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How Seed Dispersal Affects Interactions with Specialized Natural Enemies and their Contribution to the Maintenance of Diversity

H.C. MULLER-LANDAU AND F.R. ADLER

Introduction

Seed dispersal patterns affect the rate at which offspring encounter specialized natural enemies, and thereby the strength of the associated interspecific interaction (Howe and Smallwood, 1982). Relatively specialized natural enemies such as pathogens and insect herbivores are expected to be found in higher densities near plants of their host species (Janzen, 1970). Because dispersing offspring are less likely to land near a conspecific than those remaining near their maternal parent, they are presumed to be less likely to encounter specialized enemies, and thus to have a higher than average survival and growth (Ridley, 1930; Janzen, 1970; Howe and Smallwood, 1982). In line with these predictions, empirical studies have generally found that seed predation by insects declines with increasing distance from conspecific adults, while overall survival increases (Hammond and Brown, 1998; Hubbell *et al.*, 2001). Thus, both offspring and parent gain a fitness advantage from dispersal; an advantage that may be an important factor in the evolution of dispersal (Muller-Landau *et al.*, 2003).

Interactions with specialized natural enemies can contribute powerfully to the maintenance of plant species diversity (Janzen, 1970; Connell, 1971; Armstrong, 1989; Pacala and Crawley, 1992). This contribution depends fundamentally on the population-level density dependence induced by natural enemies: as a species becomes more common, its natural enemies become more common and reduce its reproductive rate; as a species becomes rarer, its natural enemies become rarer and its reproductive rate increases (Ridley, 1930; Gillett, 1962). Such population-level density dependence is the signature of a stabilizing contribution to the maintenance of diversity, *sensu* Chesson (2000). While the tropical forest literature on natural enemy effects has focused mainly on the spatial context of local seed dispersal and local enemy attack since Janzen's seminal paper (but see Schupp, 1992), theoretical

studies have demonstrated that specialized natural enemies can contribute to density dependence in populations and the maintenance of diversity in communities, even in completely non-spatial models (Armstrong, 1989; Pacala and Crawley, 1992).

Given the importance of seed dispersal in determining the strength of interactions with specialized natural enemies, and the importance of interactions with specialized natural enemies for the maintenance of diversity, it seems obvious that seed dispersal will be important in determining the contribution of specialized enemies to the maintenance of diversity. However, the form, and even the direction, of the relationship are far from obvious (Adler and Muller-Landau, 2005). On the one hand, because shorter seed dispersal distances lead to higher damage from natural enemies, we might hypothesize that natural enemy interactions will contribute most to the maintenance of diversity when seed dispersal distances are short. On the other hand, longer seed dispersal distances should lead to larger differences in the chance of encountering natural enemies between low and high population densities; thus, we might hypothesize that population-level density dependence and contributions to the maintenance of diversity will be strongest when seed dispersal distances are long. The influences of seed dispersal patterns will, of course, also depend on natural enemy dispersal patterns, which determine how enemy encounter rates change with seed dispersal distances.

Janzen (1970) predicted that longer seed dispersal distances will promote higher seedling survival and higher species diversity. The reasoning is that, as seed dispersal distances increase, the mode of the population recruitment curve shifts farther away from the parents, even as the total area under the curve increases (Fig. 18.1). Janzen further hypothesized that longer parent-offspring distances will allow more species to coexist (Janzen, 1970). Thus, higher seed dispersal distances should lead to higher diversity, facilitated by natural enemy interactions. Nathan and Casagrandi (2004) showed, in their simple spatial model, that the peak of the seedling recruitment curve does indeed move away from the adult as seed dispersal increases. But the strong link drawn by Janzen (1970) and later Hubbell (1980) between spacing dynamics and the maintenance of diversity has been shown to be faulty. Becker *et al.* (1985) showed that distance- or density-dependent predation can maintain diversity even when it does not result in a shift of the peak of seedling recruitment curve away from adults. The question remains whether such a shift in seedling recruitment due to increased seed dispersal would facilitate stronger contributions of natural enemy interactions to the maintenance of diversity.

The need for a better understanding of the consequences of seed dispersal has particular urgency today because anthropogenic influences are changing seed dispersal patterns in many populations. Abundances of vertebrate frugivores and seed dispersers in many tropical forests have been reduced by hunting and habitat fragmentation, potentially reducing seed dispersal of associated plant species (Emmons, 1989; Redford, 1992; Bond,

