THEORETICAL PERSPECTIVES ON EVOLUTION OF LONG-DISTANCE DISPERSAL AND THE EXAMPLE OF SPECIALIZED PESTS

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Abstract. Long-distance dispersal (LDD)—dispersal beyond the bounds of the local patch or cluster of conspecifics—will be most advantageous in landscapes in which large areas of suitable habitat are consistently available at long distances from established populations. We review conditions under which LDD will be selected and conclude that biotic interactions, and in particular specialized natural enemies, are likely to be one of the most important factors selecting for LDD in many species. We use simple spatially implicit and spatially explicit models to illustrate how such pests affect the evolutionarily stable strategy (ESS) for investment in LDD. Patches currently occupied by parents are more likely to be infected than distant, potentially unoccupied, patches, thus advantaging dispersal. Patchy infestations also result in higher variance in reproductive success among patches, which alone selects for increased among-patch dispersal. Both of these effects increase with the strength of the impact of infestation, and with the number of species competing for space in the community. We discuss the potential of different types of models and analytical tools to capture the impacts of pests on the evolution of LDD, and conclude that even simple models can illustrate the general relationship between pest pressure and LDD advantage, but only spatially explicit simulation models can fully elucidate the resulting ecological and evolutionary dynamics. In conclusion, we consider the potential role of selection for LDD in the spread of invasive species, and in long-term responses to habitat fragmentation and range shifts.

Key words: adaptive dynamics; density dependence; escape hypothesis; evolutionarily stable strategy (ESS); Janzen-Connell effects; long-distance dispersal; spatial ecology.

Introduction

The evolution of dispersal has provided a rich lode for theoretical exploration. A number of factors can lead to selection pressure for increased dispersal (Ronce et al. 2001), including kin selection (Hamilton and May 1977), spatiotemporal fluctuations in the environment (Comins et al. 1980, Levin et al. 1984), and decreased reproductive rates in areas of high conspecific concentrations (Levin and Muller-Landau 2000*b*). The same factors, operating on larger scales, also select for long-distance dispersal (LDD), but their relative importance differs. Long-distance dispersal is not just short-distance dispersal writ large: the mechanisms may be different, the consequences are different, and thus the evolutionary forces play different roles.

The distinction between long-distance dispersal and normal, short-distance dispersal can be made on differences in mechanism (dispersal mode) or differences in consequences (in the simplest case, dispersal distance; Nathan et al., *in press*). It is only a minority of species that show two distinct modes of dispersal, one

of which can clearly be identified as long-distance; in most species the definition of LDD has typically been made based upon arbitrary selection of a threshold distance, for example, a round number considerably higher than the mean (Nathan et al., *in press*). We suggest that when a distinction based on dispersal mode is not possible, a threshold distance for long-distance dispersal is most usefully defined with reference to the scale of spatial patterning in the population under consideration, as this is what determines how the consequences of LDD events differ from those of normal (short distance) dispersal events. Because of local dispersal and patchy environments, virtually all species exhibit local clustering of conspecifics, and this is especially true of plants and other species with sessile adults (e.g., Condit et al. 2000). As a result, autocorrelograms showing how the distance between two points affects the correlation coefficient of population density at the two points (Legendre and Fortin 1989, Legendre 1993, Palmer 2002) typically show declines from positive correlations at short distances to zero or negative correlations at long distances. Dispersal within local patches—within areas of strong positive correlation of population density (i.e., less than the correlation length)—should be considered normal, or, short-distance dispersal, while dispersal to distances larger than the scale of local patches (or correlation length) should be considered LDD. In most systems, difficulties in precisely defining the scale

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of local patches or correlation lengths will mean that such a definition of LDD retains some element of arbitrariness, as is the case with many other useful biological concepts (e.g., population).

In considering the evolution of LDD, the most important difference from the case of evolution of normal dispersal is that the payoffs are potentially much larger and are harder to quantify because they emerge from rare events over large spatial scales and multiple generations. The main benefits derive from the ability of distantly dispersed offspring to escape the local correlation length of the population, colonizing areas unoccupied by conspecifics, and in which local population expansion can subsequently occur. At long distances from established populations, the absence of specialized pests may further increase the benefits of any surviving offspring and allow for several generations of competitive advantage over other species. At these larger scales involved in LDD, environmental heterogeneity must also be considered carefully, as the habitat often emerges not as a random patchwork, but as an interplay of orderly gradients.

The mechanisms of long-distance dispersal may also differ qualitatively from those of ordinary dispersal, requiring different formulations of costs (Higgins et al. 2003). Increased long-distance dispersal may come at the cost of a lower proportion of seeds dispersed. For example, among wind-dispersed seeds, adaptations that require strong winds in order for seeds to be removed from the plant increase dispersal distances of those seeds removed (Horn et al. 2001), but may also result in more seeds not being removed during the dispersal season at all. In other cases, increases in long-distance dispersal may be a simple corollary of increase in dispersal in general, and thus the selective pressures may be difficult to disentangle. Fruit characteristics that increase gut passage time in frugivorous seed dispersers, for example, result in deposition at greater distances from the plant in general, and thereby also increase the probability that a seed will be transported long distances. In other cases, there are specific adaptations (or pre-adaptations) for long-distance dispersal. For example, pests such as the cereal leaf beetle use very different mechanisms to spread on local and landscape scales (Andow et al. 1990).

Here, we first discuss prerequisites for selection for LDD, and conditions under which such selection is likely. We argue that one of the most likely scenarios for evolution of LDD involves the influence of specialized, locally dispersing pests. We then use a variety of theoretical and modeling techniques to show how such specialized pests can select for higher rates of LDD, and how this selection varies depending on life history and abundance. Further, we use this example to review the potential of different theoretical tools to investigate LDD evolution. Finally, we discuss the implications of selection on LDD for understanding the responses of species to habitat fragmentation and range shifts, as well as the behavior of invasive species.

PREREQUISITES FOR SELECTION FOR LDD

Even though LDD alone is most often advantageous, there may be relatively weak selection specifically to enhance or maintain LDD in most species at most times. Traits that influence LDD may have myriad other effects as well, and selection on those effects may dominate. There may also simply be insufficient heritable genetic variation in LDD for selection to operate.

