Spatial patterns of seed dispersal, their determinants and consequences for recruitment

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Spatial processes are crucial for determining the structure and dynamics of populations and communities[1]. Among sessile organisms, for which seeds, eggs or larvae represent the predominant mobile stages, dispersal is the premier spatial demographic process. The seed-dispersion pattern (Box 1) not only determines the potential area of plant recruitment, but also serves as a template for subsequent processes, such as predation, competition and mating. Seed dispersal (Box 1) can contribute to species coexistence through tradeoffs between colonization ability and other characters across species[2], and through the slowing of competitive exclusion when seeds fail to arrive[3]. Dispersal also affects the rates of gene flow, and thus influences genetic structure within and among populations[4]. These connections have long been recognized[5–7]; however, with the exception of extensive research on distance- and/or density-dependent predation (Janzen–Connell effects)[8], the consequences of the actual spatial pattern of dispersed seeds remain understudied[9].

In the past decade, there have been advances in methods for characterizing seed-dispersion patterns and in extracting information about dispersal processes from these patterns[10]. Here, we begin by reviewing recent work on important, and often underappreciated, types of variation in seed-dispersion patterns. We then examine advances in understanding the processes of seed output and seed dispersal underlying these patterns. Finally, we consider progress in documenting the contribution of seed-dispersion patterns to population dynamics and spatial patterns (Fig. 1).

Patterns of variation in seed dispersal

Seed-dispersal patterns can be studied by following the fate of marked seeds from their sources[10], using genetic markers to establish the sources of seeds retrieved from their postdispersal locations[4,11], or by documenting variation in seed deposition or density with distance from sources[12]. In the last, and most common, method, the true sources and dispersal distances of seeds are not known but can be inferred in various ways (Box 2). Patterns of seed dispersal have also been inferred from patterns among seedlings; in these cases, it is difficult to disentangle the effects of seed dispersal itself from those of post-dispersal processes[9]. Whatever their methods, studies of

Growing interest in spatial ecology is promoting new approaches to the study of seed dispersal, one of the key processes determining the spatial structure of plant populations. Seed-dispersion patterns vary among plant species, populations and individuals, at different distances from parents, different microsites and different times. Recent field studies have made progress in elucidating the mechanisms behind these patterns and the implications of these patterns for recruitment success. Together with the development and refinement of mathematical models, this promises a deeper, more mechanistic understanding of dispersal processes and their consequences.

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seed dispersal are most often conducted in single populations and single seasons, over short distances and without consideration of the microsite (Box 1) upon which seeds are deposited. Such studies necessarily fail to capture important variation at larger spatial scales and longer temporal scales[13]. We refer the reader to Clark *et al.*[13] for an excellent discussion of population-level variation, and focus here on patterns of long-distance dispersal, microsite-dependent deposition and temporal variation.

Long-distance dispersal

Seed-dispersion patterns far from sources can be qualitatively different from seed-dispersion patterns near sources, because different dispersal processes can operate over different ranges of distances. Seed density almost invariably declines leptokurtically with distance, with an extended tail of long-distance dispersal (Box 3)[5,12]. Because of the inherent difficulty of sampling rare, long-distance dispersal events, empirical data are limited almost exclusively to short-distance events. However, long-distance dispersal is crucial to determining genetic structure[11], range expansion rates[14] and other important features of populations that, like long-distance dispersal itself, cannot be explained from observations of common short-distance dispersal alone[11,14]. Typically, several dispersal agents are involved. For example, seeds of the palm *Maximiliana maripa* are strongly concentrated within 20 m of the parent tree, where they are left by small mammals; however, large quantities of seeds are also found up to 2 km away, where they are defecated by tapirs (*Tapirus terrestris*)[15]. Such patterns can arise even if the same dispersal agent mediates dispersal over the entire range; for example, a small fraction of wind-dispersed seeds caught in rare updrafts is expected to reach much longer distances than the rest[16].

The rarity of long-distance dispersal events poses a unique methodological challenge in data collection on the patterns themselves[4,11,14]. Recent reviews[4,11] have emphasized the potential of genetic methods that can provide evidence of long-distance gene flow, either by comparing the genotypes of seedlings with potential parents or by examining genetic structure within and among populations[4]. However, these approaches will detect seed movement only if it results in successful recruitment; they provide no information on the total number and kind of long-distance

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dispersal events. In theory, seeds themselves could be genotyped to detect all such events, but this would require a prohibitive number of genetic analyses (at least with current methods). Another promising approach might be to follow the movement of individual seeds marked in mass quantities using chemical, radiotelemetric or other physical markers[10].

Microsite-dependent deposition

The substrate available for deposition might also affect seed-dispersion patterns – that is, seeds might be preferentially deposited or retained on some microsites. For example, wind-dispersed seeds might be more likely to end up on rough surfaces[17] than on smooth ones[18], and animal-dispersed seeds might be deposited more frequently in nesting or roosting sites[19]. The importance of differential deposition depending on microsite can be magnified when subsequent seed predation, germination, and seedling growth and survival depend also on microsite, as they often do[5,9]. There have been observations of 'directed dispersal', the disproportionate arrival of seeds at microsites with particularly favorable conditions for recruitment[6].