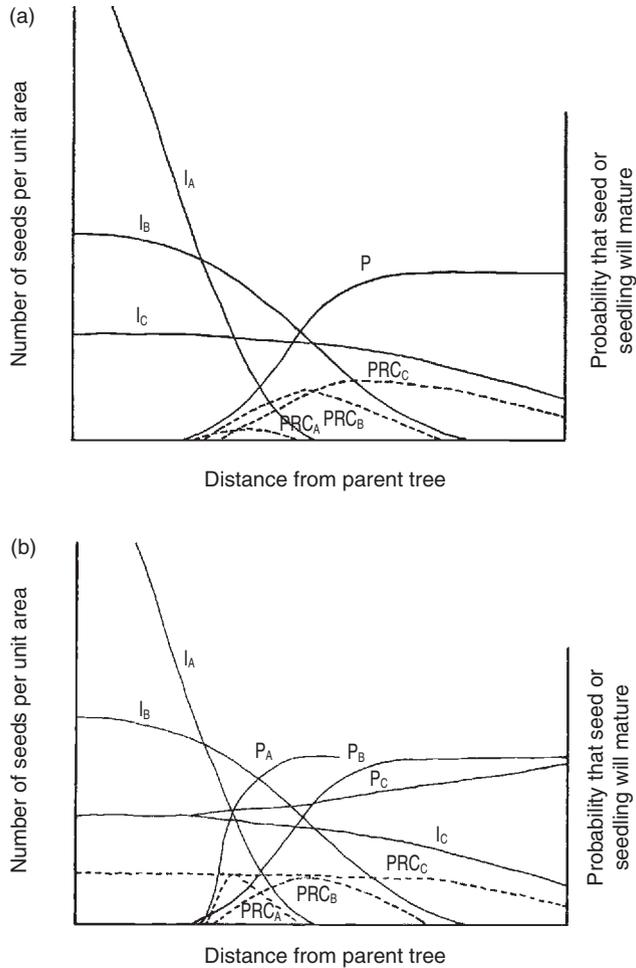


Fig. 18.1. Janzen's (1970) conception of the influences of different seed dispersal functions (I_A, I_B, I_C) on seedling recruitment curves (PRC_A, PRC_B, PRC_C) for (a) distance-responsive seed or seedling predation (P) and (b) density-responsive seed or seedling predation (P_A, P_B, P_C). Modified from Figs 4 and 5 of Janzen (1970).

1994; Wright, 2003). Anthropogenic influences may also increase dispersal of some species of plant through habitat modification, intentional and unintentional transport of propagules, as well as increases in wind velocity associated with global climate change (Soons *et al.*, 2004). Decreased (or increased) seed dispersal rates and distances potentially expose larger (or smaller) numbers of seeds and seedlings to natural enemies concentrated near parent trees, and thereby might alter the strength and influences of natural enemy interactions (Wright and Duber, 2001; Muller-Landau, 2007). Largely for this reason, many authors have warned that the potential

consequences of defaunation for tropical plant species diversity could be dire (Emmons, 1989; Redford, 1992; Bond, 1994). However, the theoretical framework for understanding the impacts expected via changes in natural enemy interactions and other aspects of population and community dynamics remains severely underdeveloped (Muller-Landau, 2007).

Our objective here is to investigate how seed dispersal distances interact with natural enemy dispersal distances to affect the strength of natural enemy interactions and the influences of these interactions on plant populations and communities. We use a simulation model that captures key features of tropical tree populations and communities, including implicit local spatial competition for resources among adults, concentration of natural enemies around adults, and enemy attack functions appropriate for pathogens and insects. We specifically examine the impacts on the proportion of offspring killed by natural enemies, the form of population-level density dependence induced by enemies, and the species diversity maintained by natural enemy interactions alone. Finally, we discuss the implications of our results for understanding the consequences of anthropogenic changes in seed dispersal distances.

Methods

Model landscape

The simulation model is discrete-space, spatially explicit and individual-based. The model landscape is a rectangular grid of cells, each of which can contain exactly one adult tree (of one species) as well as many seeds, natural enemies, and juvenile plants potentially of multiple species. Individual plants are tracked through three age or size classes: seeds, juveniles, and adults. Individual spores, eggs or offspring of natural enemies, henceforth referred to simply as 'spores', are also tracked in all simulations. To eliminate edge effects, seeds or spores that go off one side of the landscape wrap back around on the other side (i.e. the model landscape is a torus, having periodic boundary conditions).

Simulations were conducted on a landscape of 900 (30×30) adult tree grid cells. To put this in familiar units, we say that each cell (and thus each canopy tree crown) has dimensions of $10 \text{ m} \times 10 \text{ m}$. Thus, the total simulated landscape area is 9 ha.

Model processes

Simulations are in discrete time, and model processes unfold in a set order within each time-step (Fig. 18.2). Seeds first disperse around parent trees, according to specified seed production and seed dispersal functions (Fig. 18.2a). Next, spores disperse from their sources, which are here taken to be all adult trees of the host species (Fig. 18.2b). This scenario is meant to reflect

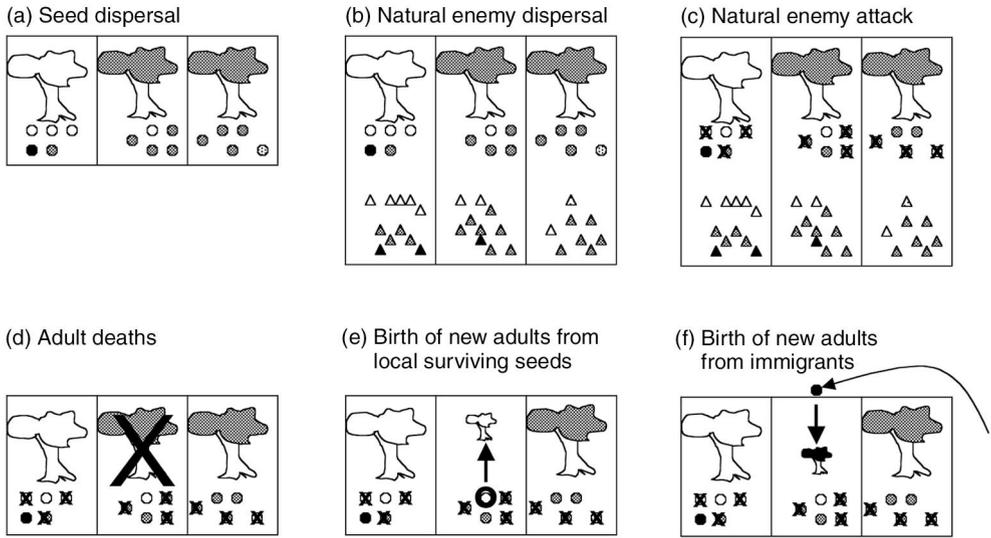


Fig. 18.2. The sequence of events that occurs during each time-step in the simulation model, in which different species are represented by different colours/stippling. (a) Seeds (circles) are dispersed away from adults according to a seed dispersal function. (b) Spores of natural enemies (triangles) are dispersed away from adult hosts according to a spore dispersal function. (c) Natural enemies attack seeds within their local neighbourhood, with the probability of a seed surviving dependent on the local density of host-specific natural enemies according to an infectivity function. (d) A fixed number of adults are randomly chosen to die. (e) A new adult is randomly chosen to replace each dead adult from among the local surviving seeds, or (f) with a small probability from an immigrant seed.

