

LETTER

When do localized natural enemies increase species richness?

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Abstract

The Janzen–Connell hypothesis states that local species-specific density dependence, mediated through specialist enemies of offspring such as fungal pathogens and insect seed predators, can facilitate coexistence of species by preventing recruitment near conspecific adults. We use spatially explicit simulation models and analytical approximations to evaluate how spatial scales of offspring and enemy dispersal affect species richness. In comparison with model communities in which both offspring and enemies disperse long distances, species richness is substantially decreased when offspring disperse long distances and enemies disperse short distances. In contrast, when both offspring and enemies disperse short distances species richness more than doubles and adults of each species are highly spatially clumped. For the range of conditions typical of tropical forests, locally dispersing specialist enemies may decrease species richness relative to enemies that disperse long distances. In communities where dispersal distances of both offspring and enemies are short, local effects may enhance species richness.

Keywords

Biodiversity, frequency dependence, Janzen–Connell effect, localized dispersal, neutral theory of biodiversity, species richness.

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INTRODUCTION

Understanding the immense local diversity of some plant communities, such as tropical forests, remains one of the most compelling problems in ecology, with a wide range of hypothesized mechanisms (Tilman & Pacala 1993; Givnish 1999; Hubbell 2001; Wright 2002). One of the leading hypotheses is that interactions with natural enemies give an advantage to rare species (Janzen 1970; Connell 1971). In particular, highly specialized herbivores or pathogens create a form of negative density dependence. As a species becomes more common, its specialized natural enemies also become more common, and its offspring are more exposed to attack and suffer higher mortality (Gillett 1962). As this form of density dependence becomes stronger, it should lead to higher species richness (Armstrong 1989; Chesson 2000).

Janzen (1970) and Connell (1971) independently added a spatial aspect to this mechanism by proposing that local dispersal of herbivores or pathogens might further enhance species richness by preventing recruitment near conspecific

adults, thus leaving more room for other species. Many studies have documented such localized effects in tropical forests (Hammond & Brown 1998) and more recently in temperate forests (Packer & Clay 2000). Hubbell *et al.* (2001) found strong reductions in survival of trees and saplings when conspecific density was high within 10 m. Large effects have also been reported in seedlings (Webb & Peart 1999; Packer & Clay 2000; HilleRisLambers *et al.* 2002), and have been shown to increase diversity during the seed to seedling transition (Harms *et al.* 2000). The universality of such effects remains uncertain (Hyatt *et al.* 2003), as does their variation with latitude (HilleRisLambers *et al.* 2002).

If effects are indeed local, do we expect them to increase species richness more than would otherwise similar non-local effects? Suppose that species richness is maintained, at least in part, by the benefits of rarity. Verbally, one can argue that short distance enemy and offspring dispersal might reduce, rather than increase, species richness relative to widely dispersing enemies and offspring. In this case, offspring experience a world where their species is effectively common because they are showered by pests

from their nearby parent. This reduction in the effective rarity of a rare species might reduce the benefits of rarity, leading to lower equilibrium species richness than with larger dispersal distances.

Several mathematical models have examined the complexities of these interacting spatial scales. Hubbell (1980) created a geometric model in which each tree creates a zone of inhibition where no member of its species can grow. Assuming that all sites in discretized space are filled, this places a lower bound on the number of species in a community that increases with the size of the zone. The actual species richness will exceed this lower bound when new species can enter the system and existing species can drift to extinction (Becker *et al.* 1985). Strengthening density dependence, even in the absence of explicitly spatial effects, stabilizes coexistence around an equilibrium (Armstrong 1989).

Localized dispersal alone, in the absence of species-specific consumers, can increase equilibrium biodiversity by increasing intraspecific competition and decreasing inter-specific competition (Ives 1988). This mechanism can maintain inferior competitors with longer dispersal distances (Shmida & Ellner 1984; Holmes & Wilson 1998; Bolker & Pacala 1999). Chave *et al.* (2002) developed a simulation model that showed that both nearest neighbour species-specific density dependence and localized dispersal increase the diversity maintained. However, this model only allows the density-dependent effect to operate on neighbouring cells and made no comparisons of the influence of density dependence at different scales.

