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PERSPECTIVE

Long-Distance Dispersal of Plants

Ran Nathan

Long-distance dispersal (LDD) of plants poses challenges to research because it involves rare events driven by complex and highly stochastic processes. The current surge of renewed interest in LDD, motivated by growing recognition of its critical importance for natural populations and communities and for humanity, promises an improved, quantitatively derived understanding of LDD. To gain deep insights into the patterns, mechanisms, causes, and consequences of LDD, we must look beyond the standard dispersal vectors and the mean trend of the distribution of dispersal distances. "Nonstandard" mechanisms such as extreme climatic events and generalized LDD vectors seem to hold the greatest explanatory power for the drastic deviations from the mean trend, deviations that make the nearly impossible LDD a reality.

Dispersal, defined as the unidirectional movement of an individual away from its place of birth (*1*, *2*), is a widespread phenomenon occurring in nearly all organisms. In plants, as in other sessile organisms, dispersal is mostly passive: Seeds or other diaspores (dispersal units) are transported away from the parent plant by vectors such as animals, wind, and water (*3*) (Fig. 1). In studying the ecology and evolution of processes such as dispersal, we usually focus our attention on the prevailing events, assuming that rare events are unimportant. Yet frequency and importance are not necessarily positively correlated. Here I highlight the rare, but disproportionately important, LDD events.

Dispersal is often portrayed in terms of the "dispersal kernel," the function that describes the probability of dispersal to different distances. The vast majority of seeds are typically dispersed short distances (*4*, *5*). The 2Dt dispersal kernel (*6*) (Fig. 2) is a "fat-tailed" distribution: LDD is more frequent than in a normal (Gaussian) or a negative exponential distribution with the same mean dispersal distance (in this case, 50 m), yet the probabilities of dispersal beyond a few hundred meters are very low. At a few hundred meters, LDD research encounters severe data limitation even for large, highly fecund trees, and data are even more restricted for most other plant species.

The fluctuating brown lines in Fig. 2 illustrate the enormous stochasticity associated with LDD. High stochasticity characterizes fecundity, the number of seeds produced, and seed-to-adult survival probability after dispersal. For a given dispersal kernel, fecundity determines how many dispersal events will actually occur, and post-dispersal survival determines what fraction of these events will lead to "effective dispersal" (i.e., successful establishment of reproductive individuals). In the hypothetical case shown in Fig. 2, the expected time for a single effective dispersal event to occur is longer than 100 billion years beyond 150 km. Nevertheless, an effective LDD event 415 km from the source, expected to occur once in almost 10^{13} years under the mean trend, may occur once in 10 years as a result of processes or events that "break the rules." Although the disparity between what is expected and what might appear seems absurd, we do have compelling evidence from many species that effective LDD events do occur far beyond the otherwise observed dispersal distances. This evidence comes from ecological studies (scales of several kilometers; see below) and biogeographical studies [e.g., multiple colonizations of remote islands such as Hawaii (*7*) and intercontinental disjunctions across the Atlantic Ocean (*8*)].

The rarity and stochasticity of LDD entail two fundamental difficulties in research: how to reliably quantify the tail of the dispersal kernel (i.e., the frequency and spatial extent of LDD events) (*5*, *9*), and how to construe the patterns, mechanisms, causes, and consequences of LDD, even if "perfect" data were available. These two difficulties and the immense variation in the spatial and temporal scales of LDD among individuals, populations, species, communities, and ecosystems (*2*, *10*) give rise to a third fundamental difficulty: how to define LDD. Indeed, any threshold distance used for identifying LDD is inherently arbitrary and case specific. Two major LDD definitions are most common (*11*): (i) an absolute threshold distance that may correspond to key biological and physical features [e.g., a distance of 250 m among patches in an experimentally fragmented forest (*12*)] and (ii) a relative threshold based on some percentile at the tail of the dispersal kernel [e.g., a fraction of 1% of all dispersed seeds having a mean dispersal distance of 500 m (*13*)].

Despite these difficulties, many researchers have become motivated by the recently renewed recognition of LDD's disproportionate importance (*1*, *2*, *5*, *10*, *11*). Classical studies have emphasized LDD's importance for colonization of oceanic islands (Fig. 1) and other remote habitats (*7*, *14*). More recent studies have shown that long jumps available through rare LDD events are much more influential than the numerous small steps available through local dispersal in determining the spread of invasive species or range expansion of native species after climatic range shifts (*6*, *15*). Rare LDD events also provide the essential link between habitat fragments (*12*) and facilitate species coexistence—for example, by enabling competitively inferior species to persist alongside competitively superior species through greater LDD capacity (*16*). In fact, LDD can facilitate coexistence even without such tradeoff between LDD capacity and competitive dominance (*13*). Indeed, LDD may also be selectively disadvantageous, as it reduces the ability to exclude competitors from occupied patches and to quickly exploit resources in newly available patches (*17*). Yet over-

