition and regional coexistence. *Ecology* **55,** 128–134.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology* **75,** 2–16.

Yeaton, R. I. & Bond, W. J. (1991). Competition between two shrub species: dispersal differences and fire promote coexistence. *Am. Nat.* **138,** 328–341.

Yodzis, P. (1986). Competition, mortality, and community structure. In: *Community Ecology* (Diamond, J. & Case, T. J., eds) pp. 480–491. New York: Harper & Row.

APPENDIX A

Computation of W_1^*

Here, we compute W_1^*. To summarize the situation, we make the symmetry assumptions (even niche spacing and closed environmental axis). The environmental conditions (E) fluctuates uniformly, F is sufficiently large such that approximately no site remains uncolonized by some species, but that not so large that every species colonizes every site, and the community is at the internal equilibrium ($X_i^* = 1/Q$, $i = 1, 2, \ldots, Q$). Then, using eqn (3) in the main text, we compute the probability that species 1 captures a randomly chosen vacant site given that it is present.

First, species 1 captures all sites at which it is present that have an environmental condition within its absolute niche. Species 1's absolute niche consists of half the distance from its niche position to that of species 2 ($1/2Q$) and half the distance in the other direction from its niche position to that of species Q ($1/2Q$). The environmental condition is within this portion of the environmental axis with probability ($1/Q$).

Next, consider the two species with niche positions immediately adjacent to species 1 (species 2 and species Q). Species 2 is absent from a randomly chosen vacant site with probability $\exp(-F/Q)$. When its absent, species 1 will win by forfeit in all environmental conditions between species 1's niche position and species 3's niche position ($1/Q$), not counting the environmental conditions already accounted for ($1/Q-1/2Q=1/2Q$). Thus, species 1 wins $1/2Q$ of the environmental conditions with probability $1/2Q\exp(-F/Q)$. Of course, an identical and independent argument can be made for the environmental conditions dominated by species Q. Thus, species 1 wins by forfeit of one of its adjacent residents with probability

$$W_1^*(1)=\frac{1}{Q}\,\mathrm{e}^{-F/Q}. \tag{A.1}$$

Next, consider the four species with niche positions immediately adjacent to species 1 (species: $Q-1, Q, 2, 3$). Species 2 and 3 are absent from a randomly chosen vacant site with probability $\exp(-2F/Q)$. When they are both absent, species 1 will win by forfeit in all of the environmental conditions between species 1's niche position and species 4's niche position ($3/2Q$), not counting the environmental conditions already accounted for ($3/2Q-1/Q=1/2Q$). Thus, species 1 wins $1/2Q$ of the environmental conditions with probability $1/2Q\exp(-2F/Q)$. Of course, an identical and independent argument can be made for the environmental conditions dominated by species $Q-1$. Thus, species 1 wins by forfeit of two of its adjacent residents with probability

$$W_1^*(2)=\frac{1}{Q}\,\mathrm{e}^{-2F/Q} \tag{A.2}$$

We repeat this process, finally accounting exactly once for each environmental condition. The probability that species 1 wins a randomly chosen available site at which it present is just the sum of all such probabilities

$$W_1^*=\frac{1}{Q}\left[1+\sum_{j=1}^{Q-1}(\mathrm{e}^{-F/Q})^j\right] \tag{A.3}$$

Equation (A.3) can be simplified as

$$W_1^*=\frac{1}{Q}\left[\frac{\mathrm{e}^{-F}-1}{\mathrm{e}^{-F/Q}-1}\right] \tag{A.4}$$

APPENDIX B

Finite Dispersal

Here, we summarize a boundary analysis for a case with a simple local dispersal bias. We assume that only a fraction m, of each plant's fecundity (F) enters the random dispersal pool, while the remaining fraction ($1-m$) disperse locally onto the parent's site.

As in the boundary analysis of infinite dispersal, we assume that Q resident species have niche positions spaced evenly over a closed environmental axis, that F is large enough so that no site remains uncolonized, and consider the fate of an intermediate invading species when the resident community is at the internal equilibrium $X_i^*=1/Q$. Furthermore, ($1-m$) is assumed to be sufficiently large that each parent leaves some progeny at its site. Then, by applying eqn (3) (from the main text) to this case, the eigenvalue governing invasion is

$$\lambda_I=1-d+\frac{d}{Q}\left[\frac{1}{2}+\sum_{j=1}^{Q-1}\mathrm{e}^{-jFm/Q}+\frac{1}{2}\mathrm{e}^{-Fm}\right.$$
$$\left.+Fm\left(\frac{1}{2}+\sum_{j=1}^{Q-1}\mathrm{e}^{-jFm/Q}-\frac{1}{Q}\sum_{j=1}^{Q-1}j\,\mathrm{e}^{-jFm/Q}\right)\right] \tag{B.1}$$

In the main body of the text, we considered the extreme case of infinite dispersal where $m=1$. Here, first note that at the other extreme, $m=0$, there is no dispersal off parent sites, there is thus no interspecific competition between juveniles, the maximum amount of winning-by-forfeit in the system and $\lambda=1$ [which is easily verifiable from eqn (B.1)]. We have numerically solved eqn (B.1) as a function of m for several cases of F, Q and d. As m decreases from 1 to 0, the invader's eigenvalue decreases monotonically towards 1. Finite dispersal reduces the pace of deterministic dynamics because of increased recruitment limitation and increased winning-by-forfeit.