In this paper we develop a simulation model and analytical approximations in continuous space that make it possible to vary the scales of both offspring and enemy dispersal (Bolker & Pacala 1999). Our model is symmetric, in that all species have identical parameters, and non-equilibrial, in that new species are constantly added to the system while others go extinct (Hubbell 2001). We test how species richness depends on the distance scales of offspring and enemy dispersal, and explain the results with an analytical approximation based on the function linking offspring survivorship to the population size of a species. Our results show how dispersal distances interact to produce subtle changes in the shape of this function, and major effects on species richness.

We show that localized dispersal can more than double standing species richness, but only when both offspring and natural enemies disperse distances less than the average distance between adults, creating highly clumped spatial distributions. When offspring disperse long distances and natural enemies disperse short distances, species richness is substantially decreased compared with cases with long-distance dispersal, although the dynamics in this case generate evenly spaced adults.

THE SIMULATION

Our model follows a fixed number N of adults placed in a continuous two-dimensional space of dimension L by L (we use a torus to avoid edge effects). The number of adults of species j is N_j , and the position of individual k of species j is given by the vector x_{jk} (for $1 \leq k \leq N_j$). The simulation tracks a series of offspring or immigrant establishment attempts. To maintain constant population size, an adult is chosen to die each time an offspring is successful.

Offspring arise either from outside or within the population. They arrive from outside with probability μ . In this case, the location of the offspring is chosen randomly and uniformly, and the species identity of the offspring is chosen with equal probability from a pool of K species. With probability $1 - \mu$, an existing adult is chosen at random to produce a single offspring. The offspring disperses a distance r chosen from the probability density function $k(r)$, in a direction chosen from a uniform distribution.

The probability that an offspring survives depends on the local density of enemies, which in turn depends on the local density of conspecific adults. The number of enemies of species j at site x , $H_j(x)$, is

$$H_j(x) = \sum_{k=1}^{N_j} b[d(x_{jk}, x)] \tag{1}$$

where $d(x_{jk}, x)$ is the distance from the k th adult of species j (at position x_{jk}) to the focal offspring at x and $b(r)$ is the density of enemies at distance r . The function b is normalized to integrate to 1. The probability an offspring of species j survives at location x is

$$\text{Probability of survival} = p[H_j(x)] \tag{2}$$

for some decreasing function p . A surviving offspring immediately becomes an adult.

In most of the results reported here, there are no impacts of the local density of adults of all species combined on either offspring or adult success. Offspring mortality depends only on conspecific density and adult mortality occurs randomly at a constant rate. In some cases, we modify these assumptions and incorporate a negative effect of interspecific crowding on adult survival. Specifically, we compute a crowding index G_{jk} for the adult at position x_{jk} as

$$G_{jk} = \sum_{(m,l) \neq (j,k)} g[d(x_{ml}, x_{jk})] \tag{3}$$

where $d(x_{ml}, x_{jk})$ is the distance from the adult at position x_{ml} to the focal adult at x_{jk} , and g is a decreasing function describing the effect. Death occurs at rate $m(G_{jk})$ for some increasing function m . For each adult, we choose a value

from an exponential distribution with mean equal to the reciprocal of this death rate, and then pick the adult with smallest value as the one to die.

Functional forms

In most simulations we use exponential functional forms for dispersal and a hyperbolically decreasing function for the probability of survival, parameterized as

$$k(r) = \frac{1}{\sigma} e^{-r/\sigma} \quad (4)$$

$$b(r) = \frac{1}{2\pi\alpha^2} e^{-r/\alpha} \quad (5)$$

$$p(H) = \frac{1}{1 + (\beta/N)H} \quad (6)$$

where the mean offspring dispersal distance is σ and mean enemy dispersal distance is α .

Other mechanisms, such as shading in trees, can make establishment directly beneath adults impossible. Other simulation methods, such as those in discrete space, also rule out extremely short dispersal distances. To test how sensitive results are to the inclusion of extremely short

dispersal distances, we modify the dispersal distance function $k(r)$ to include a threshold distance R below which no dispersers survive. Formally,

$$k(r) = \begin{cases} 0 & \text{if } r \leq R \\ \frac{1}{\sigma} e^{-(r-R)/\sigma} & \text{if } r > R \end{cases} \quad (7)$$

For those simulations including interspecific density-dependent mortality, we use an exponential function for the decay of competitive strength with distance, and a linear function for the increase in mortality with total competition, or

$$g(r) = \frac{1}{2\pi\gamma^2} e^{-r/\gamma} \quad (8)$$

$$m(G) = 1 + vG. \quad (9)$$

The parameter values and functional forms for the simulations are given in Table 1.

