THE ECOLOGY AND EVOLUTION OF SEED DISPERSAL: A Theoretical Perspective

Simon A. Levin

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544; email: slevin@princeton.edu

*Helene C. Muller-Landau

National Center for Ecological Analysis and Synthesis, 735 State Street, Santa Barbara, California 93101; email: hmuller@nceas.ucsb.edu

*Ran Nathan

Department of Life Sciences, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel; email: rnathan@bgumail.bgu.ac.il

*Jérôme Chave

Evolution et Diversité Biologique, CNRS, Université Paul Sabatier, bâtiment IVR3, F-31062 Toulouse, France; email: chave@cict.fr

■ **Abstract**   Models of seed dispersal—a key process in plant spatial dynamics—have played a fundamental role in representing dispersal patterns, investigating dispersal processes, elucidating the consequences of dispersal for populations and communities, and explaining dispersal evolution. Mechanistic models of seed dispersal have explained seed dispersion patterns expected under different conditions, and illuminated the circumstances that lead to long-distance dispersal in particular. Phenomenological models have allowed us to describe dispersal pattern and can be incorporated into models of the implications of dispersal. Perhaps most notably, population and community models have shown that not only mean dispersal distances but also the entire distribution of dispersal distances are critical to range expansion rates, recruitment patterns, genetic structure, metapopulation dynamics, and ultimately community diversity at different scales. Here, we review these developments, and provide suggestions for further research.

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*Order of the last three authors was determined by a random-number generator.

INTRODUCTION

Dispersal is defined as the unidirectional movement of an organism away from its place of birth. In sedentary organisms such as all plants and some animals, dispersal is mostly confined to a short early stage of the life cycle. In higher plants, individuals move in space mostly as seeds. Many plant species can also move through vegetative growth, but this kind of movement is not as common and typically induces relatively minor spatial change. Although nonvegetative dispersal units can be diverse and can be more appropriately described by more specific botanical terms (see van der Pijl 1982), here we use the term seed dispersal as a general expression for the dispersal of the reproductive unit of a plant.

To understand dispersal, we need to measure its spatial patterns, to explore the mechanisms that generate them, and to examine their consequences. We thus start with an overview of the empirical evidence for patterns and processes of dispersal and then discuss models describing these. The theoretical implications and explanations of dispersal are discussed in subsequent sections, starting with population spread, moving briefly through other aspects of population and community dynamics, to the evolution of dispersal. We end with a synthesis of main conclusions and directions for future research.

SEED DISPERSAL PATTERNS AND PROCESSES

Dispersal Mechanisms

The great variety of dispersal-aiding morphologies attracted the attention of naturalists as early as Aristotle (384–322 BC) and Theophrastus (371–286 BC) (Thanos 1994). For a long time, the study of seed dispersal was either anecdotal or speculative, with attempts to explain the selective value of each and every detail of a dispersal unit (Ridley 1930, van der Pijl 1982). The most commonly used classification system of dispersal syndromes is based on the agent or vector of dispersal, typically inferred from seed morphology. The principal agents of dispersal are either abiotic (wind and water) or biotic (animals and the plant itself), and the dispersal syndromes are termed, respectively, anemochory, hydrochory, zoochory, and autochory (van der Pijl 1982).

The vector-based method, and similarly any other classification of dispersal morphologies, can be refined to account for more subtle differences in the morphology of the dispersal unit, its potential dispersers, and adaptive features (van der Pijl 1982). However, as the level of detail in classification increases, the promise of theoretical generalization recedes. Furthermore, general classification methods tend to miss, and even misconstrue, important characteristics of the seed dispersal process. A key point is that dispersal is seldom mediated by a single dispersal agent and is not confined to the primary movement of seeds from the plant to the surface (Phase I dispersal) (Chambers & MacMahon 1994, Watkinson 1978). Rather, it also entails subsequent movements (Phase II dispersal) that can be mediated by other dispersal

agents. The common practice of using the morphological dispersal syndrome to distinguish short- from long-distance dispersal is therefore questionable. In fact, the actual processes responsible for long-distance dispersal (LDD) are only loosely correlated with those interpreted from seed morphology (Higgins et al. 2003).

A second major limitation of traditional classification schemes stems from the ambiguous relationships between the morphological dispersal syndrome and the contribution of the dispersal process to plant fitness (disperser effectiveness sensu Schupp 1993). Dispersal agents, even within restrictively classified groups, differ markedly in their effectiveness both quantitatively (numbers and distances of dispersed seeds) and qualitatively (treatment and deposition of seeds) (Schupp 1993). An extreme example for the importance of the quality of the dispersal agents is directed dispersal, or the disproportionate arrival of seeds to favored establishment sites in which survival is relatively high (Howe & Smallwood 1982). Wenny (2001) provides many examples and a thorough discussion of this phenomenon, which seems to be more common than previously believed.

Spatial Patterns

Dispersal is encapsulated in the seed dispersion pattern (Nathan & Muller-Landau 2000), most commonly measured in a two-dimensional setting, though it can also be measured in one (e.g., Thébaud & Debussche 1991) or three (Nathan et al. 2002b, Tackenberg 2003) spatial dimensions.

Seed dispersion patterns depend on adult dispersion patterns, their geometry and fecundity, and on the variation in the direction and distance of dispersal events. As such, they can be very complex, hence difficult to quantify. The most common practice utilizes a ground network of seed traps (Greene & Calogeropoulos 2002); direct observations (e.g., Watkinson 1978) and genetic analyses (e.g., Godoy & Jordano 2001) are used much less frequently. Dispersal studies usually cover an area where most, but not all, dispersal occurs. Quantifying seed dispersion patterns at increasingly large scales is exceedingly more difficult because more uncertainty is associated not only with the fate of rare events but even with the identity of the mechanisms operating at these scales (Higgins et al. 2003). The seed trap method soon becomes unfeasible because of the extremely huge sampling area required to detect rare LDD events (Greene & Calogeropoulos 2002). Thus, the quantification of LDD is extremely challenging (Cain et al. 2000, Nathan et al. 2003). Unconventional methods that focus on individual movements and methods that couple modeling and empirical tools are the most promising ways to estimate LDD; see Greene & Calogeropoulos (2002), Nathan et al. (2003), Wang & Smith (2002) for recent reviews.

Seed dispersion patterns reflect the totality of all individual dispersal events in a population, whereas the dispersal curve summarizes the distribution of distances traveled by seeds. Dispersal curves can in principle form any kind of distribution; cases of directed dispersal discussed above, for example, may generate complex multimodal dispersal curves (Schupp et al. 2002). The majority of empirical seed

dispersal data, however, fit a relatively simple, unimodal leptokurtic distribution, characterized by a peak at or close to the source, followed by a rapid decline and a long, relatively "fat" tail (Kot et al. 1996, Willson 1993). In the following section, we define relevant terms and discuss the mathematics of dispersal curves.

Many studies evaluate dispersal based on postdispersal (seedlings, young plants, or even adults) dispersion patterns. Although this kind of data can be collected in a cost-effective manner, it may not provide a reliable way to reconstruct dispersal. This is because data interpretation should address uncertainties involved not only with dispersal, but also with predispersal (e.g., pollination, seed production, and predispersal seed loss), and postdispersal (e.g., seed predation, germination, and seedling competition) processes (Nathan & Muller-Landau 2000, Schupp & Fuentes 1995). Such coupling is especially challenging for large-scale studies, with virtually no information available on establishment processes that follow LDD (Nathan 2001), despite their crucial importance for plant population dynamics.