Variation in LDD between species suggests that particular traits do influence LDD, yet within-species variation in these traits may be low, reducing the potential for selection upon them. For example, Nathan et al. (2002) find that seeds of tree species that have lower seed terminal velocities are more likely to be uplifted and therefore dispersed long distances than seeds of species with higher terminal velocities; however, within species, there were no significant differences in terminal velocities among seeds that were uplifted and those that were not (Horn et al. 2001, Nathan et al. 2002). Mechanistic models parameterized with real data suggest that far more of the variation in dispersal distances among wind-dispersed tree is explained by variation in wind speed (an external condition) than by variation in seed terminal velocity (Nathan et al. 2001, 2002). Insofar as variation in relevant seed and plant traits does occur, it may reflect environmental as well as genetic conditions; for example, taller trees and trees located at relatively higher elevations within a local landscape disperse seeds longer distances. Very few studies have established the genetic basis of any dispersal traits (O. Ronce, *unpublished manuscript*), much less traits specifically implicated in LDD.

Even where substantial heritable genetic variation exists in traits that affect LDD, selection on these traits may be driven largely by other factors. The rarity of LDD events and the large role of stochastic environmental factors in generating them both weaken its selective influence. For example, seed mass, which is related to the probability of LDD via uplifting in wind-dispersed tree species, also has a strong influence on seed survival and establishment probability (Leishman et al. 2000). Where LDD occurs by the same mechanisms as local dispersal, the same traits are likely to be involved, and local dispersal may be a stronger selective influence. Further empirical research is needed to identify traits affecting LDD and investigate selective pressures upon them.

Another consideration is that selection on dispersal ability occurs at multiple spatial scales, and selective forces at different scales may be in conflict. For example, Cody and Overton (1996) documented differences in dispersal ability of short-lived, wind-dispersed plants on mainland and small island subpopulations. They found that new island populations have higher dispersability than the average of mainland popula-

tions. Over time, selection within island subpopulations results in decreased dispersal potential, such that old island populations have lower dispersability than the mainland average. Thus, relatively high dispersal ability is selectively disadvantaged within local subpopulations, but favored over the whole metapopulation.

Factors Selecting for LDD

In general, we expect the strongest selective advantages to LDD in cases where patches of favorable habitat frequently appear far from established populations. New habitat must become available with sufficient frequency for selection pressure to be strong and of continuing influence; extremely rare events such as the birth of volcanic islands (Fridriksson 1975) are unlikely to suffice. Such a habitat dynamic can arise exogenously, for example through particular abiotic disturbance regimes, or endogenously, for example through interactions with powerful natural enemies.

Large disturbances, such as landslides and river meanders, can create selection pressure for LDD. Landslides commonly leave an upper area barren of seeds or vegetation, can be very large, and may take as long as 500 years to fully revegetate (Guariguata 1990, Dalling 1994). Newly exposed floodplains, created when riverbeds gradually erode and shift, show a similar dynamic of large, multigenerational disturbance (Whitmore 1990). LDD will be favored in species that specialize on habitats such as these. Climate change and accompanying range shifts can also produce the requisite landscape dynamic for a much broader array of species, as large areas of suitable habitat continually become available at long distances from established individuals.

A similar habitat dynamic can emerge endogenously when established populations create locally unfavorable conditions through resource depletion or the buildup of high densities of natural enemies. If the negative local effects are sufficient to drive populations to local extinction and subsequently allow for site recovery to more favorable conditions, then LDD and/or long-term dormancy will be advantageous, because both strategies make it possible to colonize areas in which resources have recovered or pest densities have declined. An excellent example of this is given by Fragoso et al. (2003), who document how species-specific bruchid beetles almost completely prevent recruitment in established stands of *Attalea maripa*, and how long-distance dispersal by tapirs leads to the establishment of new stands in areas where conspecifics and the associated beetle are absent.

Such specialized pests that concentrate their activities in areas of high densities of their plant host are hypothesized to be one of the most important factors maintaining high species diversity in tropical forests (Janzen 1970, Connell 1971), and are theoretically capable of maintaining very high levels of diversity (Armstrong 1989). They depress survivorship of seeds, seedlings, and saplings near adult trees, and/or in areas of high density of adults or seeds or seedlings (Hammond and Brown 1998, Harms et al. 2000). This can result in radical differences in survival of seeds dispersed short vs. long distances. For example, Fragoso (1997) observed that bruchid beetles predated 77% of seeds remaining near parents, but only 0.7% of seeds dispersed over 2 km by tapirs. Even where effects are less dramatic, somewhat increased mortality or reduced fecundity alone can be enough to prevent local regeneration of a species, given the many competing species, especially if some of the competitors have escaped the neighborhood of their own conspecific adults and associated pests. Such processes can result in fugitive species dynamics even in shade-tolerant species in mature tropical forests (Fragoso et al. 2003).

While only a limited number of species are specialized on habitats like landslides whose dynamics exert selection pressure for LDD, all species have natural enemies. Whenever these pests have limited dispersal abilities, can depress reproductive rates to the point of causing local extinction of their hosts, and themselves disappear from an area in the absence of their hosts, LDD will be advantageous to the host. In cases where the habitat dynamic favors LDD as well, pests may further multiply the advantages of long-distance dispersers. In the next two sections, we will consider the example of specialized pests in particular, and show how various methods can be used to incorporate their influence in analyses of the evolution of plant seed dispersal. While we focus on this specific example for illustration, there are parallels to the approaches taken here that can be applied to other situations where LDD provides a selective advantage, and to other systems besides plants.

Implicit Incorporation of Pest Effects

One way to incorporate the effects of species-specific pests into more general models of the evolution of dispersal is by relating the values of parameters to the influence of pests. For instance, fecundity can be allowed to reflect the proportion of seeds suffering density-dependent mortality. We will discuss ways of doing this in both spatially implicit and spatially explicit frameworks.

Spatially implicit models

In what we term a metapopulation approach (sensu Levins 1968), also referred to as an "island model," a population is considered to be distributed among many sites that are all connected through global dispersal. Seeds can either stay within the site where they are produced (nondispersers), or be dispersed "globally," that is, with equal probability to any of the other sites. These models, though highly unrealistic for most systems, can serve as useful approximations that capture many—but not all (Durrett and Levin 1994, Higgins and Cain 2002)—of the features of more complex

models, and have the advantage of being analytically tractable. They constitute a useful framework for considering evolution of long-distance dispersal, in that dispersal within a site or subpopulation can be considered local dispersal, while dispersal between subpopulations can be considered long-distance dispersal.