Box 1. Glossary

Dispersal kernel: a probability density function of the location of seed deposition with respect to the source, yielding the probability of a seed landing per unit area as a function of the distance from its source (and the direction, if relevant).

Distance distribution: the frequency distribution of distances traveled by seeds. This can be obtained from data by calculating the total seeds deposited in annuli at different distances from the source and dividing this by the total number of seeds deposited at all distances; it can be obtained from a dispersal kernel by radial integration. This is sometimes referred to as a 'dispersal curve', a term that is also applied to other graphical descriptions of seed shadows.

Microsite: a subset of sites characterized by particular environmental conditions, often grouped by their common degree of suitability for a given species at a given stage; for example, canopy gaps.

Seed dispersal: the movement of seeds away from their parent plant.

Seed-dispersion pattern: the spatial pattern of dispersed seeds; the sum of seed shadows from all sources.

Seed rain: the flux of seeds from reproductive plants, without considering space explicitly (therefore not a synonym of seed dispersal).

Seed shadow: the spatial distribution of seeds dispersed from a single plant.

Soil seed bank: the viable seeds present on or in the soil, including both those that germinate within a year of initial dispersal (the transient component) and those that remain in the soil for longer periods (the persistent component).
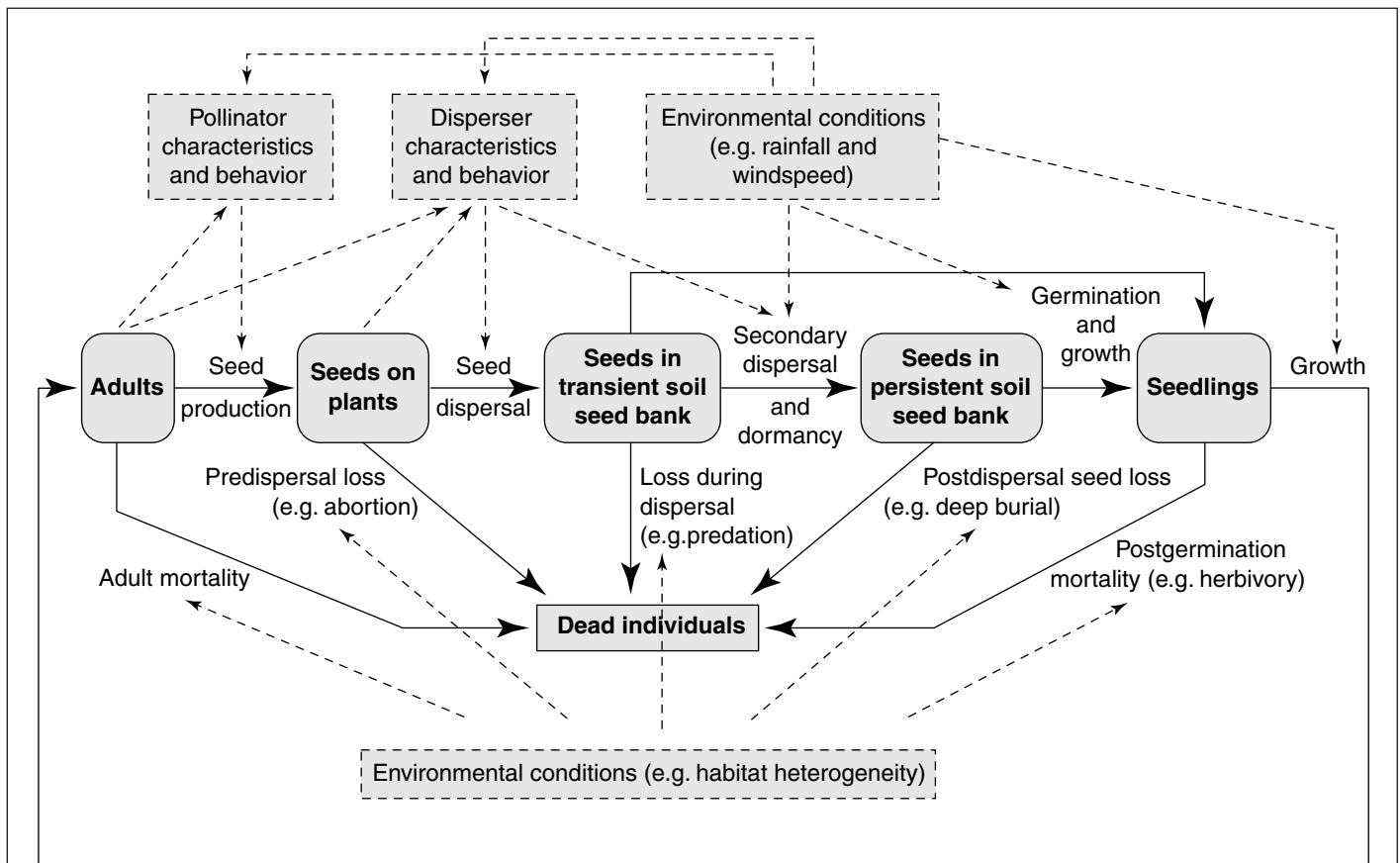