THEORETICAL MODELS OF SEED DISPERSAL

Phenomenological Models

Ultimately, we argue that understanding of dispersal requires the development of mechanistic models that can explain observed patterns. We begin, however, with a characterization of those patterns through purely phenomenological models.

SEED DISPERSAL CURVES   Data on dispersal can be represented either by the frequency distribution of dispersal distances or by the two-dimensional distance function of postdispersal seed densities. The two types have been coined, respectively, distance distribution and dispersal kernel (Nathan & Muller-Landau 2000), or one- and two-dimensional probability density functions (Cousens & Rawlinson 2001). Mathematically, a dispersal kernel is expressed in Cartesian coordinates by $P(x, y)dxdy$, the probability that a seed released at point $(0, 0)$ lands in a square of size $dxdy$ centered at the deposition site (x, y). Given the symmetries in this problem, it is easier to deal with polar coordinates r, θ, where $r = \sqrt{x^2 + y^2}$ is the distance between the release point and the deposition site, and θ is the radial angle. If dispersal is isotropic, the probability of landing in an annulus of width dr at a distance r from the point source is $2\pi r P(r)dr$. In certain cases, dispersal is directed along one preferential direction, and it can be suitably modeled as a one-dimensional process. Then, $P(x)dx$ is the probability that a seed starting at point 0 lands in the segment of length dx centered at x. It is assumed throughout this section that one-dimensional kernels are functions of x, while two-dimensional kernels are functions of r. The *seed shadow* $N(x)$ is the product of the dispersal kernel P and the total number of seeds dispersed Φ.

Dispersal curves can be estimated from seed dispersion patterns by taking into account the location, geometry, and fecundity of adults, and the directionality of the dispersal process, though the latter is usually ignored. A general problem with

such estimation is the identification of the specific source location of dispersed seeds. This has led researchers to select isolated individuals so that the seed source location is not ambiguous (e.g., Lamont 1985). However, more generally, adult plants tend to form conspecific aggregations; hence, seed shadows of neighboring individuals typically overlap. Methods for resolving the overlapping seed shadow problem are discussed in Clark et al. (1998b, 1999), Nathan & Muller-Landau (2000), and Ribbens et al. (1994).

Traditionally, three functional forms for the distance distribution were commonly fitted to dispersal data: the Gaussian, the negative exponential, and the inverse power law. The Gaussian distribution is well defined but does not fit the leptokurtic distributions that are commonly observed. The negative exponential, probably the most commonly used functional form, has a fatter tail, but not fat enough to accommodate many LDD data. The inverse power law has a fat tail, but $P(r) = a/r^\beta$ goes to infinity as r goes to zero (if $\beta > 0$); hence only functions such as $P(r) = a/(1 + br)^\beta$ can be used as general forms for dispersal kernels. A general parametric formulation encompassing all these models is

$$P(r) = \frac{a}{r^\beta} \exp(-br^\alpha) = a \exp(-br^\alpha - \beta \ln(r)), \tag{1}$$

where a, b, α, and β are parameters (Turchin 1998, p. 200). Recent studies have proposed fat-tailed distributions such as the (two-dimensional Student t) $2Dt$ (Clark et al. 1999)

$$P(r) = a(1 + br^2)^{-\alpha}. \tag{2}$$

For $\alpha = 1$, this is the Cauchy distribution (Shaw 1995). These dispersal kernels are strongly leptokurtic, with a disproportionately large fraction of the seeds dispersed far.

Short- and long-distance dispersal can be associated with different dispersal mechanisms (see Seed Dispersal Patterns and Processes above); hence the overall distribution of dispersal distances in a population may be best represented by stratified modeling, i.e., mixing several dispersal kernels such as two exponential distributions (Higgins & Cain 2002).

MOTIVATION OF MODEL FORMS   Phenomenological models are chosen mainly—if not entirely—on their ability to fit the data. However, particular modeling forms can also be justified by general assumptions about the dispersal process. The simplest example rests on a homogeneous deposition model, which implies an exponential dispersal kernel. In one space dimension, assume that a fraction ρ of the dispersed seeds that have not yet settled are deposited between x and $x + dx$, while the remaining fraction are dispersed further. This yields a differential equation for $P(x)$, $dP(x)/dx = -\rho P(x)$, whose solution on the half-line $x \geq 0$ is the exponential

$$P(x) = \rho \exp(-\rho x). \tag{3}$$

with mean dispersal distance L equal to $1/\rho$.

A simple generalization of the decay model introduces a distance-dependent decay rate, such that (in two dimensions) at point r, a seed lands at rate $\rho(r) \sim r^{\alpha-2}$. In other words, the deposition rate decreases with distance from the release point if $\alpha < 1$, and it increases with the distance from the release point if $\alpha > 1$. This produces the distribution

$$P(r) = a \exp(-br^{\alpha}), \quad r > 0. \tag{4}$$

This corresponds to Equation 1 for $\beta = 0$ and has been suggested by many authors (Clark et al. 1998b, Ribbens et al. 1994, Taylor 1978, Turchin 1998) as a practical generalization of the exponential and Gaussian models. The particular form of the decay rate could be interpreted as an intrinsic property of the disperser: the smaller the parameter α, the fatter the tail of the distribution. This could correspond, for example, to changes in the behavior of an animal disperser, which deposits more seeds near parent plants than far from them (even corrected for the area effect).

Mechanistic Models

Beyond simply justifying particular forms for phenomenological models, truly mechanistic models of seed dispersal can predict exact seed distributions (including parameter values of dispersal curves) from characteristics of the dispersal process. Mechanistic models of seed dispersal by wind have a long history, building upon available theory on wind advection. Models of seed dispersal by animals are less well developed in large part because such models require quantification of detailed behavioral information.

MODELS OF SEED DISPERSAL BY WIND   Modeling the movement of seeds dispersed by wind is analogous to modeling the movement of pollen, fungal spores, particulate pollution, etc.; thus the methodology from other fields, especially fluid dynamics, can be applied directly. One relevant set of models are plume models, specifically the tilted Gaussian plume model developed by Okubo & Levin (1989) and related work by Greene & Johnson (1989).

The tilted Gaussian plume model incorporates the joint influences of wind advection and gravity on seed movement (Okubo & Levin 1989). Advection is characterized by the horizontal velocity u (in one dimension), and seeds fall at a terminal velocity V_t that reflects the balance between gravity and friction (Greene & Johnson 1989). Seeds are released from a point of height H, disperse under the influences of diffusion and advection, and thus follow wind movement like a plume. If seed movement were entirely deterministic, then it would be determined entirely by wind speed, the height of release, and terminal velocity (Nathan et al. 2001 and references therein):

$$x = Hu/V_t. \tag{5}$$

The dispersal kernel thus peaks at x. This case ignores vertical, latitudinal, and longitudinal variation in wind speed. Of course, in reality, stochastic effects due to

fluctuations in wind speed lead to much greater variation in dispersal distances and cause the dispersal kernel to widen. Pasquill & Smith (1983) incorporated some of this variation by considering not only advection by wind along direction x, but also diffusion along the y and z axes (respectively, cross-wind and vertical directions). They were interested in the final surface distribution of light particles—particles for which the influence of gravity could be ignored (see Okubo et al. 2001a for a recent review).