For example, we can use such a model to demonstrate how variation in pest densities among sites alone will increase dispersal rates, even if pest pressure is not higher in areas of higher population densities. We assume that there are multiple individuals per patch, and that densities of individuals within a patch vary continuously. A simple way in which pests can be incorporated into this metapopulation model is to assume that there is a constant probability for each patch to be infested by pests in any generation, and that this probability is independent of the previous state of the patch. This formulation allows us to use general results of Levin et al. (1984) for the evolutionary stable strategy (ESS) of dispersal in a spatiotemporally varying environment. Levin et al. (1984) assume that there is scramble competition within patches, and that every patch reaches its carrying capacity (which varies stochastically) in every generation, and that there is a cost to dispersal such that on average only α surviving dispersing seeds can be produced for the cost of one local seed. Building on this model, if q is the probability of a pest infestation and $\gamma < 1$ is the relative reproductive output of an infested patch, then we find that the ESS rate of dispersal outside of the home patch, $\hat{D}$, is

$$\hat{D} = \frac{1 - q}{1 - \frac{\alpha}{\gamma}(1 - q + \gamma q)} + \frac{q}{1 - \alpha(1 - q + \gamma q)} \quad (1)$$

provided

$$1 > \alpha > \alpha_{crit} = \frac{\gamma}{[q + (1 - q)\gamma][(1 - q) + \gamma q]}. \quad (2)$$

For $\alpha > 1$, dispersing seeds have higher survival, and thus $\hat{D} = 1$. For $\alpha < \alpha_{crit}$, the potential advantage of bet hedging across infested and uninfested patches is outweighed by the higher mortality of dispersers, and thus $\hat{D} = 0$. Note that Eq. 2 means that, for $\alpha < 4\gamma/(1 + \gamma)^2$, $\hat{D} = 0$ under all conditions. That is, the possible benefits of pest avoidance cannot override the costs of dispersal. For $\alpha > 4\gamma/(1 + \gamma)^2$, $\hat{D} = 0$ for low q (low pest levels) and $\hat{D} = 1$ for high q; for an intermediate region of q, including $q = 1/2$ (50% infestation level), there will exist an intermediate ESS. Overall, $\hat{D}$ increases as the probability of a pest infestation or its effect increases, indicating increased selection for dispersal as the variance in yields among patches is increased.

Of course, damage due to pests is not equally probable at all sites, but is instead most pronounced in areas of high concentrations of the host (Janzen 1970, Connell 1971). We can incorporate density dependence of

pest effects, and thereby implicitly capture more of the dynamics of pest infestation. Because specialized pests are concentrated near conspecific adult plants, they will have a higher impact on nondispersing seeds than on dispersing seeds, since the latter may land on sites that have not recently been occupied by conspecific adults. A further complication is the potential feedback from changes in dispersal parameters upon the proportion of sites a species occupies.

The above result (Eq. 2) on the ESS dispersal rate, as well as many others for both spatially implicit and spatially explicit models, can be obtained in a straightforward way from a general condition determining evolutionary attractors of seed dispersal under the assumption that a single character determines dispersal, fecundity, and relative establishment success (Levin and Muller-Landau 2000a, b). Levin and Muller-Landau (2000a, b) explore tradeoffs among these characters, mediated through traits such as seed size. For example, large seeds may have reduced dispersal distance and lower fecundity, but improved competitive ability. Using a spatially explicit competition model involving multiple types competing for sites on a grid, they show that there is generally a single winning type. Conveniently, this type can be characterized as that which maximizes (locally in trait space) the quantity

$$F = [P(c)]^2 \left\{ 1 - \sum_{\mathbf{x}} [\delta(c, \mathbf{x})] \right\}^2 \quad (3)$$

where the dispersal parameter c is the evolutionarily labile character, $\mathbf{x}$ is a vector giving the displacement of a potential seed deposition site from the parent, $\delta(c, \mathbf{x})$ is the probability that a seed lands on a site displaced by $\mathbf{x}$, and $P(c)$ is the product of fecundity and seed relative competitive ability. Numerical methods are needed to evaluate $\delta(c, x)$ for most types of seed dispersal. This result is a powerful simplification in cases where it can be applied, as it transforms a game-theoretic problem, in which the strategies of two or more players must be considered simultaneously, into an optimization one involving the strategies (characters) of each species in isolation. The general result is applicable both to spatially implicit and to spatially explicit models in which space is discretized, and the density of total seeds arriving (from all individuals of all competing types combined) is constant across sites. F has no obvious simple interpretation as a single characteristic, but trades off the benefits of high reproductive success and effective dispersal.

Spatially explicit models

The spatially implicit models discussed above assume that all sites are equally connected. For most systems, however, it is important to take into account that dispersing seeds are much more likely to land at nearby sites. Of course, spatially explicit models do not lend themselves easily to formal analysis, shifting

emphasis to simulations and approximations (Durrett and Levin 1994). Here, we present a simple way in which pest-mediated effects of sibling density on seed survival can be incorporated in spatial models for the evolution of dispersal, and discuss analytical approximations that can be used in combination with such implicit incorporation of pest effects.

We can incorporate pest-mediated effects on seed survival into a spatial model of dispersal evolution implicitly by replacing functions describing the spatial distribution of dispersed seeds around parents with functions describing the spatial distribution of seeds (or seedlings) surviving after predation. Expected seed survival, like seed arrival, varies with distance from parent both due to differences in pest dispersal from the parent and due to differences in the local density of seeds. We can use information on this change in seed survival to calculate the expected distribution of surviving seeds after pest effects around isolated adults, and use this distribution in dispersal evolution models in place of the original seed shadow. For example, let us suppose that a number f of seeds are distributed around a parent tree according to a bivariate Gaussian with standard deviation of c (Clark et al. 1998), and that survival is a power-law function of local seed density (Harms et al. 2000) such that the number of recruiting seeds R is related to the local seed density S as $R = aS^b$ (with $0 < b < 1$ indicating negative density dependence). Then, through integration, we can determine that the expected number of recruiting seeds a distance x from an isolated parent is also a bivariate Gaussian, but with a higher standard deviation of dispersal distance $c/\sqrt{b}$ and with a lower number of seeds (a/b) $(2\pi c^2)^{1-b}f^b$.