soil-borne pathogens that are often lethal to seedlings and are abundant on the roots of conspecific adult trees, where they have no apparent ill effects. Seeds then either survive to become juveniles or succumb to natural enemies, depending on the density of spores of their specialized natural enemy within the same grid cell (Fig. 18.2c). Next, a set proportion of adult trees is killed at random (Fig. 18.2d). Finally, for each adult killed, a replacement is chosen from among the surviving juveniles in that grid cell or else, with very low probability, the replacement is chosen at random (uniformly) from the species pool, effectively mimicking immigration or speciation (Fig. 18.2e). There is no dormancy or persistence of seeds, spores or juveniles from one time-step to the next: only adults survive between time-steps. The adult mortality rate was set at 10% per time-step, making each time-step equivalent to 5–10 years in a typical tropical forest with an annual canopy tree mortality rate of 1–2%.

The functional forms that specify seed dispersal, spore dispersal, and the probability of seeds surviving to become juveniles match some commonly measured in the field. Seed and spore dispersal distances both follow two-dimensional Gaussian distributions (Clark *et al.*, 1998). Dispersal in all directions is equally likely. Thus, the total probability of a seed or spore

going distance r (integrating over the entire circle at this distance) is given by the probability density function

$$p(x) = \frac{2r}{\sigma^2} \exp\left(\frac{-r^2}{\sigma^2}\right) \quad (18.1)$$

where σ is the dispersal distance parameter, henceforth referred to as the dispersal scale, and mean dispersal distance is equal to approximately 0.886σ (Clark *et al.*, 1998). The number of seeds of a given species in a grid cell is drawn from a Poisson distribution with expectation equal to the sum of expected contributions from all adult trees of that species in the model landscape (with the expected contribution for any given tree to that cell calculated by integrating over 100 evenly spaced points within the cell). Similarly, the number of spores of a given species in a grid cell is drawn from a Poisson distribution with expectation equal to the sum of expected contributions from all spore sources (adults of its host species) in the landscape. Following a functional form commonly employed in epidemiological studies (e.g. Baker, 1978), the probability that a seed will become a juvenile is a negative exponential function of the local density (density within its grid cell) of spores of its natural enemies (P):

$$\Pr(\text{survival}) = \exp(-\beta P) \quad (18.2)$$

We refer to β as the infectivity. For each grid cell, the number of seeds of a species that survive to become juveniles is drawn from a binomial distribution with the given survival probability.

Simulations

At the start of each simulation, the species identity of each adult tree was assigned at random from among an initial 100 species, out of a total species pool of 200 species. Once in every 9000 births, an immigrant was chosen at random from this larger species pool (here a birth is defined as a new adult chosen to replace a dead adult). Within any simulation, all species were equivalent in every way (mortality rate, seed production, seed dispersal scale), except that their survival from seed to seedling depended on the density of a different specialized natural enemy. Similarly, all strains of natural enemy were likewise equivalent within any simulation. Across all simulations, seed production was fixed at 10,000 seeds per adult tree per time-step, spore production at 100,000 spores per adult host tree, and natural enemy infectivity (β , Eqn 18.2) at 0.001.

Simulations were run for different combinations of seed and spore dispersal scales (σ in Eqn 18.1), with each varying independently between 10, 20, 40 and 80 m (1, 2, 4 and 8 cell widths). Each combination of dispersal scales was represented by one simulation of 10,000 time-steps, or 1000 tree generations (given a mortality rate of 10% per time-step). Given the degree of temporal autocorrelation observed within any given

simulation, we sampled the simulated landscape every 200 time-steps (20 tree generations) and treated these samples as independent for the purposes of statistical analysis. To avoid transient effects of initial conditions, we discarded data from the first 1999 time-steps. We chose this threshold because species richness always plateaued between 500 and 1500 time-steps.

Analyses

We tracked three effects of natural enemies across the simulations: the average proportion of seeds killed by natural enemies, the strength of population-level density dependence, and the average species richness at equilibrium. Because natural enemy attack exclusively affected the survival of seeds to the juvenile stage (Eqn 18.2), the proportion of seeds killed by natural enemies was measured as

$$1 - \frac{\text{the number of seeds surviving to become juveniles}}{\text{the number of seeds produced}}$$

The mean proportion of seeds killed, the average equilibrium species richness and their confidence intervals were calculated from the values recorded every 200 time-steps between time 2000 and time 10,000. The strength of population-level density dependence was evaluated by analysing the relationship between births per adult and adult abundance (Fig. 18.3). In particular, we used the slope of the relationship between births per adult and adult relative abundance in the vicinity of the equilibrium abundance as our measure of density dependence (see Fig. 18.3 for details). Because all species are biologically equivalent in these simulations, all have the same equilibrium abundance within a given simulation, and thus this relationship is the same whether one species is tracked over multiple time-steps as it changes in abundance, or multiple species varying in abundance are examined at one time. We thus aggregated data for multiple species and multiple time-steps, sampling all species every ten time-steps within each sampling period of 200 time-steps (we sampled multiple times per sampling period in order to have large enough sample sizes to reliably calculate a slope for that period). For each response variable, the effects of seed dispersal and natural enemy dispersal and their interaction were analysed using ANOVA, treating each 200-time-step sample as one independent data point.