Okubo & Levin (1989) modified this example to include the influence of gravity, which becomes important for heavier particles and seeds. To take account of nonzero terminal velocity, V_t, they replaced the height term H by the expected height at distance x, that is $H - V_t x/u$. They derived a cross-wind integrated distribution that corresponds to the solution of the deterministic model mentioned above when the variance in vertical wind speed σ_w^2 goes to zero. Okubo & Levin (1989) further assumed that $t = x/u$ because the seeds are displaced at constant velocity u along the x axis. Thus, the tilted Gaussian plume model takes the form

$$P(x) = \frac{V_t}{\sqrt{2\pi}u\sigma_w} \exp\left(-\frac{(H - V_t x/u)^2}{2\sigma_w^2}\right). \tag{6}$$

This assumes that the parameters are constant in time, uniform in space, and do not vary from one seed to another. However, in reality, such variability is substantial and has important consequences for dispersal. For example, the shape of a wind-dispersal kernel will be very different if horizontal wind speed is assumed constant or to vary like Brownian motion with drift. In this example, if the wind speed varies around its mean much faster than the duration of the seed's flight, then standard tools from the theory of Brownian motion can be invoked (see below). Greene & Johnson (1989) suggested a simple generalization of the ballistic wind dispersal model (Equation 5) in which different seeds experience different wind speeds. Further, they suggested the lognormal distribution as an empirical fit to the distribution of wind speeds. From that, they deduced the one-dimensional dispersal kernel

$$P(x) = \frac{1}{x\sqrt{2\pi}\sigma_u} \exp\left(-\frac{(\ln(V_t x/u_g H))^2}{2\sigma_u^2}\right). \tag{7}$$

Here, u_g and σ_u^2 denote, respectively, the geometric mean and the variance of horizontal wind velocity u.

Spatial variation in wind speed and direction is another important issue. For example, horizontal wind speed is usually a function of height that increases roughly exponentially within a plant canopy and logarithmically above it. The influence of this vertical wind profile is discussed in Nathan et al. (2002a) in the context of the seed dispersal simulator WINDISPER (Nathan et al. 2001). WINDISPER assumes a lognormal distribution of horizontal wind speeds u, and Gaussian distributions of vertical wind speeds w (truncated to exclude net upward movements), height of release H, and seed terminal velocity V_t. For either a logarithmic (for trees in open landscapes) or an exponential (for trees within a dense forest) wind profile,

there is an analytical solution for the distance traveled by an individual seed under any combination of parameter values (Nathan et al. 2002a).

The above models provide insights into dispersal processes in various ways. Increasing model complexity and relaxing critical structural assumptions expose different layers of dispersal processes. Okubo & Levin (1989) showed that the horizontal wind speed, seed terminal velocity, and release height are the key determinants of short-distance dispersal; and there is no need to increase model complexity if the goal is to predict the local dispersal of most seeds. Nathan et al. (2001) showed that, empirically, these factors vary considerably in their relative effects. The variation in wind speed components explained most (86%) of the variation in dispersal distances of *Pinus halepensis* seeds at their study site, whereas variation in the two biological parameters (V_t and H) together explained much less (9%). Wind dispersal models should therefore include accurate estimates of wind conditions. Moreover, seeds of isolated trees are expected to travel much farther than identical seeds released from identical trees within a dense forest. These differences have important implications for tree dynamics at small and large scales (Nathan et al. 2002a).

Whereas all the above models closely match the observed dispersal data at the local scale, their relevance to LDD has been questioned (Bullock & Clarke 2000, Greene & Johnson 1995, Nathan et al. 2002a). This is because LDD of tree seeds, for example, critically depends on the fine details of turbulence structure within the forest. Nathan et al. (2002b) applied a coupled Eulerian-Lagrangian approach to model the three-dimensional flight trajectories of wind-dispersed tree seeds within and above the forest canopy. Their approach resolves the effects of canopy turbulence and explicitly incorporates excursions whose timescales are on the order of seconds. This model was parameterized from high-frequency wind measurement data for a site at Duke Forest and tested against dispersal data collected along a 45-m tower. Predictions closely matched observed data for five wind-dispersed tree species. This study revealed the crucial role for LDD of seed uplifting, by turbulent wind updrafts that result in temporally and spatially autocorrelated deviations in vertical wind velocity. Tackenberg (2003), using a stochastic Lagrangian simulator of seed flight, fed with observed sequences of high-frequency wind measurements, demonstrated that uplifting was also critical for LDD of grass seeds and concluded that LDD in grasslands is promoted by thermal updrafts.

Variation in horizontal and vertical wind speeds can be incorporated along with most of the features of the above models into a unifying random walk model of wind dispersal. It has all the same properties of WINDISPER apart from accounting for variable vertical wind profile yet is also analytically tractable (Portnoy & Willson 1993, Tufto et al. 1997, Turchin 1998). To compute the dispersal kernel in the one-dimensional case, assume that the seeds perform a biased Brownian motion vertically starting from a release point at height H. As before, seeds are dispersed by wind. Assume a downwind dispersal velocity u with variance (per unit time) in distance traveled σ_u^2 and vertical mean wind speed w with variance σ_w^2. Using Brownian motion theory (Karlin & Taylor 1981), one can find the distribution of deposition times $P(t)$:

$$\hat{P}(t) = \sqrt{\frac{H^2}{2\pi\sigma_w^2 t^3}} \exp\left(-\frac{1}{2\sigma_w^2 t}(H - wt)^2\right). \tag{8}$$

The dispersal kernel is obtained from the distribution of deposition times by the equation

$$P(x) = \int_{t=0}^{\infty} \hat{P}(t)p(x, t)\, dt, \tag{9}$$

(see also Tufto et al. 1997, Equation 12), which yields

$$P(x) = \frac{H}{\pi\sigma_u\sigma_w}\exp\left(\frac{xu}{\sigma_u^2} + \frac{Hw}{\sigma_w^2}\right)\sqrt{\frac{u^2\sigma_w^2 + w^2\sigma_u^2}{x^2\sigma_w^2 + H^2\sigma_u^2}}$$

$$\times K_1\left(\left(\frac{x^2}{\sigma_u^2} + \frac{H^2}{\sigma_w^2}\right)^{1/2}\left(\frac{u^2}{\sigma_u^2} + \frac{w^2}{\sigma_w^2}\right)^{1/2}\right), \tag{10}$$

where $K_1(x)$ is the modified Bessel function of the second kind (Gradshteyn & Ryzhik 2000). Yamamura (2002) showed that if one assumes that the distribution of deposition times (Equation 8) is a gamma distribution, the dispersal kernel is also a Bessel function. This model has many different limiting behaviors as the parameters are varied. If σ_u^2 goes to zero, the deterministic formula is recovered. To analyze this model further, introduce the nondimensional variables: $\rho = uH/\sigma_u^2$, $\eta = w\sigma_u^2/u\sigma_w^2$, $\varphi = w/u$, $X = x/H$, and $X_c = \rho^{-1}(\sqrt{1 + \eta\varphi} - 1)^{-1}$. For large distances, the dispersal kernel is $P(X) \sim X^{-3/2}\exp(-X/X_c)$. When the distance X_c gets very large, then $P(X) \sim X^{-3/2}$.