These same methods can be used to incorporate the first-order effects of negative density dependence into other dispersal kernels, such as the exponential (Turchin 1998), the Weibull (Tufto et al. 1997) and the Clark $2Dt$ (Clark et al. 1999). They account only for first-order effects because only the density of other seeds from the same parent (siblings) is taken into account. Especially in cases where dispersal is local, adults—following the patterns of seeds themselves—will tend to be spatially autocorrelated, leading to a much greater influence on conspecific seed survival than would occur otherwise. The next step is hence to incorporate information on spatial autocorrelation of adults and thus seed rain of multiple adults, in order to arrive at better approximations of the distribution of surviving seeds relative to parents. Spatiotemporal correlations in site occupancy, and resulting effects on the payoff from short- and long-distance dispersal, can be incorporated in a limited way by means of pair approximations or spatial moment equations.

Pair approximations (e.g., Harada 1999) are one method for accounting for spatial heterogeneity in the population, and its influence on dispersal success. Harada's results (1999) clearly suggest that the proportion of offspring dispersed globally increases as the relative cost of globally dispersing offspring decreases (e.g., if survival of nearby dispersers is disproportionately depressed), though pair approximations underestimate LDD by ignoring clumping at scales larger than nearest neighbors. Clumping at higher spatial scales can be incorporated through multiscale pair approximations (Ellner 2001), or by considering spatial covariances in site occupancy with distance (Bolker et al. 2000). Bolker and Pacala (1997) solve equations for the expected covariance in spatial structure in a population given a dispersal kernel and a competition kernel. Effects of pests concentrated around adults could be incorporated into the competition kernel, and thus included in the dynamics. Bolker and Pacala (1999) use moment equations to solve for the invasion conditions of a global disperser invading a local disperser, and vice versa, and provide a general framework for the case of one type of disperser invading another (their Appendix B).

While pair approximations, moment methods, and the general condition of Levin and Muller-Landau (2000a, b) are potentially useful tools for investigating dispersal evolution in spatially explicit models, simulations remain essential. For problems such as the example in the next section, even the simplest spatial models produce pair approximation equations that are not transparent, and can be solved only numerically (Harada 1999); moment approximations are even more complex (Bolker and Pacala 1999). Furthermore, the equations themselves remain approximations, which deviate from the true dynamics, as revealed in simulations (e.g., Harada 1999). Similarly, the ESS condition of Levin and Muller-Landau (2000a, b) was developed under the assumption that the total density of surviving seeds, is uniform in space; this assumption may be severely violated in communities where patchy distributions of individual species interact with negative density dependence, as considered here. Indeed, situations where long-distance dispersal is most likely to evolve are exactly those in which total seed input, and thus opportunities, vary across sites and in which important processes occur at scales greater than the correlation length of local populations and thus beyond distances typically captured in moment approximations. In contrast, simulations provide the ability to explore a greater range of assumptions efficiently.

Explicit Treatment of the Dynamics of Infestation

In the previous section, pest risks are considered implicitly, by assuming a constant relationship between species occupancy and pest level. However, the dynamics of infestation itself may introduce time lags for pests to locate adu1ts—time lags that themselves vary with the relative isolation of adults. To investigate this possibility, and its implications for the evolution of long-distance dispersal, we now turn to an individual-based, spatially explicit model that incorporates the

dynamics of pest infestation. Our model is motivated by the case of pests spreading among trees in mixed-species stands of closed-canopy forest.

Model description

In our model, space is discretized, so that the landscape consists of a square lattice of cells (with periodic boundary conditions), each capable of supporting a single tree. Individual trees are characterized as either infested (infected) or uninfested (susceptible). Dispersal of individual seeds, and infestation of one tree by another are both modeled explicitly.

We assume each tree species has two modes of dispersal, one long distance and one short distance, each governed by a Gaussian distribution, but with different dispersal distances corresponding to two different mechanisms or modes of dispersal (as in Clark 1998). The total dispersal kernel can thus be written as

$$g(x) = (1 - d)\frac{1}{2\pi\sigma^2}\exp\left(\frac{-x^2}{2\sigma^2}\right) + d\frac{1}{2\pi\lambda^2}\exp\left(\frac{-x^2}{2\lambda^2}\right) \quad (4)$$

where α and λ are the distance parameters of the normal (short) and long-distance dispersal modes, respectively, and d is the proportion of seeds that are dispersed long distances. As in the first model, we assume that there is a cost of long-distance dispersal, such that on average only $\alpha < 1$ surviving long-distance dispersing seeds can be produced for the cost of producing one surviving short-distance dispersing seed. Thus the fraction of reproductive effort expended on long-distance seed dispersal is $D = d/(d + \alpha - \alpha d)$. The probability of mortality in each time step is m, and thus trees live an average of $1/m$ time steps. The mean number of seeds produced by a tree each time step, f, depends on the proportion that are dispersed long and short distances, and satisfies $f = K/(1 - d + d/\alpha)$, where K is the total resources available for reproduction, expressed in units of the number of short-dispersing seeds that could be produced.

The influence of pests is incorporated explicitly. All young trees are susceptible when they first appear, and can be infected by conspecific infected trees. Infected trees do not recover, but remain infected and infective. We assume that death rates of adults are not impacted by infection, but that fecundity is reduced to γf (with $\gamma < 1$). A mean number of v pest propagules is produced by an infected tree each time step, and each is dispersed according to the infection kernel, $h(x)$, which is also Gaussian with standard deviation β

$$h(x) = \frac{1}{2\pi\beta^2}\exp\left(\frac{-x^2}{2\beta^2}\right) \quad (5)$$

If the dispersing pest lands on an uninfested tree of the same species as its source, the tree becomes infested.

Thus, overall, the model has three spatial scales. Population birth of susceptible individuals is governed by the dispersal kernel (Eq. 4), which is characterized by two spatial scales. One scale takes into account normal dispersal (σ) and thus is critical in determining the correlation length of the local population, while the second (λ) addresses large-scale dispersal events or LDD. These two scales are fundamentally different and nested. The third spatial scale is defined by the infective dynamics of species-specific pest populations; this scale is fixed by the infestation kernel (Eq. 5) describing the spread of pest populations.