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Fig. 1. The major causes and consequences (on ecological timescales) of patterns among seeds at various stages. Unbroken arrows represent processes, broken arrows show influences upon these processes, broken boxes denote influencing factors, and rounded boxes indicate that the dispersion patterns of that stage are of interest. The seed-dispersion pattern (the sums of seed shadows of individual plants) is in the center of the figure and is determined by the dispersion pattern of adults, their seed outputs and the forms of their seed shadows – including the distance distribution, directional bias, differential dispersal by microsite and clumping of deposited seeds. Seed output (number and quality) reflects environmental influences, including not only abiotic factors but also the biotic environment of surrounding plants and animals, and especially pollinator characters and behaviors, which are themselves influenced by both the abiotic environment and by the characteristics and distribution of plants. Seed shadows result from the responses of dispersal agents to plant characteristics, plant distribution and environmental conditions. Thus generated, the seed-dispersion pattern, combined with the spatiotemporal pattern of environmental conditions and the action of any secondary dispersers, affects postdispersal seed loss and, where applicable, incorporation into the persistent soil seed bank. The patterns of seed rain, soil seed bank and environmental conditions, along with genotype-specific effects, codetermine the pattern of seed germination and, therefore, the seedling-dispersion pattern. Subsequent survival and growth depend upon environmental conditions and possibly the spatial pattern of adults and seedlings themselves, thus the adult-dispersion pattern is obtained.

Box 2. Obtaining distance distributions from dispersion patterns

If both the source and end points of dispersed seeds are known, distance distributions (Box 1) can easily be produced. However, in most cases, only the final locations of seeds are known and there are multiple possible sources, and thus multiple possible dispersal distances, for each seed. Here, we examine the relative performance of methods for estimating distance distributions under these conditions by applying them to a simulated data set in which the true distance distributions are known.

We use a mechanistic model of wind dispersal[35] to simulate seed dispersal in a stand (Fig. I) of five adult trees (green circles) in which seed rain is quantified using 36 seed traps (open squares).

This allows us to directly calculate the true distance distributions (Fig. II) of all 15 000 seeds dispersed in the simulation (black line), as well as the distance distribution of only those 354 seeds that ended up in seed traps (blue). These differ because the seed traps do not completely sample the seed rain (in particular, none are located at long distances from trees).

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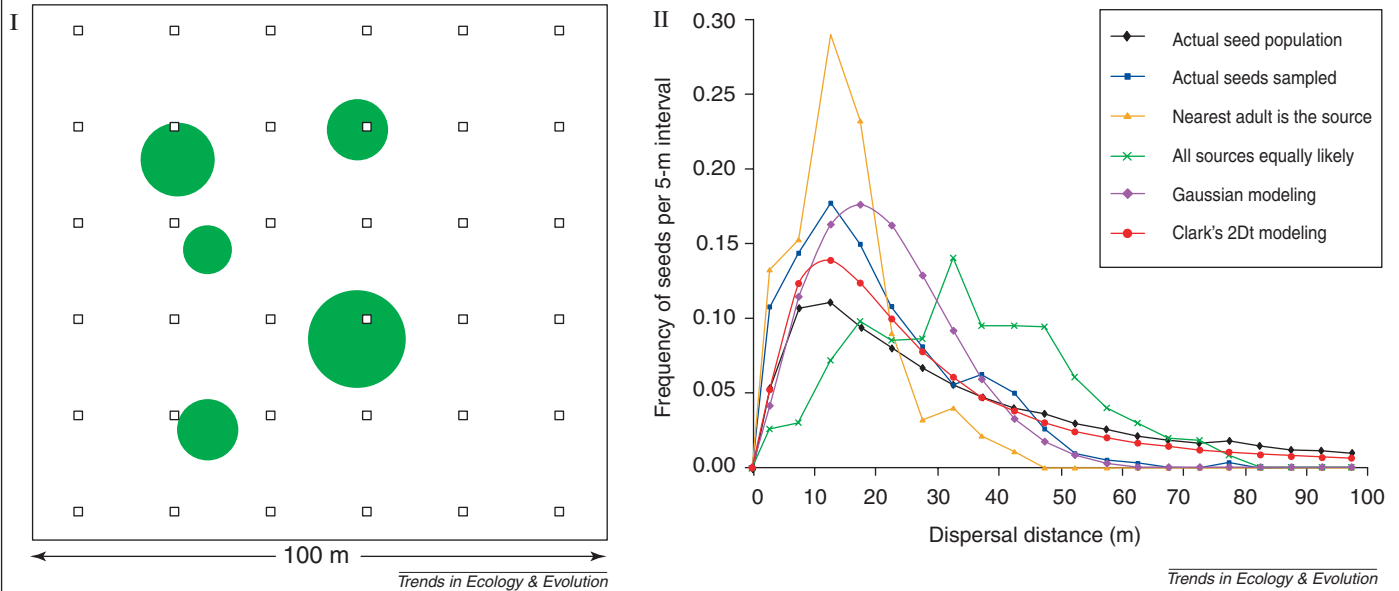
The distance distribution of the actual seed population shows that many seeds in the simulation are dispersed further than the 15–30 m that separates neighboring trees in the stand; thus, there is considerable overlap among the seed shadows of the different trees. Given this kind of overlap, there are two general sets of methods for estimating distance distributions from information on seed rain into seed traps, and on the spatial locations of trees and seed traps. We give two examples from each method, with the resulting estimates shown on the graph (Fig. II).