Portnoy & Willson (1993) developed the more difficult case of a two-dimensional, radially symmetric model with a horizontal drift velocity u and a horizontal noise term described by the variance σ_u^2. The two-dimensional model leads essentially to the same results as the one-dimensional model. With nondimensional parameterization defined by ρ, η, and φ as above, and $R = r/H$, their result is

$$P(R) = I_0(\rho R)\frac{\rho R}{\sqrt{R^2\eta + \varphi}}\left(\frac{1}{R^2\rho + \rho\eta\varphi^{-1}} + \sqrt{\frac{1 + \eta\varphi}{R^2 + \eta\varphi^{-1}}}\right)$$

$$\times \exp\left(\rho\eta - \rho\sqrt{(1 + \eta\varphi\eta)(R^2 + \eta\varphi^{-1})}\right), \tag{11}$$

where $I_0(a)$ is the modified Bessel function of the first kind, which behaves as $I_0(a) \approx (2\pi a)^{-1/2}\exp(a)$ (to within 5% for $a > 4$). We can also develop this expression for large values of R, and the dominant behavior is similar to that in the one-dimensional case.

MODELS OF SEED DISPERSAL BY ANIMALS   Skellam (1951) demonstrated that wind dispersal was inadequate for explaining observed rates of advance of

invading species, and that LDD in some cases must have involved animal vectors. Recent studies (Vellend et al. 2003) reinforce this observation. Typical models of seed dispersal by animals extend the approach described to combine a component describing animal movement and a component describing time until seed deposition. Such parameters can be estimated from statistical distributions of observed animal movements and gut retention times (or handling times, etc.) (Murray 1988). More mechanistic approaches seek to understand the rules that govern animal movements and feeding behaviors (Anderson 1982, Kareiva 1990, Neubert et al. 1995).

A very simple theoretical model of dispersal by animals makes the assumptions that (*a*) animals move randomly in space, and (*b*) deposit seeds at a constant rate during their movement. Again, the probability of displacement by a distance *r* of an animal *t* time units after it has picked up a seed follows a Gaussian distribution. The distribution of deposition times is given by an exponential function $P(t) = \rho \exp(-\rho t)$, ρ being the deposition rate as above. The resulting seed dispersal kernel, again, is obtained through Equation 9 (Broadbent & Kendall 1953, Turchin & Thoeny 1993):

$$P(r) = \frac{\rho}{2\pi D} K_0 \left(r \sqrt{\frac{\rho}{D}} \right), \tag{12}$$

where *D* is the diffusion rate for the dispersers (the animals). More complicated models could be constructed to include effects of landscape structure and variable deposition rates.

Model Assessment

A critical step in the development of models is the assessment of reliability of their assumptions and predictions. Model assessment should include evaluation of four components: structural assumptions, parameter estimates, and primary and secondary predictions (Bart 1995). In phenomenological models, structural assumptions involve, for example, the type of function and whether or not to mix two functions. In mechanistic models, structural assumptions involve, for example, whether seeds are dispersed under exponential or logarithmic wind profiles and whether seeds carried by animals are deposited at random or with some bias. Parameter estimation is crucial in both phenomenological and mechanistic approaches. Yet, good estimates for the parameters of a model are necessary but not sufficient for a good model: Ultimately, model predictions need to be compared with data. The primary predictions of dispersal models are the dispersal distances themselves, or more commonly, the predicted postdispersal seed densities or the proportions of seeds arriving at a seed trap location. Because parameters of mechanistic models are evaluated independently of the dispersal data, any dispersal data could serve to test primary predictions. Phenomenological models, however, necessitate dispersal data for their calibration; but their primary predictions can be tested against a random subset of the data not used for calibration (i.e., cross-validation).

Secondary predictions involve indirect features of the system, such as the shape of the dispersal kernel predicted by mechanistic models.

IMPLICATIONS OF DISPERSAL FOR RATES OF SPECIES ADVANCE

One of the primary motivations for studying dispersal is to understand the rates of spread of species (e.g., Okubo & Levin 2001, Turchin 1998). Models linking dispersal and rates of advance have a long history in ecology and evolutionary biology. In this section, we review classical models of species spread, recent extensions of these models, and empirical tests of the theory.

Classical Diffusion Models

One of the earliest applications of models of dispersal in ecology and evolutionary biology was to the spread of advantageous alleles. Fisher (1937) first considered the problem in genetics, writing the equation

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial x^2} + r P (1 - P) \tag{13}$$

for the frequency P of the favored allele entering a new (linear) habitat. Here D is the diffusion coefficient, and r is the intrinsic rate of natural increase. The assumptions underlying this equation are that individuals move via random walk, in small steps, with no directional bias, and that population growth is logistic (Okubo & Levin 2001). In reality, one should write coupled equations for genotypes, since it is individuals rather than genes that move, and derive Equation 13 from these equations (Aronson & Weinberger 1978), but the reduced model (13) is a good approximation.

Based on Equation 13, Fisher reasoned that the eventual (asymptotic) rate of spread of the allele would be

$$2\sqrt{Dr}. \tag{14}$$

Kolmogorov et al. (1937) established this result formally, for general growth functions $f(P)$ (see Okubo et al. 2001b).

In an ecological setting, the seminal paper extending these results was that of Skellam (1951), who was interested in the rates of advance of invading species. Skellam embedded the problem in a broader framework that considered more complicated dispersal kernels in multiple spatial dimensions. He also derived the equivalent of Equation 13, for the population density P.

The nonlinear term can be ignored in the determination of asymptotic speeds, because densities are low enough at the front that growth is essentially exponential. For more general growth functions, this is also true, but nonlinearities can be important early in spread if there are multiple possible equilibria, resulting in the equation

$$\frac{\partial P}{\partial t} = D\frac{\partial^2 P}{\partial x^2} + rP. \tag{15}$$

No real front forms in this case because population size is growing (or declining) exponentially. Skellam addressed this by assuming that there is a cut-off level P* below which either the spreading population would not be detected, or population density would be too low to sustain spread, and defined the position of the front as the value(s) of x where population density equals that threshold. By symmetry, even in one dimension there will be two such points, and their locations will advance asymptotically at the speed given in Equation 14. Equation 13 assumes no bias in movement, such as might arise owing to advective forces like winds or water flow, or simply tactic movement in the case of animal or microbial dispersal. For constant advection, the speed is given by Equation 14 relative to a frame of reference moving with the advection.

In two or three spatial dimensions, the essential problem and conclusions are the same, at least in homogeneous habitats. The basic equation, in two dimensions, without advection, is given by

$$\frac{\partial P}{\partial t} = D_x\frac{\partial^2 P}{\partial x^2} + D_y\frac{\partial^2 P}{\partial y^2} + f(P). \tag{16}$$

If diffusion is isotropic, then a point release will eventually spread in circular fronts, at the speed given by Equation 14; nonisotropic diffusion will lead to elliptical patterns with different rates of spread in different directions. Without density dependence, arbitrary initial distributions can be treated as superpositions of point releases, yielding the same result; with density dependence, the picture becomes a bit more complicated, and the details again must depend on the specific form.