We find evolutionarily stable strategies by starting with a single type (a single d), which can mutate. Selection and the continual introduction of new variation through mutation together result in evolution of the LDD fraction to its evolutionarily stable value. We compare the evolutionarily stable dispersal strategies among systems in which parameter values vary, and report here the patterns with changes in the cost of LDD (α) and the number of species. We also track the mean densities of susceptible and infested individuals of each species, and the spatial structure of the community as a whole.

In order to allow for a large number of simulations with different parameter values, the total size of the landscape was kept relatively small and dispersal distances were restricted accordingly. Results are reported here for simulations on grids of 100×100 cells, with $\sigma = 1$ and $\lambda = 5$. If the area occupied by a single canopy tree is ~10 m across, then this corresponds to a landscape of 100 ha, short dispersal-distance standard deviations of 10 m, and LDD standard deviations of 50 m. In order to verify that our results were not significantly affected by the chosen scales, we also repeated a subset of simulations on larger and smaller grids and with longer and shorter dispersal distances; all the qualitative results we report below remained unchanged.

Model results

Examination of the model landscape reveals examples of exactly the sort of spatial host–pest dynamics that were expected. Snapshots of the grid show areas where a species has become absent following a pest infestation, areas where it has recently reinvaded and is expanding in the absence of its pests, and areas where the pest has recently located a susceptible population and is spreading within it (Fig. lA). These dynamics become more pronounced in more diverse communities, where abundances are lower and thus escape from pests in space becomes more feasible. If we look at the spatial correlation structure of species occupancy, we see an initial steep decline in the probability of encountering conspecifics with distance from an occupied cell corresponding to the scale of normal dispersal, followed by a more gradual decline over the scale of long-distance dispersal to the mean value for the landscape (Fig. 1B, filled circles). Similarly, the probability of encountering an infested conspecific declines with distance from an infected individual (Fig. 1B, open
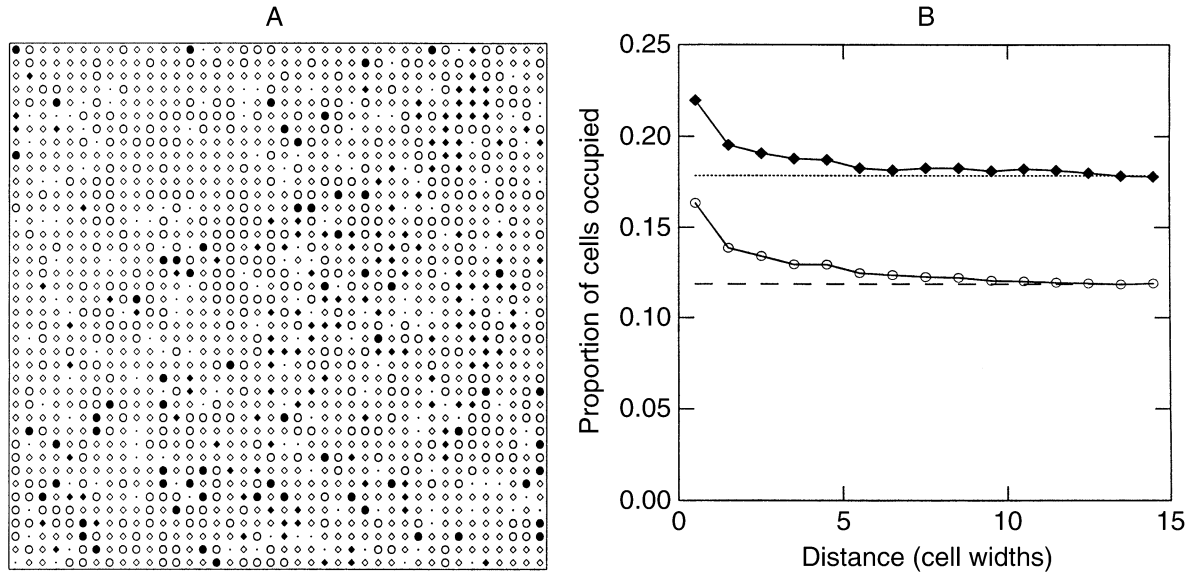
Fig. 1. A map of part of the model landscape, showing (A) the spatial structure of occupancy and infestation and (B) a graph of the spatial correlation structure for one point in time in one particular simulation. In the map (A), the focal species is shown with filled symbols, the other four species with open symbols. Susceptible individuals are indicated with circles, and infested individuals with diamonds, while dots show empty cells. In (B), the filled diamonds show the probability that a cell is occupied by a conspecific as a function of distance from an occupied cell, with the dotted line indicating the mean probability over the whole landscape. The open circles show the probability that a cell is occupied by an infected conspecific as a function of distance from an infected individual, with the dashed line giving the mean probability over the landscape. Both figures are based on data from a simulation conducted on a 100×100 lattice (only a subset of which is shown in panel (A), with short-distance dispersal $\sigma = 1$, long-distance dispersal $\lambda = 5$, pest dispersal $\beta = 2$, mortality $m = 1$, reproductive resources $K = 16$, virulence $v = 16$, pest effect on fecundity $\gamma = 0.6$, relative survival/cost of dispersers $\alpha = 0.625$, and thus ESS investment in LDD $D = 0.015$.

circles), reflecting both decreases in the number of conspecifics as shown above and decreases in the probability that conspecifics are infected.

The results of the spatially explicit model confirm the general patterns we obtained with the much simpler spatially implicit models, and provide additional insight into the combination of factors that lead pests to enhance selection for LDD. Higher survival and lower costs of LDD (lower α), lead of course to higher levels of LDD (Fig. 2). Further, we find that higher species diversity is associated with higher levels of LDD (Fig. 2 and 3D). This is due to the decreased density of conspecific infected individuals at higher diversity, especially among sites encountered by individuals dispersing long distances (Fig. 3B). Two factors contribute to this decreased density. First, simply because there are more species, each species has a lower abundance, and thus the probability of encountering any conspecific is reduced (Fig. 3A). In addition, the prevalence of infection in the community overall is reduced at higher diversities, because it is harder for the infection to spread, thereby influencing selection on LDD (Fig. 3C). This secondary effect, which leads to a change in the relationship between species abundance and pest effect across communities of different diversity, emerges only from a model such as this one in which the dynamics of infection are explicitly incorporated.