We test for spatial clumping by simulating a variant of Ripley's K (Ripley 1981). We first compute the number of individuals of the same species within a given distance. We then compare this with 1000 simulations with randomized species identities.

SIMULATION RESULTS

We simulate 100 adults in a 1 ha area to roughly match the density of trees in a typical tropical forest, and use $K = 1000$ species in the species pool. We examine a realistic range of mean offspring dispersal distances σ (Clark *et al.* 1999; Muller-Landau *et al.* 2002) and mean enemy dispersal distances α (Wright 1983; Fitt *et al.* 1987; Hubbell *et al.* 2001; Muller-Landau *et al.* 2004) of 1–50 m. For the small region we are simulating, a distance of 50 m is equivalent to a dispersal distance of infinity, with offspring and adult positions effectively uncorrelated. Results are based on at least four simulations of 4000 steps (deaths), sampled at 2000, 3000 and 4000 steps.

Increasing the strength of intraspecific density dependence as a result of natural enemies (increasing the parameter β) leads to greatly increased species richness. In the absence of intraspecific density dependence ($\beta = 0$), this small community maintains only about six species (Table 2). The species richness is generally doubled with stronger intraspecific density dependence ($\beta = 10$).

With a fixed strength of intraspecific density dependence (β), a combination of short-distance offspring dispersal and short-distance enemy dispersal leads to higher species richness than with long-distance dispersal of offspring or enemies, as predicted by Janzen (1970) and Connell (1971). However, long-distance offspring dispersal and short-distance enemy dispersal leads instead to significantly lower

Table 1 Variables, parameters, and functions in the simulation

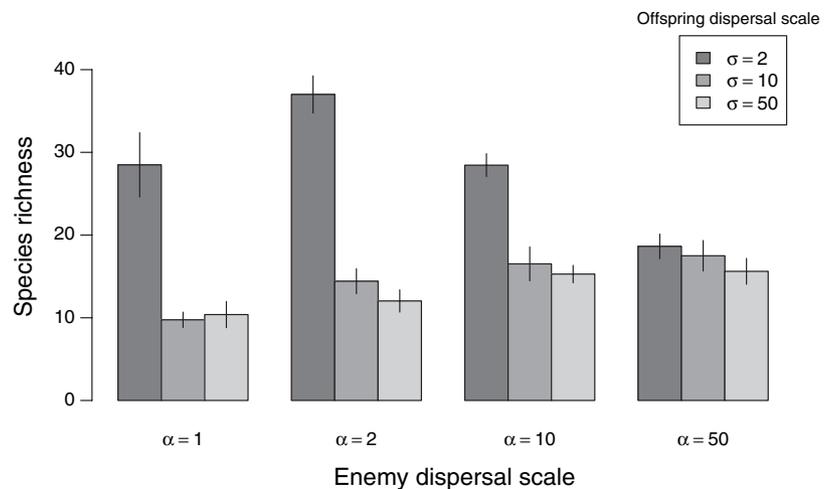
Parameters	Values
L , Length and width of simulated landscape	100 m
N , Total population size	100
K , Number of species in the species pool	1000
μ , Probability a new individual immigrated	0.01
β , Parameter describing frequency dependence	0, 5 or 10
α , Mean enemy dispersal distance	1–50 m
σ , Mean offspring dispersal distance	1–50 m
R , Threshold distance for offspring survival	2–10 m
γ , Scale of interspecific density dependence	2–50 m
v , Increase in adult mortality because of crowding	0.1
Functions	Forms
$k(r)$, Probability density function for offspring dispersal	Exponential, Gaussian, Cauchy
$b(r)$, Probability density function for enemy dispersal	Exponential, Gaussian, Step
$p(H)$, Offspring survivorship as a function of enemy number	Reciprocal of linear
$g(r)$, Effect of adult on another adult at distance r	Exponential
$m(G)$, Adult mortality as a function of adult effects	Linear