Empirical Tests of the Theory

Everything discussed so far relates to the general reaction-diffusion model (e.g., Equation 13) and its extensions. How good are the assumptions underlying this model, and how well do the predictions agree with observations? In general, the assumption of random walk is a convenience, representing ignorance of local stochastic factors that determine actual movements. The convenience can be justified, however, if in some statistical sense, the observed patterns do not differ from the predictions of the theory.

Skellam examined a number of empirical examples—in particular, the oaks in England following the recession of the glaciers, and the muskrats introduced into Bohemia by an incautious Czech prince. Although much of his focus was in interpreting patterns and mechanisms, Skellam did conclude that the spread of oaks was too rapid to be explained by simple diffusion, confirming the calculations of Clement Reid (Clark et al. 1998a, Reid 1899, Turchin 1998). Rates of Holocene postglacial spread of many temperate tree species were estimated by Davis (1976), Huntley & Birks (1983), Delcourt & Delcourt (1987), and MacDonald (1993),

among others. The pollen record shows an individualistic response of tree species, with average rates of spread on the order of 200 m/yr. Reid's paradox (Reid 1899, Skellam 1951) highlights the discrepancy between these estimated high spread rates, and the observed dispersal distances of nearly all species, which typically average no more than a few tens of meters. We return to this in Tails and Rates of Advance of Populations below.

Nonlocal Transport, and Non-Gaussian Kernels

Equation 13 describes a diffusion approximation for a stochastic process, provided redistribution is the result of a large number of small steps. Alternatively, redistribution can be treated as a discrete event, with consequences that can be encapsulated in a single "kernel function." The approach is especially appropriate for situations where growth and dispersal occur sequentially rather than simultaneously, as for annual plants. Skellam (1951) developed the basic approach, in which a dispersal kernel represented the probability distribution for the terminal point of a seed released at a given position. Based on this, one can develop models of population redistribution while taking into account the details of influences on individuals. Mollison (1977) showed how consideration of redistribution kernels with nonlocal transport could change fundamentally the predictions about spread.

In recent years, a number of investigators have built on the framework developed by Skellam & Mollison. Notable among these have been Weinberger (1978), Aronson (1985), Fife & McLeod (1977), van den Bosch et al. (1988), van den Bosch (1990), Kot & Schaffer (1986), Kot et al. (1996), and Neubert et al. (1995, 2000). The simplest model follows annual populations that are sedentary during most of their lives, such as plants or intertidal sessile invertebrates, and that disperse their propagules at the end of a season. Thus the number of propagules n satisfies the equation

$$n_{t+1}(x) = \int_{-\infty}^{\infty} \phi(x, y) f(n_t(y)) \, dy, \tag{17}$$

where the kernel $\phi(x, y)$ is the probability density function for the endpoint x of a dispersal event originating at y. Often, but not necessarily, $\phi = k(x - y)$, a function of $(x - y)$ alone. In this case, the probability of dispersing a given distance is independent of the point of origin (Neubert et al. 2000). The second term in the integral represents growth between dispersal events, or more precisely the number of propagules per adult.

The advantage of Equation 17 is that k need not take the Gaussian form, consistent with diffusive spread, and hence can capture LDD events and multimodal dispersal. Numerous examples in the plant literature illustrate the inadequacy of the Gaussian dispersal kernel, and the associated diffusion approximations (Cain et al. 1998; Davis 1976, 1987). Weinberger (1978) showed that, under reasonable conditions, the solutions to Equation 17 again converge to traveling waves, with speed

$$c = \min_{s \in S}\{(\ln(f'0)m(s))/S\}. \tag{18}$$

Here, $f'(0)$ is the growth rate of the population when it is rare, and

$$m(s) = \int\limits_{-\infty}^{\infty} k(x)e^{sx}\,dx \tag{19}$$

is the moment-generating function for the kernel (Kot 1992; Kot et al. 1996; Neubert & Caswell 2000; Neubert et al. 2000; Weinberger 1978, 1982). S is the set of positive s for which the integral in Equation 19 converges (Neubert et al. 2000). Furthermore, to assure convergence to a wave front, one further assumes

$$0 \le f(n) \le nf'(0). \tag{20}$$

More generally one can consider delays owing to dispersal, overlapping generations, multiple dimensions, and other complications; but these are beyond the scope of this review. Equation 17 provides a natural bridge from explicit dispersal kernels to the problem of spread.

Tails and Rates of Advance of Populations

Whereas most seeds fall near the parent plant, and most larvae disperse short distances, it is the tail of the dispersal distribution that is of central importance in the spread of species (Mollison 1977, Skellam 1951, Turchin 1998). Both Skellam and Mollison emphasized the inadequacy of the diffusion approximation when long-distance transport is important. Reid's paradox (see Empirical Tests of the Theory, above) that rates of spread in the paleontological record far exceed that expected based on observed mean dispersal distances can be resolved if the tails of the distribution are sufficiently fat (Clark 1998, Clark et al. 1998a, Higgins & Richardson 1999).

Skellam (1951) and Mollison (1977) both emphasized the importance of focusing on the dispersal kernel, and all its moments, in the prediction of spread. The approach has been extended effectively by van den Bosch et al. (1988), van den Bosch (1990), and Kot et al. (1996). Kot et al. (1996) (see Equation 17) showed that one should distinguish three types of dispersal kernels, and that the diffusion approach works only for those with exponentially bounded tails.

IMPLICATIONS OF DISPERSAL FOR POPULATION DYNAMICS AND COMMUNITY ORGANIZATION

Implications of Dispersal for Population Dynamics

Dispersal plays an important role not only in range expansion (see Implications of Dispersal for Rates of Species Advance above) but also in determining the spatial and genetic structure of populations at local and landscape scales.

LOCAL POPULATION DYNAMICS   Dispersal patterns directly affect the spatial structure of populations, equilibrium population densities, and rates of population dynamics. All other things being equal, shorter dispersal distances and more clumped seed deposition will tend to result in more clumped seedling and adult distributions (Hamill & Wright 1986), slower rates of exploitation of newly available sites, and lower equilibrium abundances (Bolker & Pacala 1999). In general, however, these effects are strongly modified by the spatial pattern of abiotic and biotic influences on establishment, growth, and survival (Schupp & Fuentes 1995). A species with long dispersal distances may nonetheless exhibit a clumped spatial distribution and low equilibrium abundance if the locations in which it can successfully establish are rare and clumped (Hamill & Wright 1986). Such spatial variation in the probability of seed success is ubiquitous in plant populations and must be considered in evaluating the impact of dispersal patterns (Schupp & Fuentes 1995). This is especially important when the probability of seed deposition itself depends upon habitat conditions (Nathan & Muller-Landau 2000). Disproportionately high seed deposition in favorable habitats (so-called "directed dispersal;" see Dispersal Mechanisms, above) has the potential to enhance greatly recruitment rates and thereby affect population dynamics (Wenny 2001).