Make *a priori* assumptions about the origins of seeds in each trap: these assumptions can be used to assign presumed dispersal distances to each seed and thus to obtain the frequency distribution of these distances for all seeds in all traps.

- Assuming that the nearest adult is the source (yellow) leads to underestimation of dispersal distances whenever at least some seeds originate from plants farther away than the nearest neighbor. This assumption will work best when seed shadows overlap very little.

- Assuming that all possible sources are equally likely (green) leads to overestimation of dispersal distances whenever seeds are more likely to go shorter distances. This assumption will be least problematic if seed shadows of all possible seed sources overlap completely and show little decline in expected seed densities with distance from the source over the range of distances investigated, and if all plants are identical in their seed production.

Assumptions can also be based upon specific knowledge of the relative seed production of adults or of the dispersal process. For instance, mechanistic models of dispersal (Box 3) can be used to estimate the expected number of seeds each adult would disperse to each trap, and, therefore, the expected sources of seeds in traps[25].

Use inverse methods to fit models specifying distance distributions: this recently developed method relies on numerically intensive calculations of the likelihood of obtaining the observed data on seed-dispersal patterns (Box 1) given a particular model specifying seed shadows of the mapped seed sources[47,50,51]. Some set of plausible phenomenological or mechanistic models (Box 3) having a limited number (typically, two to four) of free parameters must first be specified; the best model and the best parameter values are chosen from among them on the basis of the fit to the data. Distance distributions can then be calculated from the fitted model.

This method will work well under a wide variety of degrees of overlap, provided seed trapping or census sites are well distributed with respect to distances to possible sources. It will almost invariably do better at capturing the true distance distribution than either of the above methods, as is demonstrated in the example (Fig. II) in which Gaussian (purple) and Clark's 2Dt (red) (Ref. 51) dispersal kernels (Box 1) are fitted to the simulated data.

The major disadvantage of this method is that it is difficult to estimate confidence limits in the distance distribution corresponding to the fitted model, particularly at the distribution tail[10], because these depend strongly upon the particular assumptions made (note the differences between the Gaussian and 2Dt fits) and because the effects of any errors in the data can easily be magnified.

Classic examples are the deposition of mistletoe seeds on the stems of their host plants by passerine birds, the dispersal of elaiosome-bearing seeds by ants to the nutrient-rich nest environment, and the burial of pine seeds by nutcrackers and jays in xeric habitats. New studies suggest that directed dispersal is more common than previously believed. For example, male bellbirds (*Procnias tricarunculata*) preferentially disperse the seeds of the Neotropical tree *Ocotea endresiana* to canopy gaps[20] (Fig. 2). Deposition rates of seeds might also be influenced not only by the substrate of the focal site, but also by that of surrounding sites. This has been shown for the ballistically dispersed temperate herb field pepperweed (*Lepidium campestre*), for which dispersal distances depend on the height of the vegetation surrounding the parent plant[21].

Temporal variation
Temporal variation in population-level seed production (especially masting[22]) has been an active area of study for many years, but temporal variation in dispersion patterns of the seed rain (Box 1) and the soil seed bank (Box 1) is pursued less often. Such variation can arise from differences in

the relative seed output of individuals over time (a common phenomenon[23]) or from differences in the seed-dispersal process itself. The few studies that report data for multiple periods, whether within or across years, generally do find variation in seed dispersion. For example, ants dispersed *Trillium grandiflorum* seeds significantly longer distances and deposited them in larger aggregations in one year than in the next[24]. Temporal variation might be evident only in parts of the landscape; for example, seed-dispersion patterns of the wind-dispersed Mediterranean tree Aleppo pine (*Pinus halepensis*) are interseasonally variable far from, but not near to, seed sources[25]. The effects of temporal variation in seed dispersal can be moderated by the presence of a persistent soil seed bank (Box 1), which inherently averages over multiple years. Thus, dispersion patterns of wind-generated seed rain in yellow birch (*Betula alleghaniensis*) were variable over four years, showing some significant similarity in spatial patterns only in the two mast years in which most trees were fruiting; by contrast, the spatial patterns of the soil seed bank were relatively consistent[26].

The mechanisms behind the patterns

Seed-dispersion patterns are determined by the spatial pattern of reproductive adults, their seed outputs and their seed shadows (Box 1). To understand variation in seed-dispersion patterns we need to understand variation in seed output and seed dispersal resulting from differences in plant and/or disperser characteristics and environmental conditions (Fig. 1).