Table 2 Simulated species richness with a variety of parameter values*

α	σ	Effects of β			Effects of γ			Effects of R		
		$\beta = 0$	$\beta = 5$	$\beta = 10$	$\gamma = 2$	$\gamma = 10$	$\gamma = 50$	$R = 2$	$R = 5$	$R = 10$
2	2	6.0	31.5	36.0	42.7	38.4	37.6	21.7	16.8	15.2
2	10	6.4	13.6	15.8	14.4	15.0	14.0	18.0	17.0	16.7
2	50	6.1	10.9	11.0	10.3	11.9	11.5	16.1	17.1	15.1
10	2	5.7	22.7	28.1	36.0	29.3	28.1	25.1	17.3	19.2
10	10	7.3	14.2	16.9	19.1	17.3	18.7	17.7	15.7	16.2
10	50	6.6	12.6	15.7	14.2	15.3	14.9	17.7	16.7	16.9
50	2	6.6	15.6	18.1	30.2	21.0	19.4	16.1	17.7	14.8
50	10	6.3	13.7	17.9	17.8	18.2	16.9	17.7	16.2	18.3
50	50	5.9	13.0	15.3	16.6	15.6	15.1	16.3	14.3	15.1

*Except as noted, all results use $\beta = 10$, $\gamma = 0$, and $R = 0$. Standard errors are all less than 1.0.

Figure 1 Species richness as a function of mean enemy dispersal distance α for a range of mean offspring dispersal distances σ , with error bars showing ± 1 SE. Parameters as in Table 1 with $\beta = 10$, no interspecific density dependence ($\gamma = 0$) and exponential forms for $k(r)$ and $b(r)$.



species richness (Fig. 1). Results with different offspring and enemy dispersal distance functions are qualitatively similar, but the peak species richness occurs in some cases for a larger enemy dispersal distance (F. R. Adler & H. C. Muller-Landau, unpublished data).

Interspecific density-dependent mortality (non-zero values of γ and ν) increases species richness when it operates at a scale of a few metres, and then only when mean offspring dispersal distances are very short (Table 2). Otherwise, it has no effect.

Earlier authors have hypothesized that higher diversity is associated with a more regular distribution of individuals within a species (Janzen 1970). We thus examined the spatial patterns of individual species after the number of species had reached equilibrium.

The combination of short-distance offspring and enemy dispersal that produces the highest species richness generates highly clumped distributions of adults of a given species (Fig. 2a; $P < 0.001$), as do all cases with short-

distance offspring dispersal (results not shown). In contrast, the scenario with long-distance dispersal by offspring and short-distance dispersal by enemies that produces the lowest species richness generates relatively regular distributions of the individuals within a species (Fig. 2b). Statistically, the spatial pattern is regular for distances less than 3 m ($P < 0.05$). With long-distance dispersal, the spatial patterns are indistinguishable from the null model.

To test whether high diversity and clumping disappear when extremely short-range offspring dispersal is eliminated, we modified the dispersal distance function $k(r)$ to include a threshold distance required for successful dispersal (eqn 7). Even a relatively small threshold ($R = 2$ m or about 20% of the mean distance between adults) largely removes the increased species richness when dispersal distances of both offspring and enemies are short (Table 2), and simultaneously nearly eliminates the intraspecific clumping.