Habitat favorability may itself not only affect but also be affected by the population spatial pattern. Proximity to parents or other conspecific adults may impact recruitment negatively if the activities of seed predators, pathogens, or other natural enemies are concentrated around parent trees (Connell 1971, Hammond & Brown 1998, Janzen 1970), or positively if parent trees provide a favorable microenvironment for recruitment (Tewksbury & Lloyd 2001) or are associated with higher local availability of mutualists such as mycorrhizae (Wilkinson 1997). Empirical studies have shown that many if not most plant species suffer increased mortality in areas of higher densities of conspecific seeds, seedlings, or adults (Harms et al. 2000, HilleRisLambers et al. 2002). Given a particular negative relationship between conspecific density and survival, the number and spatial pattern of successful recruits will depend upon seed dispersal patterns. In general, higher rates of seed dispersal will lead seeds to experience lower conspecific densities and thus higher survival. Depending on the exact dispersal and survival functions, seedling densities may decrease, increase (McCanny 1985), increase and then decrease (Janzen 1970), or remain unchanged with increasing distance from parents (McCanny 1985).

METAPOPULATION DYNAMICS   Dispersal strategy has a very direct impact on a species's abundances and distribution among different subpopulations and its overall persistence in the whole metapopulation.

When patches are identical in suitability for the target species, dispersal rates among patches, within-patch population growth rates, and patch-carrying capacity alone will determine metapopulation dynamics since they determine rates of colonization and stochastic extinction. Most theoretical studies have used island models in which all patches (subpopulations) are equally connected through global

dispersal. In these models, higher rates of dispersal alone lead to occupancy in greater numbers of subpopulations, increased mean subpopulation and overall metapopulation abundance, and longer-term persistence (Hanski 2001). Of course, these effects may be diminished or reversed if dispersal is associated with increased mortality (Hanski 2001). Spatially explicit metapopulation models in which dispersal rates among pairs of patches are distance-dependent provide additional insight into the relative importance of fecundity, short- and long-distance dispersal on colonization rates and thereby metapopulation dynamics. Higgins & Cain (2002) use such a model to demonstrate that fecundity, interpatch distances, and the rates and distances of LDD all had significant, interacting effects on colonization rates and overall dynamics, while short-distance dispersal was unimportant. They incorporated a stratified dispersal kernel (see Theoretical Models of Seed Dispersal, above), and their results imply that important gains in understanding can be made by relaxing the standard assumptions. Metapopulations with restricted dispersal and/or high degree of isolation can generate complex spatial patterns even in homogeneous environments (Hanski 2001).

When patches differ in such a way that competitive ability of a species varies among them, these differences will interact with dispersal to determine metapopulation structure and dynamics. Given stochastic and asynchronous variation in conditions among patches, dispersal can be an effective bet-hedging strategy, potentially allowing metapopulation persistence through dispersal from one transiently favorable site to another, even when the expected growth rate in all local populations is negative (Metz et al. 1983). Given fixed differences in conditions among patches, dispersal between source and sink patches can provide the means for a species to occur frequently outside the bounds of its fundamental niche (Pulliam 1988). In such source-sink metapopulations, dispersal is strongly asymmetrical from source to sink. Dispersal can provide a rescue effect (Brown & Kodric-Brown 1977) for small populations (in either sink or source habitats) facing high risk of extinction. Less frequently, dispersal may increase extinction risk of small isolated populations, especially in sink habitats, if the number of emigrants exceeds the number of immigrants. Matrix population models can provide a useful approach for approximating patch models in which colonization and survival rates differ among patches and among successive early recruitment stages (Horvitz & Schemske 1986).

GENETIC STRUCTURE   Dispersal has profound effects on the genetic structure of populations (Malécot 1948; Wright 1943, 1969), and this can be used to infer the phylogeographic structure of plants (Petit & Grivet 2002). In plants, genes are dispersed either through haploid pollen or diploid seeds, and inheritance may be maternal (e.g., chloroplast DNA in angiosperms), paternal (e.g., chloroplast DNA in conifers), or biparental (e.g., nuclear DNA). Classical models of isolation by distance (Kimura 1953, Wright 1943) have been used to analyze the development of genetic structure of populations. In general, higher levels of long-distance gene flow act to reduce local genetic correlation, while higher levels of short-distance

gene flow act to increase it (Wright 1969). These models have been generalized in various ways recently, for example to consider uniparentally inherited genes (Hu & Ennos 1999) or local density-dependence (Barton et al. 2002).

Implications for Communities

Just as seed dispersal is important to population structure and dynamics, it also is important to community structure and dynamics—specifically, to local species composition and its spatial and temporal turnover. We can divide the effects of seed dispersal on communities into two categories: those that result from general limits to dispersal or migration ability in all species, and those that result from differences among species in dispersal ability—differences associated with trade-offs between dispersal ability and other traits. We refer to these as effects of overall dispersal rates and dispersal trade-offs, respectively. These effects are clearly related, but have distinct theoretical implications.

OVERALL DISPERSAL RATES   The effects on community structure and dynamics of overall dispersal or migration rates among local communities depend fundamentally on the nature of local competitive interactions. In the extreme (neutral) case in which all species are competitively equivalent, dispersal and speciation rates alone determine local and global diversity patterns. In the opposite extreme of such strict competitive hierarchies that only one species is suited for any given site, dispersal has little effect on diversity.

In neutral models, increasing dispersal increases the number of species competing for sites, increasing local community species richness and evenness (alpha diversity, sensu Whittaker 1972) while decreasing turnover among communities (beta diversity) and total metacommunity species richness (gamma diversity) because species can drift to extinction faster (Chave et al. 2002, Hubbell 2001). These effects are exactly analogous to those found in neutral models in population genetics discussed above. Building on those results (Kimura 1953, Malécot 1948), we can compute the expected species-area curves, relative abundance distributions, rates of turnover in space, and other measures of community structure directly from dispersal and speciation rates (Bramson et al. 1996, 1998; Chave & Leigh 2002).

As local community dynamics become less neutral, with increased local competitive differences among species, dispersal rates become relatively less important to diversity patterns but still can exert substantial effects. When species have competitive differences that vary among areas, the effects of dispersal are weaker than in the neutral model. Because continuing immigration can allow some locally inferior species to persist in areas where they would otherwise be eliminated, local diversity can be enhanced in a community-level "mass effect" (Shmida & Ellner 1984). Where local competitive ability is negatively frequency-dependent (e.g., owing to life-history niche differences or negative density-dependent recruitment), the effects of dispersal are stronger than in the neutral model because

immigrants that represent locally new types are disproportionately advantaged (Chave et al. 2002). In contrast, in communities in which local competitive dynamics are positively frequency-dependent, increased dispersal is most likely to reduce local as well as total diversity. Extensive dispersal among communities homogenizes species composition, and eventually makes competitive ability dependent on global rather than local abundances, thus facilitating domination by the single most abundant species (Amarasekare 2000, Karlin & MacGregor 1972, Levin 1974).

The importance of dispersal in real communities can be tested empirically in a number of ways (Nathan & Muller-Landau 2000). The strongest test involves experimental manipulation of seed dispersal patterns, but except for seed addition experiments (which manipulate seed number as well as spatial pattern), such tests are rare. Where experiments are impractical, simulations using empirically parameterized population and community models are a good alternative (Ribbens et al. 1994). Comparison of empirical population and community patterns with those expected under models with varying influences of seed dispersal provides a final, albeit weaker, means of assessing the relative importance of dispersal (Condit et al. 2002, Schupp & Fuentes 1995).