Tests of robustness

A key simplifying assumption of our main simulations is that adult host plants are the source of natural enemies. In reality, many natural enemies that attack seeds and seedlings are found in high concentrations around adults only because there are many seeds and/or seedlings there, not because the adult plants themselves are an important reservoir. If the source of natural enemy spores or inoculum is not the adult trees, but

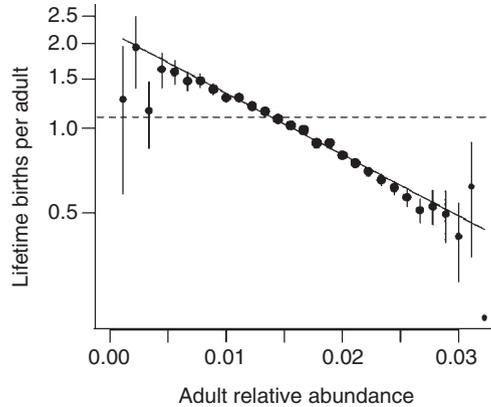


Fig. 18.3. To calculate population-level density dependence we first calculated the average lifetime births per adult for each adult relative abundance (filled circles; vertical lines show 95% confidence intervals). We then regressed $\log(\text{lifetime births per adult})$ against adult relative abundance (solid black line), weighting each abundance by the number of occurrences (circle size reflects this weighting). The slope of the regression line is our measure of population-level density dependence; steeper (more negative) slopes indicate stronger density dependence. The horizontal dashed line indicates the birth rate at which the population neither increases nor decreases in abundance. The example here is from a simulation in which seed and natural enemy dispersal scales were both 40 m.

rather the seeds or seedlings previously killed by the natural enemy, then the spatial distribution of sources of natural enemies changes as the seed dispersal distance changes, and we might expect different effects of seed dispersal distances on the maintenance of diversity.

To evaluate such a possibility, we ran simulations in which natural enemies dispersed from dead seeds, rather than from adult trees. Because natural enemy densities can vary considerably within the area of an adult tree and do not immediately spread over such an area, these simulations were run with a finer grid for natural enemies and seeds superimposed over the coarse grid for adults – specifically, there were 25 of these seed and natural enemy cells per adult cell (each effectively $2\text{ m} \times 2\text{ m}$). Because tracking natural enemies in this way greatly slowed the simulations, these simulations were done on a smaller grid of 400 (20×20) adult cells, over fewer time-steps (1000), with only 20 species, and without immigration or speciation. Seed and natural enemy dispersal scales were 10 or 40 m (1 or 4 adult cell widths). Each killed seed resulted in the production of 100 spores of the natural enemy. A parallel set of simulations was done with natural enemies dispersing from adult trees, and each adult tree producing 100,000 spores. We examined the proportion of seeds killed by natural enemies and the population-level density dependence under each set of dispersal distances within each set of simulations. The effects on species richness could not be evaluated in parallel with the main simulations because there was no immigration in these sets of simulations.

Results

Dispersal and total mortality

As expected, longer seed dispersal distances led to lower total mortality due to natural enemies (Fig. 18.4a). This effect was strongest for the shortest enemy dispersal scales, decreasing as enemy dispersal increased, but remained significant at all the scales examined here. Further, for any given seed dispersal scale, enemy dispersal scales that were relatively similar to the seed dispersal scale resulted in the highest mortality; this effect was most pronounced for longer seed dispersal scales. Seed dispersal scale, enemy dispersal scale, and the interaction of the two, all had significant effects on total mortality, explaining 65.2, 19.2 and 15.5% of the variation, respectively (Table 18.1).