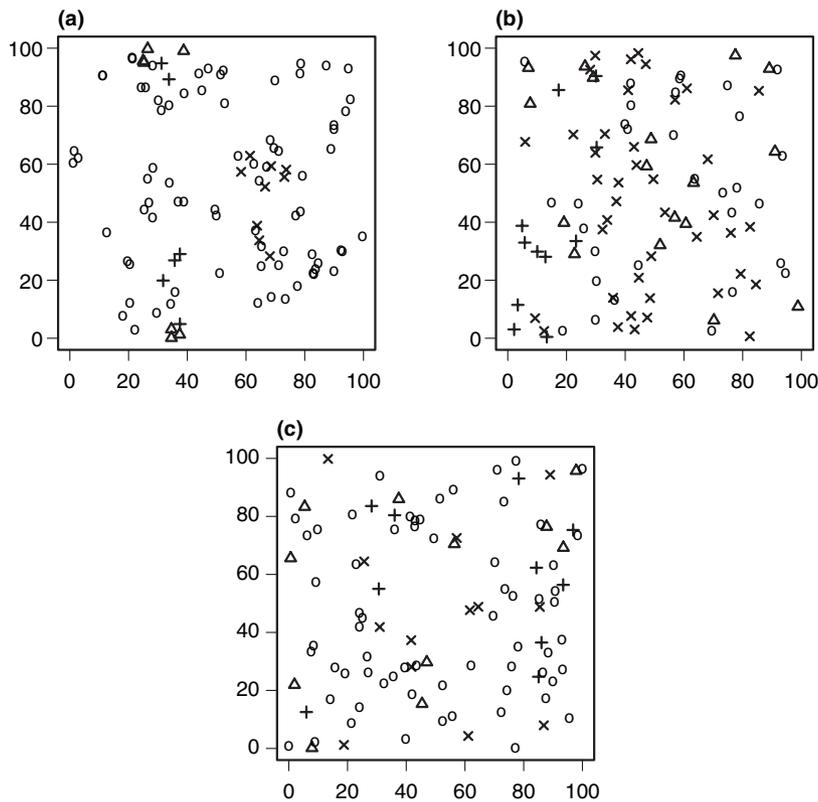


Figure 2 Spatial distribution of individuals (at the end of a 4000 step simulation) with parameters that produce three different species richness levels. The three most abundant species in each case are shown with cross, triangle and plus signs, and all others are shown with open circles. Parameters as in Fig. 1 with (a) $\alpha = \sigma = 2m$ (35 total species), (b) $\alpha = 1m$, $\sigma = 10m$ (nine total species), and (c) $\alpha = \sigma = 50m$ (18 total species).

APPROXIMATING THE SIMULATION

We developed a mathematical approximation to gain insight into the factors leading to different levels of diversity in the simulations.

The frequency-dependent Moran model

The number of members of any given species follows a random walk on the integers from 0 to N . As in the Moran model of population genetics, maintenance of species is a battle between losses because of drift and gains because of migration or mutation (Ewens 1980; Hubbell 2001).

If q_i is the stationary probability that a species has i members, then q_0 is the probability that a given species is not present. The probability that any given species is present is then $1 - q_0$. As the species are identical, the expected number S of species maintained from a pool of K species is

$$S = K(1 - q_0) \tag{10}$$

(Yokoyama & Nei 1979; Takahata & Nei 1990). To find the probabilities q_i , we quantify the probability of gaining or losing a member.

In the absence of interspecific density dependence, the probability that a focal species gains a member when it has i individuals is

$$u_{i+1} = (1 - \mu) \frac{i}{N} \left(1 - \frac{i}{N}\right) p_i + \frac{\mu}{K} \left(1 - \frac{i}{N}\right) \hat{p}_i. \tag{11}$$

As in the simulation, μ is the migration probability, N is the total population size, and K is the size of the species pool. The crucial values are p_i , the average probability of survival of an offspring that originates in a population with i members of its species, and \hat{p}_i , the average probability of survival of an offspring that originates through migration into a population with i members of its species. The first term is the product of the probability $1 - \mu$ that the offspring originated within the patch, the probability i/N that it is of the focal species, the probability $1 - (i/N)$ that the individual chosen to die is of another species, and the probability of survival p_i . The second term is the product of the probability μ/K that a migrant arrives of the focal species, the probability $1 - (i/N)$ that the individual chosen to die is of another species, and the probability of survival \hat{p}_i . For simplicity, we assume that all species are equally likely to arrive.

The probability of losing a member when there are i individuals of the focal species is

$$d_i = (1 - \mu) \frac{i}{N} \left(1 - \frac{i}{N}\right) M_i + \mu \left(1 - \frac{1}{K}\right) \frac{i}{N} \hat{M}_i. \tag{12}$$

Here, the first term is similar to that in eqn 11, except that M_i is the probability of survival of an offspring of another species that originates in a population when the focal species has i members. In the second term, $1 - (1/K)$ is the probability that a migrant is not of the focal species, and \hat{M}_i is the probability such a migrant offspring survives if the focal species has i members.

Solving this model for the equilibrium distribution q_i requires forms for the survivorship probabilities p_i , M_i , \hat{p}_i and \hat{M}_i . To simplify the problem, we make the following approximations, which generalize an approach to computing diversity of the immune system developed by Yokoyama & Nei (1979) and Takahata & Nei (1990).

- (1) K is sufficiently large that all immigrants are new species (as in the infinite-alleles model of population genetics). If we assume that any offspring of a new species survives, this implies that $\hat{p}_i = 1$ for all i .
- (2) No species becomes abundant, so that $1 - (i/N) \approx 1$.
- (3) As no species is common, $M_i \approx M$ for some constant M .
- (4) As all immigrants are of new species, $\hat{M}_i = 1$.

With these approximations, we arrive at the simplified equations

$$u_{i+1} = (1 - \mu) \frac{i}{N} p_i \quad \text{for } i \geq 1 \tag{13}$$

$$u_1 = \frac{\mu}{K} \tag{14}$$

$$d_i = (1 - \mu) \frac{i}{N} M + \mu \frac{i}{N}. \tag{15}$$

If the values of p_i and M were known, these equations can be solved recursively to find the equilibrium. In particular,

$$u_{i+1} q_i = d_{i+1} q_{i+1} \tag{16}$$

by equating the probabilities of entering and leaving each state.