DISPERSAL TRADE-OFFS   The models discussed above all assume that dispersal rates are equivalent for all species; but in reality, seed dispersal varies widely among plant species together with other characters. Not all trait combinations are found, however—allocation and design limitations result in trade-offs that limit possible combinations, and selection eliminates others. Strategic trade-offs between the ability to disperse long distances and other traits can thus potentially enable niche differentiation that contributes to stable, equilibrium, species coexistence.

Trade-offs between the ability to colonize new sites (involving high dispersal rates and/or fecundity) and the ability to compete for sites upon arrival have long been hypothesized to contribute to stable species coexistence (Skellam 1951). Theoretical studies have demonstrated how such trade-offs potentially can contribute to ecologically (Hastings 1980, Tilman 1994) and/or evolutionarily (Geritz et al. 1999) stable coexistence of many species by allowing competitively inferior species to persist as fugitives in areas unoccupied by more dominant but less vagile species. Importantly, such coexistence requires either strong competitive asymmetry, as in the classic competition-colonization trade-off model in which sites held by weak competitors are instantaneously taken over by arriving strong competitors (Hastings 1980, Tilman 1994), or strong demographic stochasticity, insuring that the superior competitor's seeds do not reach all sites (Kisdi & Geritz 2003). Alternatively, trade-offs between dispersal and other traits such as fecundity, may enable equilibrium coexistence in spatially variable habitats (Yu & Wilson 2001).

There are a number of ways to test for the presence of competition-colonization trade-offs among species and to evaluate their importance to community dynamics and structure. The most direct and definitive test is experimentally to add seeds of all species: If a competition-colonization trade-off is present, this should result in

an increase in the abundance of a subset of species that are competitively dominant and are ordinarily seen later in succession (Pacala & Rees 1998). Two studies involving addition of seeds of multiple co-occurring grassland plant species both found that seed addition increased the relative abundances of larger-seeded species within the community (Jakobsson & Eriksson 2000, Turnbull et al. 1999). This is in accordance with the idea that larger-seeded species are the better competitors and the poorer colonizers, and that a competition-colonization trade-off mediated by seed size drives successional patterns in this community (Pacala & Rees 1998). This idea is further reinforced by the finding (Moles & Westoby 2002) that seed addition is more likely to increase abundance in larger-seeded species. The presence of competition-colonization trade-offs also can be documented by analyzing correlations among relevant traits (Leishman et al. 2000). This is a weaker test, especially since many such correlations, for example fecundity-establishment trade-offs, can result in merely neutral dynamics (Yu & Wilson 2001).

EVOLUTION OF DISPERSAL

As we have seen, dispersal strategies have important implications for populations and communities, and thus not surprisingly, for fitness. As a result we expect strong selection on dispersal-related traits. Theoretical work on dispersal evolution has a long history (Hamilton & May 1977, Van Valen 1971), and recent years have seen an explosion of studies in this area (Gandon & Michalakis 2001) in part because of the increasing ease of simulating ever more complex scenarios under which dispersal can evolve. These theoretical studies have increasingly clarified how different factors can affect selective pressures on dispersal, although there remains a dearth of corresponding empirical work to test or parameterize theoretical models (Ronce et al. 2001).

The payoff of a dispersal strategy depends fundamentally on the strategies of other individuals in the population because these determine the number of competitors encountered by dispersing and nondispersing individuals and their relatedness. Thus the evolution of dispersal must be considered in a game-theoretic context. We search for strategies that are evolutionarily stable strategies (ESS)—strategies that cannot be invaded by any other strategy (Maynard Smith 1982). Further, to be evolutionarily accessible via mutation by small steps under the standard assumptions on quantitative genetic traits with continuous genetic variation, such a strategy must also be an evolutionary attractor, that is, be convergence stable (Eshel 1983) and a neighborhood invader strategy (NIS), making it an ESNIS (Levin & Muller-Landau 2000). Such strategies, and also (attracting) evolutionary branch points, can be sought using methods of adaptive dynamics (Geritz et al. 1997). Alternatively, genetic structure may be modeled explicitly, for example, in terms of selection at one or more genes (Vincent & Brown 1988).

The major forces selecting for dispersal are kin competition, inbreeding depression, and spatiotemporal variability in environmental conditions. Because pollen dispersal distances typically exceed seed dispersal distances and thus are much

more important in determining the level of inbreeding (Ennos 1994), inbreeding depression is likely to be relatively unimportant in selection for dispersal among plants; thus we do not consider it further. Here we review work demonstrating how the remaining factors contribute to dispersal evolution—work that helps explain differences in dispersal strategies among species and the coexistence of multiple dispersal types within communities. It is important to note that the optimal dispersal strategy will also depend on how dispersal trades off with other traits, and on coevolution between dispersal and other characters.

Kin Competition

A universal advantage of a strategy incorporating dispersal over a strategy of no dispersal is that dispersers can win sites from nondispersers, but nondispersers can never win sites from dispersers (Hamilton & May 1977). Dispersal can allow some individuals to escape competition with kin for the home site and instead potentially compete with and take over sites held by unrelated individuals having a different dispersal propensity. Thus, even in a model in which dispersal is costly, in which there is no variation in environmental quality or crowding and no inbreeding depression, non-zero dispersal rates will be selected. This result was powerfully demonstrated by Hamilton & May (1977) using an island model of an asexually reproducing annual plant species in which each patch had one individual. If dispersing individuals incur a survival reduction c (that is, they survive at rate $1-c$ relative to nondispersing individuals), the ESNIS fraction of offspring to disperse outside the parent patch, D, is

$$D = \frac{1}{1+c}. \tag{21}$$

Thus, if there is no cost to dispersal, all the offspring should disperse, and even if dispersal is very costly (almost always lethal), half the offspring should disperse.

For more general island models having multiple individuals per site and different breeding systems, the influence of kin competition on dispersal rates can be assessed by considering the relatedness of individuals within and among patches (Frank 1986, Gandon & Michalakis 2001). In general, as patch size increases, relatedness within the home patch decreases, the benefits of dispersal for escaping kin competition decrease, and thus the optimal dispersal fraction decreases (Comins et al. 1980). Outbreeding reduces the optimal dispersal fraction because it reduce relatedness within patches; indeed, for high cost of dispersal, the optimal dispersal rate in outbred populations is zero (Hamilton & May 1977, Taylor 1988).

Qualitatively similar results hold for rates of dispersal under more realistic, spatially explicit dispersal models. This was demonstrated early in stepping-stone models—models in which dispersing offspring go only to neighboring sites (Comins et al. 1980). As the number of sites to which dispersal occurs decreases, relatedness between the home site and these sites increases, reducing selection for dispersal. Thus, the ESNIS dispersal fraction declines as the spatial scale of dispersal decreases (Comins et al. 1980, Gandon & Rousset 1999).

If dispersal to different distances is controlled independently, then the evolutionarily stable dispersal strategy is one in which the fitness gains of dispersal to all distances is equilibrated (Rousset & Gandon 2002). In particular, Rousset & Gandon (2002) show that dispersal is associated with two types of costs: the direct cost paid by the disperser (in increased mortality or equivalent), and the indirect cost due to competition with related individuals. At the ESNIS set of dispersal strategies, the product of direct and indirect benefits should be the same at different dispersal distances (Rousset & Gandon 2002).