DISCUSSION

General considerations

Both simple and complex models indicate that in the presence of specialized, locally dispersing pests, LDD provides an advantage, even when it comes at considerable cost in fecundity or competitive ability. This advantage emerges whenever pests depress reproductive rates and disperse locally, as was seen in models run under a wide range of pest virulence, pest effect, host fecundity, etc. Given the ubiquity of such natural enemies (e.g., Packer and Clay 2000, HilleRisLambers et al. 2002), we can surmise from the low proportion of seeds dispersed long distances among terrestrial plants that there are severe constraints or costs associated with LDD. This idea is also supported by comparison with marine systems, where LDD is much easier to accomplish, and is also very common (Jablonski and Lutz 1983, Kinlan and Gaines 2003).

The costs and payoffs of LDD vary with the abundance of a species and its distribution. Species that are common everywhere will have less to gain from LDD, because their pests are likely to be similarly ubiquitous, and they will face equivalent competitors (conspecifics) in all sites. This effect is clearly seen in our simulation results. At the opposite extreme, we speculate that species that are very rare everywhere may also benefit less
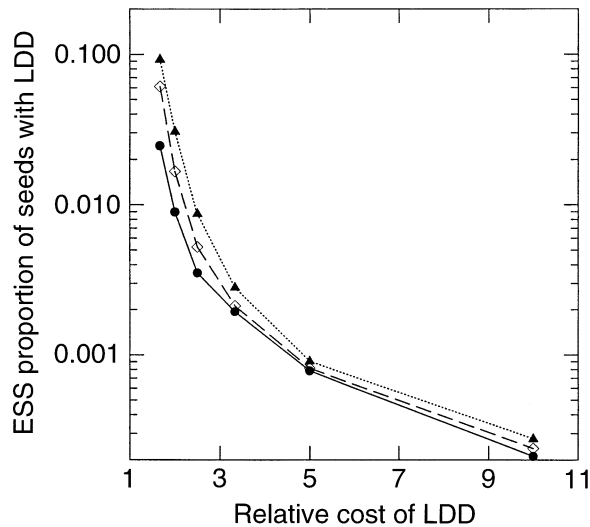
FIG. 2. As the relative cost of long-distance dispersers, $1/\alpha$, increases, the ESS proportion of seeds that are dispersed via LDD, d, decreases. The investment in LDD also increases as the number of species in the community increases from 1 (solid line, filled circles) to 4 (dashed line, open diamonds) to 6 (dotted line, filled triangles). The ESS dispersal distances were found for communities on a 100×100 lattice (with periodic boundary conditions), with short-distance dispersal $\sigma = 1$, long-distance dispersal $\lambda = 5$, pest dispersal $\beta = 2$, mortality rate $m = 1$, reproductive resources $K = 16$, virulence $v = 16$, and pest effect on fecundity $\gamma = 0.6$.

from LDD, because it will be easy to escape areas of high conspecific density even without it, and their pests are likely to be rare. As a result, we hypothesize that the benefits of LDD will be highest among species of intermediate and/or spatially variable abundance, where the probability of infestation differs the most between normally and distantly dispersed offspring.

Life history traits will also influence the relative benefits of LDD, and thus its prevalence. The ability to enter long periods of dormancy may potentially provide many of the same benefits as LDD, just as dispersal and dormancy provide alternative benefits more generally (Cohen and Levin 1991). In the case of pests in particular, dormancy too may allow organisms to increase the probability that their offspring will emerge in a relatively enemy-free environment. Thus, where dormancy is a viable strategy, we can expect lower frequencies of LDD. Species with high reproductive rates and thus faster population growth potential may also experience increased benefits of LDD, because they can expand further in the time before pests rediscover the population.

These life history patterns hold to varying degrees when selection for LDD is due to other factors. When disturbance regimes or other abiotic landscape dynamics create the necessary favorable patches far from established populations, dormancy that allows species to persist in such sites from one period of favorable conditions to the next will provide an alternative strategy

that can reduce selection for LDD. However, under conditions of range shifts, dormancy is highly unlikely to provide a viable alternative, unless range shifts are repeated and dormancy is very long-term. High reproductive rates will increase the potential benefits of LDD under both abiotic landscape dynamics and range shifts, just as they do with species-specific pests. Trends with abundance, however, are likely to differ.

Future directions

The question of the evolution of a complete dispersal strategy—incorporating normal and long-distance dispersal—is inherently a question that involves multiple scales and many aspects of an organism's life history and habitat. Future work should consider changes across scales of multiple factors, both biotic and abiotic, including advective flows of wind and water as well as the distribution and dynamics of competitors and pests (see Levin et al. 2001).

Any particular analytic approach to LDD will be of limited utility, so multiple approaches are useful. As in Keymer et al. (2000), it may be possible to represent multispecies community models as dynamic landscape models of individual species, that is, as models in which a single population interacts with a dynamic landscape of favorable and unfavorable patches. This approach is especially likely to be useful for abiotic landscape dynamics, where methods of geostatistics (Isaaks and Srivastava 1989) can be applied to generate landscapes with particular spatiotemporal habitat correlation (e.g., Hill and Caswell 1999). Similarly, recent work by Lewis (2000), Lewis and Pacala (2000), and Clark et al. (2001) provide analytical tools to understand the consequences of LDD for range expansion rates, tools which may also prove useful for understanding selection. Finally, insights may be gained by comparison with the parasitology literature, where models of selection on within-host expansion and between-host transmission provide an analogy to within-population growth and between-patch LDD.

Ultimately, however, progress in understanding the evolution of LDD is limited not so much by the available theoretical techniques as by the dearth of relevant data. Very little is known on how LDD trades off with other life history traits within populations, on levels of within-population variability in LDD, or on its heritability—all critical factors in building realistic models of dispersal evolution. Until such empirical data are in hand, models will be unable to inform explanations of the evolution of LDD in any particular system, and will continue to serve only to illustrate general patterns and principles.