The solution must satisfy three conditions:

- (1) $\sum_{i=0}^N q_i = 1$ because these are defined as probabilities
- (2) The average number in each species $\sum_{i=0}^N i q_i$ must equal N/K .
- (3) The average survival probability for an offspring that originates in the population is

$$M = \frac{\sum_{i=0}^N i q_i p_i}{\sum_{i=0}^N i q_i}. \tag{17}$$

If the values of p_i are known, we choose a value for M , solve this system numerically for q_i , compute the resulting

value of M from eqn 17, and iterate the process until the values of M and q_i converge (Yokoyama & Nei 1979; Takahata & Nei 1990). When $p_i = 1$ for all i , this model corresponds to the standard neutral theory, and predicts the same level of species richness (Hubbell 2001).

Comparison with simulations

The survival probabilities (the values of p_i) measured from simulations can be used to compute M , the q_i and $S = K(1 - q_0)$ to test for consistency with the simulations. Using a wide range of parameter values, the approximation captures much of the variation, including the lower species richness when the mean enemy dispersal distance is small and the mean offspring dispersal distance is large (Fig. 3).

The species richness predicted by this model can be expressed compactly with generating functions (F. R. Adler, unpublished data). Here we present results from solving for the species richness using two simple functional forms for the p_i . Figure 4(a) shows the simulated probabilities p_i for the three cases illustrated in Fig. 2. Minimum species richness occurs when the mean enemy dispersal distance is small but the mean offspring dispersal distance is large. This produces a probability of survival that is roughly constant for all $i > 0$. When the mean dispersal distances of both enemies and offspring are large, species richness is moderately low. In this case, the probability of survival follows the survivorship function $p(H)$ itself (Table 1) because there are no local effects. Maximum species richness occurs when the mean dispersal distances of both enemies and offspring are small. This generates a probability

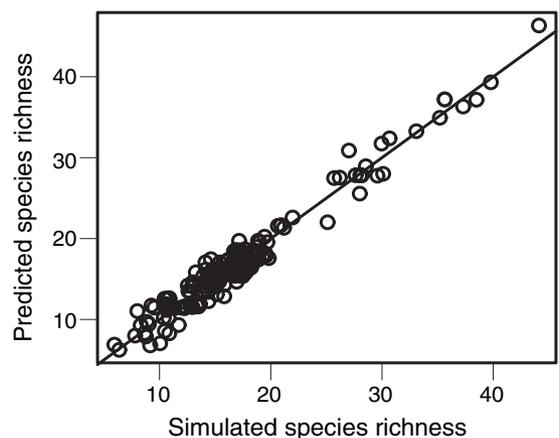


Figure 3 Comparison of simulated species richness with that predicted from using survival probabilities measured in the simulations. The diagonal represents equality, and each dot represents a different simulation, covering the range of parameter values and functional forms in Table 1.