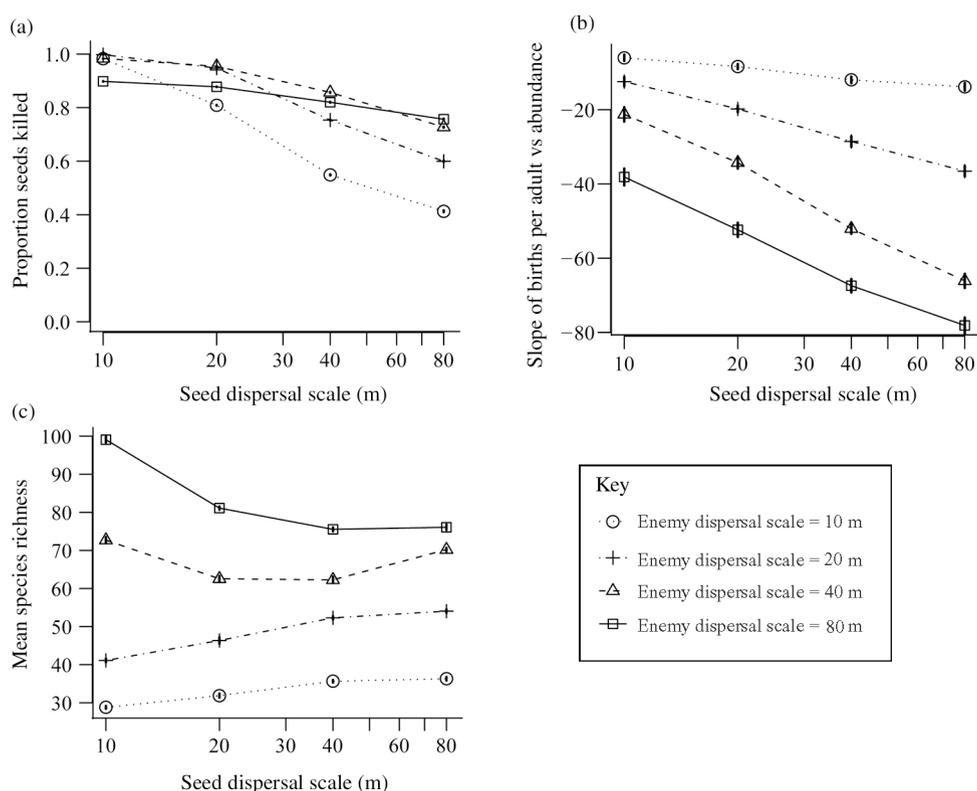


Fig. 18.4. Effects of seed and natural enemy dispersal scales on (a) total seed mortality due to natural enemies, (b) population-level density dependence as quantified by the slope of the relationship of births per adult to adult relative abundance (more negative slopes reflect stronger density dependence) and (c) mean equilibrium species richness maintained in the model community. The points show means across samples for a given set of parameter values; 95% confidence intervals on the means were plotted as vertical bars but are so narrow that they are not visible.

Table 18.1. ANOVA results for effects of seed dispersal scale, enemy dispersal scale, and their interaction on juvenile survival, population-level density dependence and species richness; all effects are significant at $P < 0.0001$, denoted by ***.

Independent variable	df	F-ratio		
		Juvenile survival	Density dependence	Species richness
Seed dispersal	3	118375.1 ***	1048.5 ***	225.3 ***
Enemy dispersal	3	34862.9 ***	2953.9 ***	19895.5 ***
Seed dispersal × Enemy dispersal	9	9386.5 ***	86.8 ***	620.9 ***
Error	624			

Dispersal and population-level density dependence

Longer seed dispersal distances also led to stronger population-level density dependence (Fig. 18.4b). That is, there was a stronger decrease in recruitment with adult density when seed dispersal scales were longer. This effect was strongest for the longest enemy dispersal scales and more modest as enemy dispersal decreased, but remained significant at all the scales examined here. Longer enemy dispersal scales also resulted in stronger density dependence, an effect that was more pronounced at longer seed dispersal scales, and was stronger overall than the effect of seed dispersal scales. Seed dispersal scale, enemy dispersal scale, and the interaction of the two, all had significant effects on density dependence, explaining 23.5, 66.1 and 5.8% of the variation, respectively (Table 18.1).

Dispersal and equilibrium species richness

The effects of seed dispersal scale on the equilibrium species richness maintained depended on enemy dispersal scale (Fig. 18.4c). For long enemy dispersal scales, species richness was highest at short seed dispersal scales; in contrast, for short enemy dispersal scales, species richness was highest at long seed dispersal scales. The effects of enemy dispersal scale alone were straightforward and much stronger: for any given seed dispersal scale, increased enemy dispersal scale always increased species richness. Seed dispersal scales, enemy dispersal scale, and the interaction of the two, all had significant effects on species richness, explaining 1.0, 89.7 and 8.4% of the variation, respectively (Table 18.1).

While the proportion of seeds killed by natural enemies and the strength of population-level density dependence were both correlated with species richness as expected, the influence of seed dispersal on species richness cannot be predicted from the influence of seed dispersal on either of these variables (Fig. 18.5). The proportion of seeds killed was positively correlated with species richness overall ($r = 0.24$, $n = 640$), and shorter seed dispersal always increased the proportion of seeds killed, but did not necessarily

increase species richness (Fig. 18.5a). Population-level density dependence was negatively correlated with species richness ($r = -0.72, n = 640$), and longer seed dispersal always made this density dependence more negative (indicating stronger population regulation), but did not necessarily increase species richness (Fig. 18.5b). The effects of enemy dispersal on species richness also could not be predicted from the effects on the proportion of seeds killed, but could be predicted from the effects on population-level density dependence. That is, increased enemy dispersal distances sometimes increased and sometimes decreased the proportion of seeds killed, yet always made population-level density dependence more negative and always increased species richness.

Robustness of results to the source of natural enemies

The qualitative effects of seed dispersal scale and natural enemy dispersal scale on the proportion of seeds killed and population-level density dependence were the same whether natural enemies dispersed from adult trees or from killed seeds (Fig. 18.6). In both cases, the proportion of seeds killed was higher at the lower seed dispersal distance and at enemy dispersal scales closer to seed dispersal scales, although both effects were smaller when natural enemies dispersed from killed seeds (Fig. 18.6a,b). Population-level density dependence was consistently stronger under the