Seed output

Seed output varies considerably among plants as a result of differential fecundity[22,23], as well as differential predispersal seed loss. Variation within populations is determined partly by plant size[27]. Site quality influences plant size and also has a direct effect on resources available for reproduction; for example, light availability was positively correlated with seed production in the woodland herb primrose (*Primula vulgaris*)[28]. Year-to-year variation in crop size depends partly upon weather conditions. Among tropical trees, seed production is highest in years of high insolation that follow several years of lower insolation, because these conditions increase the plant resources available for fruitset and also favor pollinators[29]. Local genetic structure and self-incompatibility systems can determine the degree of inbreeding and outbreeding depression, and thus the number and quality of seeds produced[30]. Predispersal losses of seeds as a result of abortion or predation also vary among individuals and between years; no factors that consistently explain the variation have been identified[31].

Seed dispersal

Seeds of most plants are dispersed by multiple agents[32]. Therefore, their seed shadows are determined by the combined effects of seed displacement by all dispersal agents that move seeds from the parent plant (primary or Phase I dispersal) or from subsequent locations (secondary or Phase II dispersal). Although often overlooked, secondary dispersal can greatly affect seed shadows and increase dispersal distances[33]. Given this complicated picture, it is not surprising that seed dispersal is often characterized simply by the fitting of phenomenological models to the total seed shadow (Box 3). However, progress is being made in the development of a mechanistic understanding of seed dispersal (Box 3), especially for abiotic agents, providing the background for the development of mechanistic models that incorporate multiple dispersal agents.

Box 3. Phenomenological and mechanistic models of seed dispersal

Mechanistic models predict seed-dispersion patterns (Box 1) directly from characteristics of plants and their dispersal agents. Although complicated to develop and parameterize, they have the advantage that changes in seed densities are truly predicted, rather than merely fit. Because all parameters correspond directly with real features of the study system, the effects of variation in the operative factors upon seed-dispersion patterns can also be examined and generalization to other systems is possible.

Thus far, mechanistic models have been applied mainly to seed dispersal by wind[16,34,35]. Here (Fig. I), we display an example of a dispersal kernel (Box 1) obtained from such a mechanistic wind model (blue) for parameter values giving a mean dispersal distance of 20 m (Ref. 35); note that it has a relatively fat tail (Fig. I) even though this particular model does not incorporate the influence of updrafts.
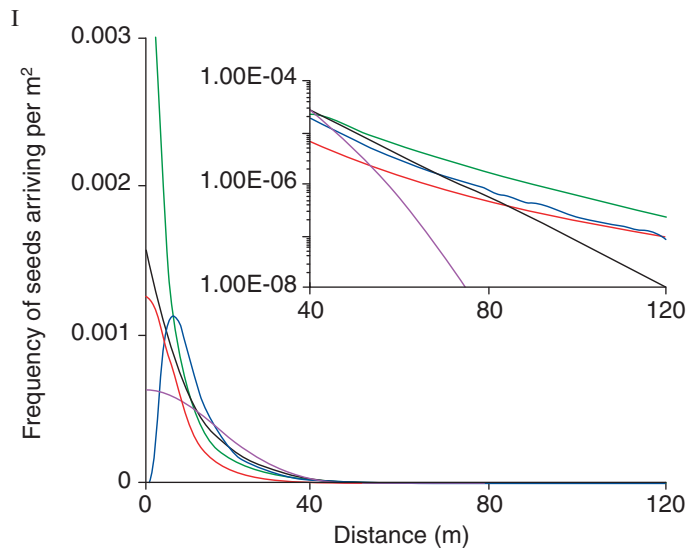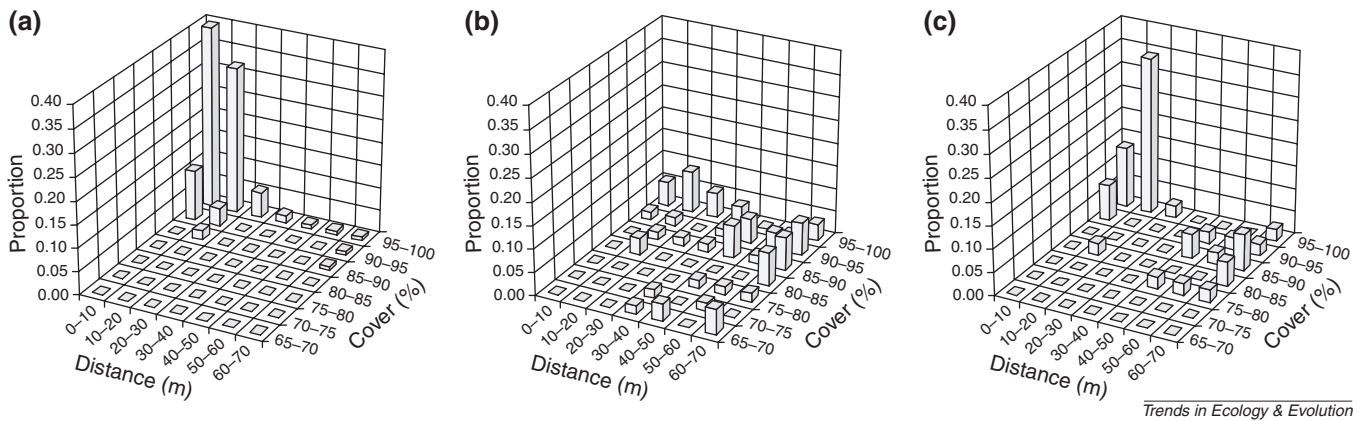
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Phenomenological models have long been used to fit data on seed densities as a function of distance from their source[10]. Although simple to apply, they have the disadvantage that their parameters do not relate directly to particular characteristics of the plant or disperser. Because they can be obtained only by fitting data, and not through *a priori* predictions, they do not provide a basis for generalization beyond studied systems. In Fig. I, we display examples of dispersal kernels from four functions that have been used to fit dispersal data – exponential (black), Gaussian (purple), exponential family fat tailed (exponent 0.5; green) and Clark 2Dt (red) – all parameterized to have a mean dispersal distance of 20 m.