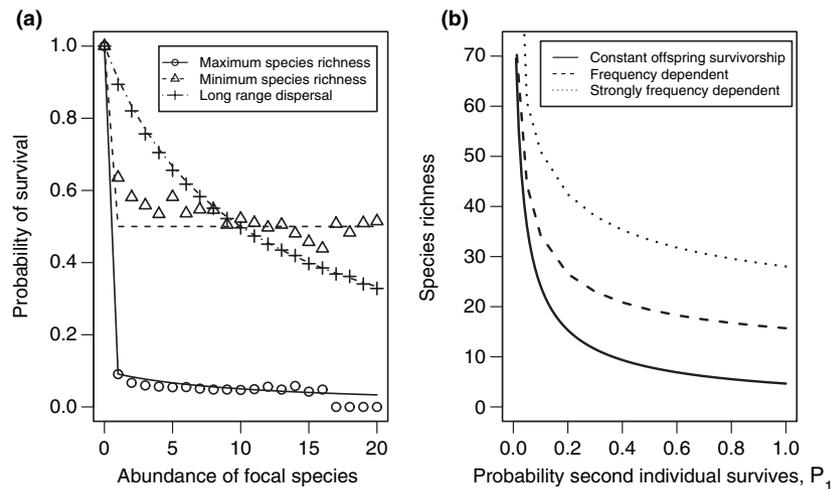


Figure 4 (a) The probability of survival as a function of population size for the three sets of parameter values used in Fig. 2. Probabilities are averaged over the last 3000 steps of one 4000-step simulation in the maximum diversity and long-distance dispersal cases, and over the last 3000 steps of three 4000-step simulations in the minimum diversity case (to reduce sampling error). They are fit, by eye, with simple functions. In the minimum species richness case, we approximate the probabilities with $p_i = 0.5$ for $i > 0$. In the long-distance dispersal case, we use $p_i = 1/(1 + 0.1i)$ [substituting $\beta = 10$ and $N = 100$ into $p(H)$]. In the maximum species richness case, we use $p_i = 0.1/(1 + 0.1i)$ for $i > 0$. (b) Predicted species richness as a function of the probability p_1 a second individual survives for two different forms for the survival probability curve. In the constant case, p_i is constant for $i > 0$ (solid line). Higher species richness occurs in the frequency-dependent case ($\beta = 10$, dashed line) and the strongly frequency-dependent case ($\beta = 100$, dotted line).

of survival that decreases quickly with small population size and continues to decrease slowly thereafter, and can be fit by a multiple of the survivorship function.

We can use these functional forms to examine the effects of different parameter values. The case with constant p_i for $i > 0$ is described by the single parameter p_1 . The case paralleling the survivorship function $p(D)$ can be modelled with the function

$$p_i = \frac{p_1}{1 + (\beta/N)i} \quad (18)$$

for $i \geq 1$. The parameter β describes the effective strength of frequency dependence and p_1 is a fitted parameter, which can be thought of as the probability that the second individual of a species survives. Both lower values of p_1 and higher values of β lead to higher species richness in a more or less additive way (Fig. 4b). The high species richness seen when both offspring and enemies move short distances results from the combined effects of a low p_1 (the offspring of the first adult in the plot are unlikely to survive) and a high β (subsequent offspring are even less likely to survive).

DISCUSSION

Our results show that the mean dispersal distances of offspring and specialized natural enemies have strong and

interacting effects on species richness in model communities. When natural enemies disperse short distances while offspring move longer distances, species richness is substantially lower than with long-distance dispersal of both offspring and enemies (Fig. 1). In this case, the adults of a given species are regularly spaced (Fig. 2b). In contrast, when both offspring and natural enemies have highly localized dispersal, with mean distances less than or equal to the average distance between adults, species richness is greatly increased. In this case, the adults of each species are clumped (Fig. 2a). When enemies move long distances, the dispersal distance of offspring has no effect on species richness.

The differences in species richness result from differences in the shape of the function linking species abundance to offspring survival. When offspring survival decreases rapidly and steadily with increasing conspecific adult abundance, species richness is high; when this function is relatively flat, species richness is low (Fig. 4). When both offspring and enemies disperse long distances, this function declines slowly and steadily because the expected number of enemies encountered by any given individual increases steadily with conspecific adult abundance. When both offspring and enemies disperse very short distances, this function declines rapidly and steadily because extreme clumping of conspecific adults and concentration of their offspring and enemies in these clumps elevates the probability that offspring encounter enemies. When offspring disperse relatively long

distances and enemies short distances, this function levels off because offspring are influenced primarily by enemies from their own parent.

Whether shorter offspring and enemy dispersal increases or decreases species richness in a particular community depends on the scales of dispersal and successful recruitment relative to the externally set density of adults in the community. The enhancement in species richness seen here in simulations with very short offspring and enemy dispersal is possible only because most offspring and enemies disperse distances shorter than interadult distances expected under a uniform distribution, and because offspring are not inhibited from establishing at such short distances. If offspring dispersal is disallowed at distances less than half the mean interadult distance, or if establishment at similarly short distances from adults of any species is inhibited because of crowding effects, then the species richness enhancement because of short dispersal distances by both offspring and enemies disappears (Table 2 with $R = 5$).

In our simulations, interspecific density-dependent mortality at small scales can interact with localized offspring dispersal to increase species richness even in the absence of specialized natural enemies (F. R. Adler and H. C. Muller-Landau, unpublished data), as has been seen in other studies (Bolker & Pacala 1999; Chave *et al.* 2002). However, the reduced species richness created by natural enemies with short distance dispersal interacting with longer distance dispersal by offspring appears to be a novel result.