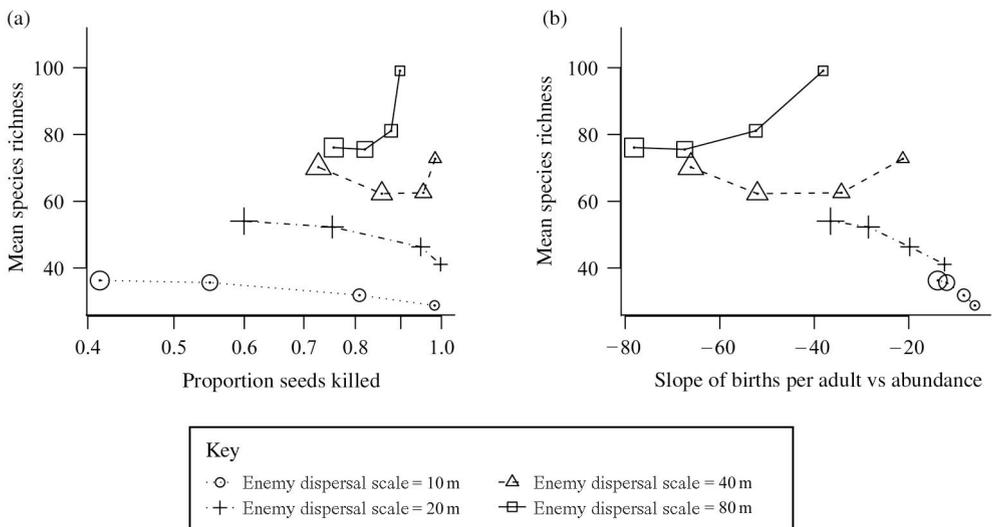


Fig. 18.5. The relationships of species richness to (a) the proportion of seeds killed and (b) the population-level density dependence across simulations varying in seed and enemy dispersal scales. Symbol size increases with seed dispersal scale, while symbol and line type reflect enemy dispersal scale as shown in the key. 95% confidence intervals are not shown, as they are generally smaller than the size of the symbols.

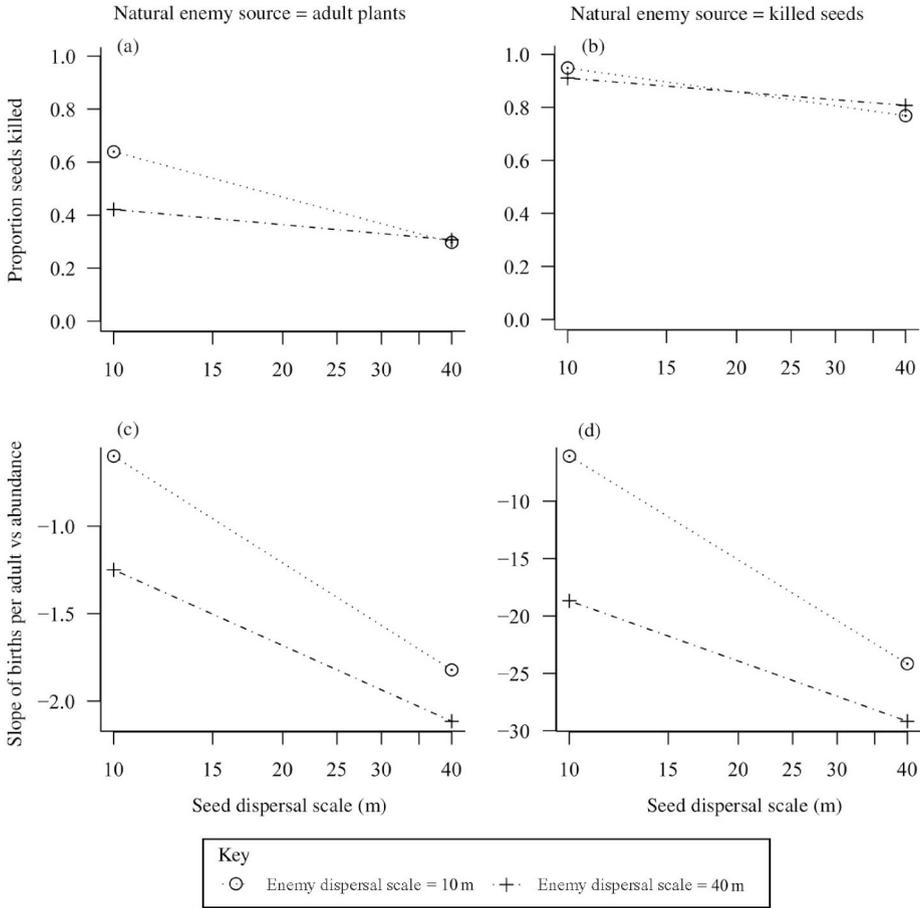


Fig. 18.6. The effects of seed and natural enemy dispersal scales on (a, b) total seed mortality due to natural enemies and (c, d) population-level density dependence in simulations in which the source of natural enemy spores is either (a, c) adult plants of the host species or (b, d) seeds of the host species recently killed by natural enemies.

longer seed dispersal distance and longer natural enemy dispersal distance in both sets of simulations (Fig. 18.6c,d). Overall, density dependence was much stronger when natural enemies dispersed from killed seeds.

Discussion

The complex effects of dispersal on species richness

The results of this study demonstrate that the effects of dispersal distances on the diversity-maintaining influence of natural enemy interactions are complex. In particular, seed dispersal distances have opposite effects on

the magnitude and the density dependence of mortality induced by natural enemies. Increased seed dispersal distances reduced total mortality due to natural enemies, but increased the population-level density dependence of such mortality. Increased natural enemy dispersal distances sometimes increased and sometimes decreased total mortality, depending on how they related to seed dispersal distances, yet always increased population-level density dependence of mortality.

Stronger population-level density dependence represents a stronger stabilizing force that should maintain higher diversity in the community, but it was not always associated with higher species richness in our simulations. We hypothesize that the higher species richness found for shorter seed dispersal distances when enemy dispersal distances are long reflects an effect of seed dispersal alone, rather than an interaction with natural enemies. In neutral models without natural enemies, in which species richness maintained represents a simple balance between speciation (or immigration from outside the model landscape) and stochastic extinction, shorter seed dispersal distances are associated with higher species richness in the landscape as a whole (Chave *et al.*, 2002). This occurs because shorter seed dispersal distances reduce the rates at which species can change in abundance because more offspring land on cells already occupied by conspecifics, essentially slowing drift to extinction or dominance. When we completely eliminated natural enemies from our model, we observed this effect, with higher species richness at shorter seed dispersal distances (data not presented).