The functional forms most commonly used are the inverse power law, the negative exponential[12] and the Gaussian; each has a single free parameter. The inverse power law possesses the unique disadvantage of having a singularity (infinite density) at zero, and thus it cannot be used as a dispersal kernel. Of the two proper density functions, neither the negative exponential nor the Gaussian have sufficiently fat tails to account for long-distance dispersal (Fig. I). Other functions that are leptokurtic enough, such as more fat-tailed members of the exponential family of dispersal kernels[14], typically overestimate dispersal near the source (Fig. I). The failure of all these functions to fit short- and long-distance dispersal simultaneously has motivated the recent development of dispersal kernels that are the sums of a discrete[52] or a continuous [Clark 2Dt (Ref. 51)] set of exponential family models – their greater number of parameters (five or more and two, respectively) allows greater flexibility and thus better fits everywhere (Fig. I and Box 2).

Mechanistic models can successfully predict seed dispersal by wind[34,35] using information on wind conditions and plant attributes. The relevant plant attributes include the aerodynamic properties of diaspores (seeds plus wings or other dispersal appendages) and the height from which they are released[36]. Given that intraspecific variation in these plant characteristics is relatively low, variation in wind conditions explains the overwhelming majority of intraspecific variation in dispersal distances[35].

Fig. 2. Directed dispersal is evident in a study by Wenny and Levey[20], which documented dispersal distances and microsite (Box 1) biases for all seed dispersers of the common shade-tolerant Neotropical montane tree *Ocotea endresiana*. The distance to the nearest conspecific tree, and the canopy cover of all sites at which seeds were deposited, was recorded. These *O. endresiana* seeds are dispersed by five species of birds: black guan (*Chamaepetes unicolor*), resplendent quetzal (*Pharomachrus mocinno*), emerald toucanet (*Aulacorhynchus prasinus*), mountain robin (*Turdus plebejus*) and three-wattled bellbird (*Procnias tricarunculata*). (a) Wenny and Levey[20] found that the first four bird species dispersed seeds near trees, and at random with respect to canopy cover. (b) However, male bellbirds disproportionately dropped seeds in gaps, where they advertise to females from song perches, often long distances from fruiting trees. (c) Because sites with somewhat lower canopy cover had greater seedling survival, overall seedling recruitment showed two peaks: one in typical understory sites near parents and one in relatively more open sites far from parents. *Reproduced, with permission, from Ref. 20.*

The major challenge lies in determining the speed and direction of winds experienced by dispersing diaspores, because these depend upon small-scale variations in wind behavior and upon differential seed release under different weather conditions, both of which remain poorly understood. Comprehension of important processes, such as long-distance dispersal[11,14,16] and differential deposition of wind-dispersed seeds, awaits further developments in these areas.

In theory, knowledge of animal behavior and plant characteristics can be combined to predict seed dispersal by animals, just as knowledge of wind behavior can be used to explain wind dispersal. However, in practice, the behavior of animals is even more complex and less well understood than that of wind, depending not only upon abiotic conditions and vegetation, but also upon abundances and characteristics of alternate food sources, competing species and predators. Studies of individual disperser–plant interactions in particular populations can, and often do, document behavioral patterns (including foraging activity, movement patterns, gut retention time and habitat use) in sufficient detail to explain overall distance distributions (Box 1) and differential dispersal by microsite (Fig. 2). Nevertheless, qualitative attempts at generalization across species – for example, through classification of plants according to their fruit morphology and of animals by their diets – have had mixed success[37]. Some promising recent studies have taken a more continuous and quantitative approach. For example, seed mass and morphology were related to the retention time of seeds in an animal's coat, and thus to dispersal distance, in 13 plant species dispersed epizoochorously by wood mice (*Apodemus flavicollis*)[38]. Longer retention times corresponded to genetic estimates of more gene flow among three other epizoochorously dispersed species[39]. Similarly, bird and seed size together determined foraging activity and gut retention times of three species of turacos, and thus their dispersal of tropical tree seeds[40]. These results show that mechanistic frameworks can provide a good basis for isolating the relative contributions of the many factors involved in determining seed-dispersion patterns, even if true quantitative and predictive models of animal dispersal remain a distant goal for most systems.