In tropical forests, we expect that shorter dispersal distances will decrease the strength of negative density dependence and thereby species richness; in other plant communities, short dispersal may instead increase species richness. In tropical forests, adult trees inhibit the growth of nearby saplings into adults by casting shade and depleting soil resources. As a result, the spatial distribution of adult trees of all species combined is more regular than a random distribution, in contrast to the distributions observed in our short dispersal simulations. Under these conditions of regular adult distributions and the inhibition of recruitment near adults, short dispersal distances weaken rather than enhance the species richness promoted by specialized natural enemies. In other plant communities in which the distribution of all adults combined are clumped and establishment near adults is not inhibited, short dispersal distances may result in increased species richness. These conditions may be met in desert plant communities.

Our models are highly abstracted, and leave out many biologically relevant factors. They explicitly treat only the effects of adults, not the effects of other offspring on natural enemy densities and thereby survival. Given that the offspring distribution is determined largely by the adult distribution in our model, this might not seem to matter. However, in reality, seed deposition patterns are not

determined entirely by adult distributions: there may be disproportionate or directed dispersal to particular habitat types, and seeds may be locally clumped even after accounting for differences in distances from adults and habitat because of the behaviour of seed dispersers (Howe & Smallwood 1982; Schupp 1993; Fragoso *et al.* 2003; Muller-Landau and Hardesty, in press). One study suggests that adult distributions play a more important role in seedling survival than do local seedling densities (Barot *et al.* 1999). Another, however, finds that local conspecific seed density explains more of the variation in seed-to-seedling survival probability than does the local distribution of adults and saplings (Muller-Landau *et al.* 2004). More work is required to determine how the distributions of seeds, seedlings, saplings and adults influence natural enemy distributions and thus offspring survival.

We have also collapsed the time scales of growth and natural enemy establishment, assuming that offspring become adults immediately and that all adults support enemies, ignoring the fact that enemies need to find adults. If this latter factor was included, the proportion of adults with enemies could well be an increasing function of adult density. The shape of this function will depend on adult spatial pattern and enemy dispersal distances. For example, if natural enemies move short distances and offspring disperse long distances, then there may be a relatively abrupt increase in the proportion of adults infested at a percolation threshold at which the adults are sufficiently connected to allow the enemies to move through the population. In contrast, if offspring move short distances so that adults are clumped, then enemies may be able to reach most adults even at relatively low adult densities.

The behaviour of our enemies is a simplified cartoon, assuming complete specificity and a lack of behavioural response to different local host densities. Vertebrate herbivores have been shown to eat seeds down to a more or less uniform density (Bustamante & Simonetti 2000), perhaps some sort of giving-up density (Brown 1988). For seed predators with territories and slow numerical response, higher seed density can lead to lower seed predation through a sort of herd immunity (Schupp 1992; Wills *et al.* 1997).

Our models maintain adult numbers at a constant level in the landscape as a whole, while leaving local densities unconstrained. In simulations where numbers were not kept constant, the low survivorship resulting from highly localized offspring and enemy dispersal resulted in a lower number of adults and lower species richness (F. R. Adler and H. C. Muller-Landau, unpublished data). Differences in density have been proposed to explain some of the diversity differences in tropical forests (Pitman *et al.* 2002).

Our models neglect differences between species. First, within a given community, species differ in the strength of localized effects. In some studies, rare species show the

largest density-dependent effects (Hubbell *et al.* 2001), while in others only the dominant species show an effect (Condit *et al.* 1992; Penfold & Lamb 1999). Klironomos (2002) suggests that stronger effects in rare species are precisely what keeps these species rare.

Second, species could differ in other life-history parameters, such as birth and death rates. While small differences in these parameters can significantly change the number of species coexisting in neutral models (Yu *et al.* 1998), models including intraspecific density dependence may be more robust. Furthermore, tradeoffs, such as those between competition and colonization, can enhance diversity, and might interact in unexpected ways with localized enemies (Pacala & Tilman 1994; Bolker & Pacala 1999; Chave *et al.* 2002).

Diversity promotion depends on more aspects of natural enemies than their dispersal distances, including degree of specificity, reproduction rate, and ability to survive dispersal and locate new hosts. Our goal has been to demonstrate that local species-specific density dependence alone has the potential to increase or to decrease species richness, depending on the spatial scales of offspring and enemy dispersal. The next challenge is to assess the influence of these mechanisms in real communities by parameterizing models through detailed measurements of dispersal distances and other characteristics of natural enemies, and making detailed comparisons with abundance and spatial data. Such tests would show whether the large differences in predicted species richness might be relevant in real communities.

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