In real communities, this neutral effect enhancing species richness at short seed dispersal distances is likely to be much weaker than the density-dependent effect enhancing species richness at long seed dispersal distances. The lower the rate of species introductions (whether considered immigration or speciation events) as a fraction of the number of births in the community, the weaker this neutral effect will be, because the species richness maintained in neutral models is strongly positively dependent on the immigration/speciation rate. In our simulations presented here, we implemented a high rate of species introduction because this magnified the differences between the scenarios, and allowed us to capture the qualitative effects without the much larger landscapes and longer simulation times that would have been necessary to observe statistically significant effects given realistically low immigration and speciation rates (Chave *et al.*, 2002). Immigration at these small spatial scales becomes part of the internal dispersal dynamics at larger spatial scales – dynamics that are themselves dependent on dispersal distances – and ultimately, at the largest scales, the only such introductions arise through speciation. Real communities are expected to have much lower speciation rates than the rate of introductions in our simulations, and therefore species richness should respond much more strongly to population-level density dependence than to seed dispersal alone.

We conclude that the effects of dispersal on population-level density dependence should be excellent predictors of the effects on species

diversity in real communities. Longer seed dispersal distances and longer natural enemy dispersal distances both led to stronger population-level density dependence, and thus should both lead to stronger contributions of natural enemy interactions to the maintenance of diversity. In effect, longer dispersal distances of either seeds or natural enemies cause the frequency of seed–enemy encounters to depend more strongly on the overall abundance of the host, rather than merely its local abundance. This in turn leads to larger changes in survival with changes in host abundance – stronger disadvantages when common, and stronger advantages when rare. This is stronger population-level density dependence, and it directly contributes to stronger maintenance of diversity at a community level.

Therefore, Janzen (1970) was right about the final effect – longer seed dispersal distances (and longer-foraging natural enemies) do result in stronger contributions of natural enemies to species diversity – even if he was wrong about one of the prerequisites; that is, seedling density need not peak some distance away from parents in order for distance- or density-responsive enemies to promote diversity. Janzen (1970) was also correct that the proportion of seeds killed by natural enemies will decrease as seed dispersal distances increase. As he recognized, the simple proportion of seeds killed by natural enemies does not predict contributions to the maintenance of diversity. Under short seed and natural enemy dispersal distances, many more seeds are killed, but the difference between the proportion killed at high and low host abundances is minimal, because seeds are always near parents, and thus near enemies, whether their species is common or rare.

The importance of local competition

The contrasts between the effects on diversity in these simulations and in our previous study (Adler and Muller-Landau, 2005) highlight the importance of local resource competition for structuring populations and communities. In our previous model, adults could establish arbitrarily close to each other, and therefore shorter seed dispersal distances led to ever higher levels of clumping of adults both at the population and community levels. Because the total number of adults in the landscape was constrained, this was also associated with ever larger areas of empty space within the model landscape. Thus, as seed dispersal distances became shorter, seeds suffered a double increase in attack of locally concentrated natural enemies – attack due to their increasing proximity to their own parents, and attack due to the increasing proximity of other conspecifics clustered ever more closely around their parents. This led to stronger density dependence at shorter dispersal distances, and thus higher diversity. When conspecific clumping was reduced by imposing a minimum establishment distance from parents (but not from other adults) on seedlings, shorter dispersal distances led to only a small increase in species diversity (Adler and Muller-Landau, 2005). In this chapter, the discrete-space nature of the landscape

effectively imposed a minimum establishment distance from any existing adult (parent, other conspecific or heterospecific), which is perhaps more realistic for a closed-canopy forest; under these conditions shorter dispersal distances always reduced density dependence.

Strong local resource competition in tropical forests and many other plant communities prevents the pronounced clumping that appeared in the model of Adler and Muller-Landau (2005), and thus precludes the diversity-enhancing effect of short dispersal found there. Large trees (> 30 cm in diameter) of all species combined in a Panamanian tropical forest have a spatial pattern that is the opposite of clumped: it is more regular than a random distribution (H.C. Muller-Landau, 2004, unpublished results; data available at <http://ctfs.si.edu/datasets/bci/>). To implicitly represent this local resource competition and capture the effects on community spatial pattern, we used a discrete space model with regularly spaced adults in this study. The convention of a regular rectangular grid with one adult tree per cell is common in forest models, and indeed in spatial models of plant communities in general (Hubbell, 2001; Chave *et al.*, 2002). Discrete- and continuous-space models have various advantages and disadvantages in general (Durrett and Levin, 1994; Bolker, 2004). The particular choice of continuous formulation in our previous study enabled analytical treatment (Adler and Muller-Landau, 2005). Furthermore, different models are appropriate for different communities. The results of Adler and Muller-Landau (2005) are likely to apply well to communities in which the spatial scales of seed and natural enemy dispersal are shorter than the spatial scales of resource competition, and in which strong overall clumping of adults can and does develop; desert plant communities may be a good example. The results from the current study should better predict effects in closed-canopy communities such as tropical forests.

Robustness of the results

Our model is obviously a simplification of the complexities of plant and natural enemy dynamics in real communities. Some of the simplifying assumptions are intended to narrow our focus to the question at hand (e.g. the assumption that all species are identical); others are made to speed up simulations to reasonable timescales (e.g. the size of the grid). Many of these assumptions have quantitative effects on the results; however, the qualitative patterns that we observe are robust to more realistic assumptions regarding the sources of natural enemies and many other aspects of plant–enemy interactions.