Consequences for recruitment

Seed dispersal determines the potential rates of recruitment, invasion, range expansion and gene flow in plant populations, with long-distance dispersal hypothesized to be disproportionately important to all of these[11,14]. However, although recruitment cannot occur without seed arrival, seed arrival is no guarantee of recruitment. We need to consider postdispersal processes to understand the importance of dispersal (or of particular dispersal processes) to the spatial patterns and dynamics of plant populations. After all, differential deposition on different substrates will not matter if seedling success is essentially identical on all of them and if the substrates are randomly distributed; temporal variation in seed dispersal will be of little consequence if there is a large, persistent soil seed bank; and even large variation in the density of seeds deposited might be of limited importance if there is strong, positively density-dependent mortality as a result of predation or competition. By contrast, even low levels of long-distance dispersal might be disproportionately important if those seeds benefit from reduced competition in new habitats or from a rare genotype advantage. Consideration of establishment processes focuses our attention on the details that matter.

Overall, the importance of seed-dispersion patterns is reflected in the degree to which the abundance and distribution of recruits depends upon the pattern of seed availability (seed limitation), rather than upon the pattern of establishment success (establishment limitation) (Box 4), including differences owing to the quality of individual seeds or to genotype–microsite interactions. This question has been addressed in several ways. In all approaches, the ability to assess the importance of dispersal to population processes as a whole is limited by the stage to which processes and/or patterns are considered, because the contribution of dispersal to numbers and patterns at one particular stage might not reflect the contribution to patterns at a later stage[9].

Comparing patterns in the field

The importance of the seed-dispersion pattern to spatial patterns at subsequent stages has been addressed most often through field studies comparing patterns across stages; for example, by using spatial correlograms[41],

partial Mantel tests[41], geostatistics[42] and other spatial statistics to evaluate the concordance between spatial patterns among arriving seeds and among established seedlings[9]. Genetic demography studies of changes in the spatial patterns of genotypes through the life cycle can also reveal genotype- or phenotype-specific effects, which might cause the sources and dispersal distances of seeds recruited into the adult population to vary considerably from those at earlier life stages[43]. In both cases, the simplest analyses compare spatial distributions of different stages at a single period[44]; however, these might result in erroneous conclusions if there is strong temporal variation in seed dispersal or recruitment[9]. Such problems are avoided if studies follow cohorts and compare spatial patterns over time. In one study, Houle[26] found that postdispersal seed density of yellow birch was positively correlated with subsequent first-year seedling density in one cohort, but not in another. Such mixed results are typical[9], and presumably reflect the varying importance of seed dispersal in different systems and at different times. However, lack of concordance might sometimes reflect insufficiently precise characterization of the dispersal process itself, or of soil seed bank dynamics, as is the case when seedlings establish at sites where no seed availability was documented. Correlations between seed dispersion and subsequent recruitment alone might also be misleading if analyses fail to take account of correlated differential dispersal, which might result in correlations between seed success and seed arrival across microsites[9].

Experimental manipulations
The most straightforward way to assess seed limitation (Box 4) is to add seeds at a density thought to be saturating and compare the resulting seedling numbers with control plots in which seed availability is not augmented. Many sowing experiments find a

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Box 4. Decomposing recruitment limitation

Total failure to recruit at a given site or recruitment at less than maximum density can be the result of failure of seeds to arrive and/or the lack of suitable conditions for establishment. Consider, for simplicity, the case of either seed arrival at saturating density or failure of seeds to arrive and patches either entirely suitable or entirely unsuitable for establishment of a single individual (Table I) – we define *a*, *b*, *c* and *d* as the number of patches in each of these categories, respectively:

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Seed	Patch	
	Suitable	Unsuitable
Arrival	*a*	*c*
No arrival	*b*	*d*

Obviously, in reality there is a gradation of site quality and seed arrival; however, these ideas generalize to any situation in which recruit density is a nondecreasing function of the density of seeds arriving.

We can calculate indices of the influence of individual factors by calculating how many sites would be won if that factor were not limiting, but all other limitations were still present and thus the proportion of those sites lost because it is limiting. By analogy with the concept of realized niches, we refer to these as measures of realized limitation:

$$\text{Realized seed limitation (RSL)} = 1 - \frac{a}{a+b} = \frac{b}{a+b}$$

$$= 1 - \frac{\text{abundance given actual seed rain and actual establishment conditions}}{\text{potential abundance given saturating seed rain and actual establishment conditions}}$$

$$\text{Realized establishment limitation (REL)} = 1 - \frac{a}{a+c} = \frac{c}{a+c}$$

$$= 1 - \frac{\text{abundance given actual seed rain and actual establishment conditions}}{\text{potential abundance given actual seed rain and ideal establishment conditions}}$$