Implications for ecology and conservation

LDD is disproportionately important for many ecological processes, including range expansion and responses to reserve placement (Caswell et al. 2003). In investigating the role of LDD in fundamental and ap-
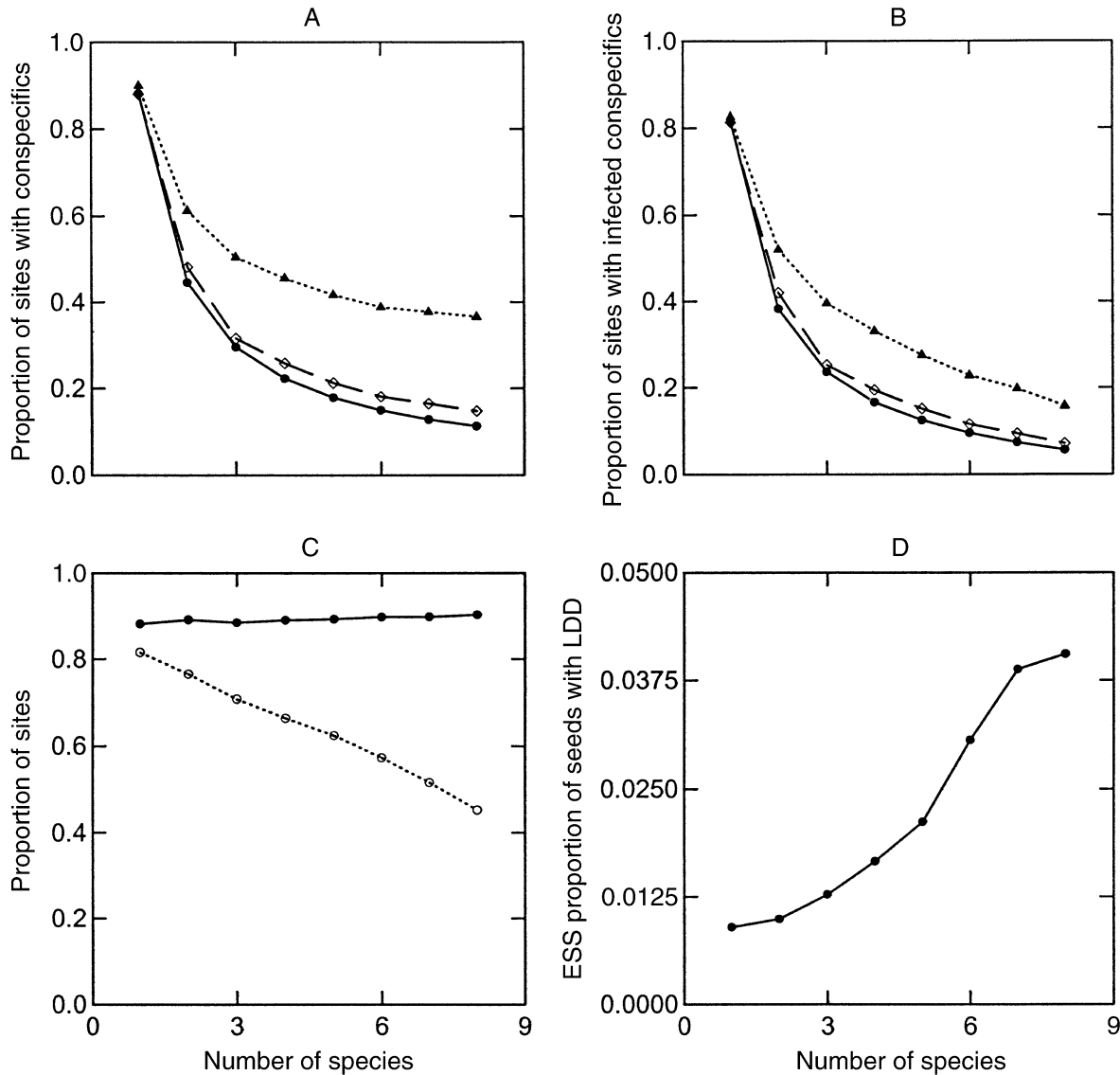
FIG. 3. The effect of species diversity on the proportion of occupied cells, the infestation rate, and the ESS investment in LDD. (A) As the number of species increases, the proportion of cells occupied by conspecifics decreases (solid line, filled circles), and concomitantly the proportion decreases for cells encountered by dispersing offspring, more so among long-distance dispersers (dashed line, open diamonds) than among short-distance dispersers (dotted line, filled triangles). (B) The proportion of individuals that are infested conspecifics decreases even more drastically (symbols as before). (C) Overall, the proportion of cells that are occupied increases slightly (solid line, filled circles), and the proportion of cells occupied by infested individuals of some species decreases (dotted line, open circles). (D) Thus, the ESS proportion of seeds dispersed via LDD, d, increases as the number of species increases. Results for communities on a 100×100 lattice (with periodic boundary conditions), with short-distance dispersal $\sigma = 1$, long-distance dispersal $\lambda = 5$, pest dispersal $\beta = 2$, mortality rate $m = 1$, reproductive resources $K = 16$, virulence $v = 16$, pest effect on fecundity $\gamma = 0.6$, and relative survival/cost of dispersers $\alpha = 0.5$.

plied ecological questions, it is important to consider not only the current capacity of a species for LDD, but also its likelihood of evolving a different rate of LDD. While physical constraints may limit the possible rates of LDD that can evolve, evolution within those constraints may be rapid where selection pressures exist and there is sufficient genetic variability (Peroni 1994, Cody and Overton 1996).

The potential for evolution of different levels of LDD may be especially important in understanding the spread of invasive species, the effects of habitat fragmentation, and responses to global climate change. For example, as favorable habitat becomes increasingly fragmented and isolated within an inhospitable matrix, selection against LDD because of reduced habitat availability may more than outweigh selection for LDD due

to range shifts, and result in slower range expansion than under past climate changes.

Last but not least, human influences are rapidly changing the costs and benefits of LDD, and thereby changing selection pressure on it. Humans have long been important LDD vectors, and the increasing global movement of people and their goods is in parallel increasing the opportunities for those individuals that can hitchhike with these vectors, and grow and reproduce in the environments in which they are then deposited. Understanding long-distance dispersal, and the characteristics that preadapt organisms for success in the environments humans are creating, may provide us with powerful insights for managing pests and invaders, and for conserving valued species.

LITERATURE CITED

Andow, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. Landscape Ecology **4**:177–188.

Armstrong, R. A. 1989. Competition, seed predation, and species coexistence. Journal of Theoretical Biology **141**: 191–195.

Bolker, B., and S. W. Pacala. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. Theoretical Population Biology **52**:179–197.