An aspect of kin competition that has only recently received theoretical attention is parent-offspring competition, although it was discussed early on by Hamilton & May (1977). The potential for parent-offspring competition arises when there are overlapping generations. When parents senesce—so that the probability of parental mortality changes with age—there is selection for an increase in the dispersal fraction with increasing maternal age (Ronce et al. 1998).

Spatiotemporal Variability in the Environment

Spatiotemporal variability in the environment leads to selection for increased dispersal, which allows for bet-hedging over uncertainty (Gadgil 1971). This is true only, however, when the quality of the environment varies in both space and time. Fixed spatial variation in habitat quality selects against dispersal when dispersal is not habitat-dependent, because dispersal tends to move individuals from better habitats with higher abundances to poorer habitats with lower abundances (Hastings 1983). Fixed, synchronous temporal variation alone also has no effect on selection for dispersal in simple models (Ellner & Shmida 1981).

The effect of habitat variability in the absence of kin competition was first demonstrated by Comins et al. (1980). In their island model of annual plants with discrete, nonoverlapping generations, there are an effectively infinite number of individuals per patch, and thus, relatedness within a patch is zero, and there is no kin competition selection for dispersal. Each patch has a probability x of becoming extinct in any given generation. Then the ESNIS dispersal fraction is

$$D = \frac{x}{1 - (1 - x)(1 - c)}, \tag{22}$$

where c is as before the survival cost of dispersal. Note that if dispersal is very costly, then the optimal dispersal fraction approaches the probability of extinction of a patch (Van Valen 1971).

Levin et al. (1984) extended this work to more general types of uncorrelated environmental variation. They showed that for arbitrary stationary distributions of environmental variation, identical among sites, the dispersal fraction will depend on the normalized harmonic mean of the distribution of site quality. As long as there is some probability of patch extinction, the dispersal fraction will always be nonzero, no matter the cost of dispersal. However, if there is zero probability of patch extinction (harmonic mean greater than zero), then there will be some threshold dispersal cost beyond which the ESNIS is zero dispersal (Levin et al.

1984). Chaotic population dynamics, which produce a special kind of endogenous variation among patches, also favor dispersal (Holt & McPeek 1996).

While the above models support the intuitive conclusion that dispersal should increase as environmental stability decreases, this need not always be the case. Ronce et al. (2000) find conditions under which dispersal rates can decrease as the extinction rate of patches increases. They relax the assumption that carrying capacity is always reached in one generation, and thus allow for potentially multiple generations of growth within patches (see also Levin et al. 1984 for an earlier version of such a model). This increases the benefits of staying home, and thus decreases the ESNIS dispersal fraction. Further, as the extinction rate increases, more patches are below carrying capacity, and as a result, there is a region of parameter space where dispersal rates decrease with increasing extinction rate (Ronce et al. 2000).

Thus far, we have considered the effects of environmental variability only on the potential for evolution of strategies of fixed dispersal fractions in the island model—that is, the fraction dispersed does not change with local conditions. Yet there is extensive evidence that in many systems, dispersal is dependent on local density or habitat quality (Travis & French 2000). Such conditional dispersal strategies will generally be advantageous whenever crowding varies among patches (Levin et al. 1984, Metz & Gyllenberg 2001, Travis & Dytham 1999). Their relevance to plant populations deserves further consideration.

Even more importantly, we must extend results on dispersal fractions in island models to dispersal strategies in explicitly spatial habitats. In the past few years, a number of studies have made this leap using spatially explicit simulation, and most consider both habitat heterogeneity and kin competition together. Qualitative conclusions regarding the effects of spatiotemporal variation are the same as in island models (Heino & Hanski 2001). However, explicit spatial structure allows for consideration of the effects of realistic levels of spatial autocorrelation in habitat as well, and this has produced some novel results. In autocorrelated landscapes, "fat-tailed" dispersal kernels are favored, while uniform distributions are favored in random landscapes (Hovestadt et al. 2000). When spatial and temporal variability exhibits red rather than white noise (increasing rather than constant variance with time or distance), there is reduced selection for dispersal (Travis 2001). In models with relatively constant spatial variation in landscape quality, different dispersal rates evolve in narrow corridors and on the boundaries of good habitats than in the centers of habitats, with potentially important implications for conservation (Travis & Dytham 1999).

INTEGRATION AND FUTURE DIRECTIONS

The growing interest in dispersal is matched by increasing recognition of the value of models in describing, exploring, and predicting dispersal processes and patterns (Bullock et al. 2002, Clobert et al. 2001, Levey et al. 2002).

Phenomenological models fitted to data describe the pattern of dispersal distances, and the successes and failures of different models together have illuminated the fact that the distribution of dispersal distances is generally strongly leptokurtic. We advocate increased caution when inferring dispersal from patterns of establishment: Pre- and postdispersal processes should be separated from dispersal because they can significantly alter dispersal patterns. Yet, for the same reason, it is crucial to investigate better how these three basic recruitment processes are interrelated, e.g., how fecundity affects LDD and how LDD itself affects seed survival. Of particular interest are habitat-specific seed deposition rates (see Dispersal Mechanisms and Spatial Patterns, above), which appear to be very important for many species and have rarely been accommodated in any phenomenological models.

Mechanistic models have provided important insight into which aspects of the dispersal process are most important in determining dispersal distances, in general, and LDD events, in particular. In the case of seed dispersal by wind, mechanistic models have demonstrated the importance of not only average wind velocities but also the correlation structure of windspeeds, especially the incidence of updrafts. Further development of mechanistic models, especially of seed dispersal by animals, is an important direction for future research. This requires, first and foremost, a solid knowledge of the natural history of the relevant dispersal processes—knowledge that can be used to inform decisions about which details are crucial to include in the model and which are not. Model development also requires high-quality data on the operative factors for parameter estimation and on dispersal patterns at small and large scales for testing model predictions. Theoretical tools and pre-existing models from probability theory, fluid mechanics, animal behavior (e.g., optimal foraging theory), and other fields within and beyond ecology are likely to be useful in designing, simplifying, and solving (finding closed-form solutions to) mechanistic models.

Theoretical studies of the implications of dispersal for range expansion, population dynamics, and community structure, as well as of dispersal evolution, indicate that the shape of the dispersal kernel is fundamental. Nevertheless, most conclusions to date have relied upon very simplified, unrealistic models of dispersal, in particular global, nearest-neighbor, or Gaussian dispersal models. This work has provided qualitatively useful results, indicating that, in general, higher rates of dispersal are associated with faster range expansion, presence in more subpopulations, higher local diversity (genetic and species), and lower turnover in space. Yet, further advances that more precisely characterize the importance of dispersal depend critically upon models that incorporate realistic dispersal patterns, including habitat-specific seed deposition. In addition, we emphasize the importance of rigorous model assessment.

New technological advances promise to reduce the typically high uncertainty involved with quantifying dispersal processes, especially those operating at large scales, for a larger array of species and dispersal modes. Although the magnitude of inherent (nonreducible) uncertainty (Clark et al. 2001) is unknown, a potential for high inherent uncertainty does exist. This raises the question of how plants,

facing high uncertainty in the behavior of the (external) dispersal agent, can still gain some control over the distance their seeds travel and eventually their fate. Such questions provide an important avenue for future theoretical studies, encompassing both ecological and evolutionary aspects of seed dispersal research.

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