Alternatively, we can calculate the degree to which a factor would be limiting if no other factors were limiting – measures of fundamental limitation:

$$\text{Fundamental seed limitation (FSL)} = 1 - \frac{a+c}{a+b+c+d} = \frac{b+d}{a+b+c+d}$$

$$= 1 - \frac{\text{abundance given actual seed rain and ideal establishment conditions}}{\text{potential abundance given saturating seed rain and ideal establishment conditions}}$$

$$\text{Fundamental establishment limitation (FEL)} = 1 - \frac{a+b}{a+b+c+d} = \frac{c+d}{a+b+c+d}$$

$$= 1 - \frac{\text{abundance given saturating seed rain and actual establishment conditions}}{\text{potential abundance given saturating seed rain and ideal establishment conditions}}$$

These quantities can be assessed using simulation models of the processes or directly from field data. Sowing experiments, in which seeds are added at saturating densities, directly provide information on RSL (= 1 – density in controls / density in experimental plots). They also provide information on FEL, through comparisons between mean densities observed when seedfall is saturating (and thus only establishment limitation is operative), with maximum densities observed under saturating seedfall and ideal establishment conditions (FEL = 1 – mean density in experimental plots / maximum density possible). FSL is approximately the proportion of sites not reached by seeds, and thus can be estimated from information on where seeds arrive. If the sites where seeds arrive are a random sample from possible sites, then REL will be the same as FEL. However, if seedfall is disproportional to favorable or unfavorable sites, REL will differ. Sowing experiments directed only at sites that receive some seeds, or the combination of information on microsite-specific establishment success and the relative abundance of microsites (Box 1), can be used to calculate REL in these cases.

Both seed and establishment limitation can be further decomposed into parts to focus upon the limiting effects of particular dispersal or establishment processes. For example, Clark *et al.*[47] decomposed seed limitation into contributions as a result of the local nature of seed dispersal (dispersal limitation) and of the limited number of seeds alone (source limitation). Establishment limitation could be similarly decomposed to isolate the effects of distinct mortality agents, such as seed predation and seedling herbivory. However, if density-dependent effects, owing to predation, parasitism or disease, are so strong that they 'overcompensate' (such that beyond some level higher seed densities have lower seedling yields), then the concept of 'saturating' seed densities becomes untenable and thus calculation of limitation measures would require a different basis for comparison.

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significant effect of the experimental increase in seed abundance upon population recruitment and, therefore, on community composition[45]. However, because sowing is usually done at a single density (not necessarily saturating) and

results reported only for the treatment as a whole, these experiments say little about the absolute degree of seed limitation, or of the relative importance of seed supply compared with other factors in natural communities, although they could be designed to do so (Box 4). More sophisticated experiments could examine the relative importance of seed limitation at different distances from parents by comparing the seedling yield of the observed seed-dispersal pattern with that of alternative experimental distributions; these have rarely been undertaken (but see Ref. 46). The performance of such experiments at appropriate spatial and temporal scales is difficult, especially where large and long-lived species are involved; not surprisingly, most seed-manipulation studies have been conducted on grasses and forbs[45].

Models parameterized from field data
Finally, information gleaned from field studies of seed dispersal and recruitment might be combined in models and the relative importance of each process assessed using simulations in which single factors are varied[47] (Box 4). This modeling approach allows for the assessment of the importance of each process not only for total recruit numbers, but also for other measures, such as the spatial pattern of recruits (to which it has not yet been applied). Further, it might be possible to test model predictions using manipulative experiments.

Prospects for integration

Not all of the patterns and sources of variation in seed dispersion that we discuss here will prove important to understanding seed dispersal or its consequences in every system. To determine which features are important we need longer term, larger scale, integrated studies, of the kind that have generated crucial insights into marine systems[48]. These studies not only provide more information on variation among populations and individuals, across microsites, in time and at long distances from sources, but also link these to their consequences for recruitment. Extensive natural history data have been collected on seed-dispersion patterns, dispersal-agent behavior and establishment success in many systems[5–7,9,12]; however, most of these data are on small spatial scales and short temporal scales[13], and are not closely linked to each other. Herrera[49] provides a rare example of a long-term study on seed dispersal by birds[37]; we know of no comparable studies on seed-dispersion patterns themselves. Increasing recognition of the importance of large-scale studies, combined with more sophisticated technology and more efficient molecular tools, which can supply more accurate data on individual dispersal events[4,11], provides bright prospects for further progress.

Today, the greatest challenge is to link these patterns to the mechanisms underlying them, because it is understanding of the mechanisms that will facilitate generalization to unstudied sites and species. Studies of the behavior of animal dispersers should examine consequences for dispersal patterns more explicitly, and test predictions based on disperser behavior against field data. In this way, we might hope to develop a mechanistic and predictive understanding of seed dispersal by animals, of the kind that continues to be elaborated for dispersal by wind and other abiotic agents. Finally, studies of mechanisms also should consider implications for recruitment – evaluating the relative importance of seed dispersion to observed population densities, dynamics and spatial patterns.

Spatial ecology, and the mathematical techniques that have been developed to explore it, provides a context and tools for developing a deeper understanding of dispersal processes and their consequences[10], and for applying these insights to management[32]. Such advances will depend upon the use of models to integrate information from field studies and thus to explore large-scale consequences that cannot be tested easily in the field.

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