In this chapter we have presented results demonstrating that the qualitative effects of seed and natural enemy dispersal distances on diversity maintaining forces are the same whether natural enemies disperse from adult host plants or recently killed seeds. The effects on species richness could not be evaluated because of the shorter time span of the runs and the concomitant lack of inclusion of immigration, but we

expect that these would also be qualitatively the same, because species richness is driven by effects of population-level density dependence and seed dispersal distance alone. The similarity in the qualitative effects reflects the fact that under Gaussian seed dispersal, seed densities are considerably higher under adult trees and decline with increasing distance so that, in practice, the areas under adult trees are the main source of natural enemies even when these are explicitly produced by dead seeds. If seed dispersal patterns were such that there was no concentration of seeds under parent trees, then the two scenarios would be expected to diverge.

While we did not conduct simulations relaxing other assumptions, we can infer their effects from theory and the results of other studies. All other things being equal, a larger model landscape or a higher immigration rate will support higher species richness for all dispersal scales (Chave *et al.*, 2002), but will not affect the direction of changes with dispersal scale. An increase in natural enemy infectivity will increase the proportion of seeds killed, but will leave qualitative patterns unchanged (Adler and Muller-Landau, 2005). If species of plant vary in their competitive abilities, susceptibility to natural enemy attack, or seed or natural enemy dispersal scales, then their reproductive rates will equilibrate at different relative abundances; however, each species' reproductive rate will still be negatively density-dependent, and thus, as long as a species' equilibrium abundance is non-zero, natural enemy interactions will help maintain it in the community. If natural enemies are specialized at a higher taxonomic level than species, for example at the generic level as seems most common for insects and pathogens (Gilbert and Sousa, 2002; Novotny and Basset, 2005), then the impacts on diversity depend on how effects of a given natural enemy vary across species. Effects that are identical across all species in a genus would contribute to maintenance of generic diversity, but not to the maintenance of species diversity within genera. In the more realistic case of unequal effects across multiple affected plant species and by multiple shared natural enemies, the natural enemies contribute to the maintenance of species diversity the degree that different species are most limited by different natural enemies, i.e. different factors, as stated in classic competition theory.

Implications for understanding effects of changes in seed dispersal patterns

The effects of seed dispersal distances on natural enemy interactions in this study shed light on the potential impacts of anthropogenic changes in seed dispersal patterns for population viability and community diversity. In considering the implications, we must take into consideration that these changes affect different species to differing degrees (with some species completely unaffected), in communities where seed dispersal already varies among species. Thus, we cannot simply extrapolate from differences between simulations in which seed dispersal distances of all species are higher or lower – we must take variation among species into account.

The first direct effect of reduced seed dispersal distances on interactions with natural enemies is elevated mortality due to specialized natural enemies concentrated around parents (Janzen, 1970). Because these reductions in seed dispersal affect some, but not all, of the species in a community, the affected species will be at a relative disadvantage and will be expected to decrease in abundance. Such changes in abundance alone can lead to profound changes in community structure. However, the most important question from a conservation perspective is whether these declines will continue to local extinction. The many density-dependent factors that stabilize plant populations and communities have the potential to prevent such extinctions by ensuring that, at some lowered abundance, the reproductive rate of the affected species will be high enough for it to maintain itself (Muller-Landau, 2007). These factors include not only interactions with natural enemies, but also habitat niche differentiation and temporal partitioning of varying environmental conditions, among others (Chesson, 2000; Barot, 2004).

Unfortunately, the results shown here suggest that reduced seed dispersal not only increases mortality due to natural enemies and thereby decreases survival at any given abundance, it also reduces the strength of the population-level density dependence of mortality due to specialized natural enemies. Shorter seed dispersal scales led seeds to continue to encounter their natural enemies at high rates even when the abundance of their conspecifics in the overall landscape was very low. This implies that species whose seed dispersal is decreased will derive less benefit from rarity, and are more likely to continue to decrease in abundance to extinction. On the other hand, species whose seed dispersal is enhanced are likely to not only experience elevated survival but also increased density dependence. Thus, their increase is more likely to be checked before they achieve monodominance.

To what degree are these predictions regarding the effects of changed seed dispersal on density dependence and diversity sensitive to the details of our model? Incorporation of additional complexity or changed functional forms for natural enemy dynamics could result in quite different influences of changed seed dispersal distances on density dependence and diversity. For example, if natural enemies have a minimum population size larger than that supported by a single host individual, then natural enemies and the mortality they induce could locally disappear before the host reaches extinction. This could elevate host reproductive rates sufficiently to facilitate persistence, or even increases to a level at which the natural enemy reappears. Similarly, relaxing the degree of host specialization of natural enemies, adding dependence of enemy movement distances on host availability, adding seed or spore dormancy, and many other potential changes could have major impacts on how seed dispersal affects density dependence. In general, however, we expect the qualitative result found here to be relatively robust – decreased seed dispersal will decrease the density dependence of natural enemy interactions, and thereby reduce the potential for species declines to stop short of extinction.

Conclusions

Seed dispersal clearly plays an important role in structuring plant interactions with specialized natural enemies. In this chapter we demonstrated the importance of seed dispersal distances to the magnitude and density dependence of mortality due to natural enemies. But dispersal distances are only one facet of seed dispersal patterns (Muller-Landau and Hardesty, 2005) – habitat-specific deposition and clumping of seed rain irrespective of habitat are likely to further affect natural enemy interactions. Furthermore, the specific influences of all these factors depend on the details of natural enemy life history – specificity, longevity, movement distances, reproductive rates, etc. Ultimately, we need to better understand these and other details of plant and natural enemy biology, and incorporate this understanding into mechanistic models in order to elucidate the influences of seed dispersal on natural enemy interactions, and specifically on the density-dependent, and consequently diversity-enhancing, effects of natural enemies on plant populations and communities.

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