Bolker, B. M., and S. W. Pacala. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. American Naturalist **153**:575–602.

Bolker, B. M., S. W. Pacala, and S. A. Levin. 2000. Moment methods for ecological processes in continuous space. Pages 388–411 *in* U. Dieckmann, R. Law, and J. A. J. Metz, editors. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, UK.

Caswell, H., R. Lensink, and M. G. Neubert. 2003. Long-distance dispersal and invasion speed: applications to conservation. Ecology **84**:1968–1978.

Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. American Naturalist **152**:204–224.

Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. American Naturalist **157**:537–554.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in Southern Appalachian forests. Ecological Monographs **68**:213–235.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology **80**: 1475–1494.

Cody, M. L., and J. M. Overton. 1996. Short-term evolution of reduced dispersal in island plant populations. Journal of Ecology **84**:53–61.

Cohen, D., and S. A. Levin. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. Theoretical Population Biology **39**:63–99.

Comins, H. N., W. D. Hamilton, and R. M. May. 1980. Evolutionarily stable dispersal strategies. Journal of Theoretical Biology **82**:205–230.

Condit, R., et al. 2000. Spatial patterns in the distribution of tropical tree species. Science **288**:1414–1418.

Connell, J. H. 1971. On the roles of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 *in* P. J. den Boer and G. R. Gradwell, editors. Dynamics of populations. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeek, 1970. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Dalling, J. W. 1994. Vegetation colonization of landslides in the Blue Mountains, Jamaica. Biotropica **26**:392–399.

Durrett, R., and S. Levin. 1994. The importance of being discrete (and spatial). Theoretical Population Biology **46**: 363–394.

Ellner, S. P. 2001. Pair approximation for lattice models with multiple interaction scales. Journal of Theoretical Biology **210**:435–447.

Fragoso, J. M. V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. Journal of Ecology **85**:519–529.

Fragoso, J. M. V., K. M. Silvius, and J. Correa. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology **84**:xx–xx.

Fridriksson, S. 1975. Surtsey: evolution of life on a volcanic island. Butterworth, London, UK.

Guariguata, M. R. 1990. Landslide disturbance and forest regeneration in the Upper Luquillo Mountains of Puerto Rico. Journal of Ecology **78**:814–832.

Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. Nature **269**:578–581.

Hammond, D. S., and V. K. Brown. 1998. Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. Pages 51–78 *in* D. M. Newbery, H. H. T. Prins, and N. D. Brown, editors. Dynamics of tropical communities. Blackwell Science, Oxford, UK.

Harada, Y. 1999. Short- vs. long-range disperse: the evolutionarily stable allocation in a lattice- structured habitat. Journal of Theoretical Biology **201**:171–187.

Harms, K. E., S. J. Wright, O. Caldern, A. Hernndez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature **404**: 493–495.

Higgins, S. I., and M. L. Cain. 2002. Spatially realistic metapopulation models and the colonization–competition trade-off. Journal of Ecology **90**:616–626.

Higgins, S. I., R. Nathan, and M. L. Cain. 2003. Are long-distance dispersal events in plants usually caused by non-standard means of dispersal? Ecology **84**:1945–1956.

Hill, M. F., and H. Caswell. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. Ecology Letters **2**:121–127.

HilleRisLambers, J., J. S. Clark, and B. Beckage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature **417**:732–735.

Horn, H. S., R. Nathan, and S. R. Kaplan. 2001. Long-distance dispersal of tree seeds by wind. Ecological Research **16**:877–885.

Isaaks, E. H., and R. M. Srivastava. 1989. Applied geostatistics. Oxford University, New York, New York, USA.

Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biological Reviews **58**:21–89.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist **104**:501–528.

Keymer, J. E., P. A. Marquet, J. X. Velasco-Hernandez, and S. A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. American Naturalist **156**:478–494.

Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology **84**:2007–2020.

Legendre, P. 1993. Spatial autocorrelation—trouble or new paradigm. Ecology **74**:1659–1673.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio **80**:107–138.

Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pages 31–57 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. CAB International, Walingford, UK.

Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. Theoretical Population Biology **26**:165–191.

Levin, S. A., J. Dushoff, and J. E. Keymer. 2001. Community assembly and the emergence of ecosystem pattern. Scientia Marina **65**:171–179.

Levin, S. A., and H. C. Muller-Landau. 2000*a*. The emergence of diversity in plant communities. Comptes Rendus de L'Académie des Sciences, Sciences de la Vie **323**:129–139.

Levin, S. A., and H. C. Muller-Landau. 2000*b*. The evolution of dispersal and seed size in plant communities. Evolutionary Ecology Research **2**:409–435.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Lewis, M. A. 2000. Spread rate for a nonlinear stochastic invasion. Journal of Mathematical Biology **41**:430–454.

Lewis, M. A., and S. Pacala. 2000. Modeling and analysis of stochastic invasion processes. Journal of Mathematical Biology **41**:387–429.

Nathan, R., G. G. Katul, H. S. Horn, S. M. Thomas, R. Oren, R. Avissar, S. W. Pacala, and S. A. Levin. 2002. Mechanisms of long-distance dispersal of seeds by wind. Nature **418**:409–413.

Nathan, R., G. Perry, J. T. Cronin, A. E. Strand, and M. L. Cain. *In press.* Methods for estimating long-distance dispersal. Oikos.

Nathan, R., U. N. Safriel, and I. Noy-Meir. 2001. Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. Ecology **82**:374–388.

Packer, A., and K. Clay. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature **404**:278–281.

Palmer, M. W. 2002. Scale detection using semivariograms and autocorrelograms. Pages 129–144 *in* S. E. Gergel and M. G. Turner, editors. Learning landscape ecology: a practical guide to concepts and techniques. Springer-Verlag, New York, New York, USA.

Peroni, P. A. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. American Journal of Botany **81**:1428–1434.

Ronce, O., I. Olivieri, J. Clobert, and E. Danchin. 2001. Perspectives on the study of dispersal evolution. Pages 341–357 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford, UK.

Tufto, J., S. Engen, and K. Hindar. 1997. Stochastic dispersal processes in plant populations. Theoretical Population Biology **52**:16–26.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Massachusetts, USA.

Whitmore, T. C. 1990. An introduction to tropical rain forests. Clarendon Press, Oxford, UK.

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