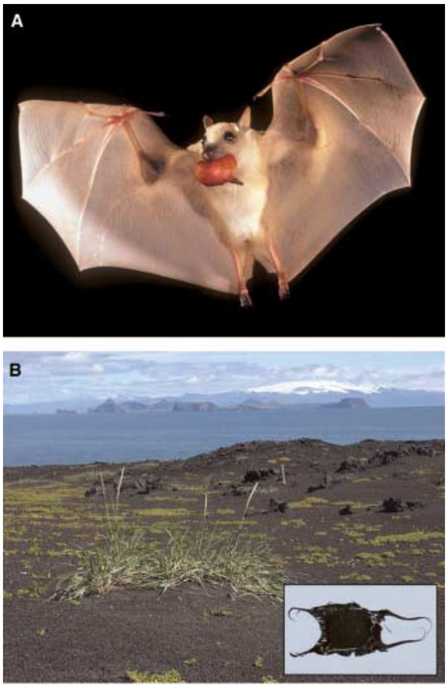

Fig. 1. (**A**) *Epomophorus* sp. carrying a fig in Kenya. Large mammals, birds, and bats are traditionally considered LDD vectors. (**B**) LDD can also be mediated by abiotic factors such as strong storms, floods, and ocean currents that enabled plants such as sea sandwort (*Honckenya peploides*; front and back) and lyme grass (*Leymus arenarius*; middle) to colonize Surtsey, a volcanic island erupted from the ocean 33 km south of Iceland and 4.8 km from the nearest island seen in the background. LDD can also be mediated by "nonstandard" vectors. For example, seeds of five plant species with no known adaptation for water dispersal were drifted ashore attached to a "mermaid's purse" (inset), the egg capsule of the common skate (*Raja batis*). [Photographers: (A) Merlin D. Tuttle, Bat Conservation International; (B) Borgþór Magnússon and Sturla Fridriksson (inset), *Surtsey Research Progress Report* **6**, 25 (1972)]

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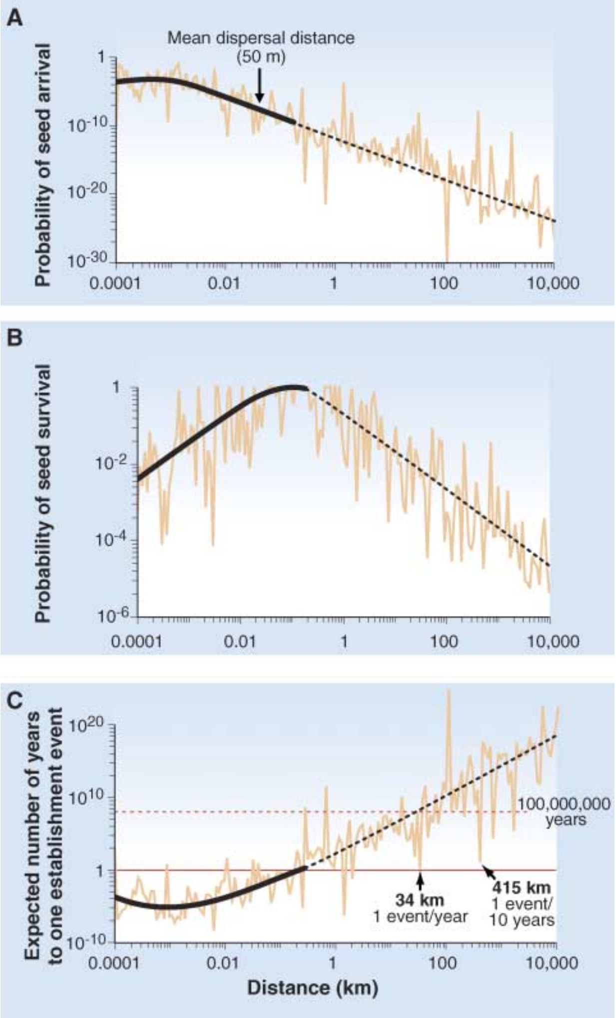

Fig. 2. Multiple temporal and spatial scales associated with LDD of seeds. The transition from bold to dashed lines at 0.2 km indicates the range of distances over which dispersal (and perhaps also survival) becomes practically unquantifiable by current methods; the fluctuating brown lines represent the stochastic deviations from the mean trend. (**A**) 2Dt dispersal kernel [see text; shape = 1.01, scale = 1050 m^2, mean dispersal distance = 50 m: values corresponding to the best LDD performance among tree species analyzed by (*6*)]. (**B**) Seed-to-adult survival kernel, combining a phase of increase [negative exponential mortality; survival = $1 - \exp(-0.04x)$] up to 200 m, and a phase of decrease (inverse power law; survival = $200x^{-1}$) farther away. The increasing survival phase follows the escape hypothesis, which postulates higher density-dependent predation and competition near the parent tree; the decreasing survival phase follows general spatial autocorrelation phenomena in which environmental conditions tend to be less similar, hence less suitable, farther away. (**C**) The expected number of years for establishment of one individual, calculated as the inverse of the product of dispersal (A) and survival (B) probabilities and the source strength defined as a population of 10^6 individuals, each with an annual fecundity of 10^4 seeds. LDD events over much of the range are extremely unlikely. Yet, as exemplified by the two cases indicated by arrows (C), large stochastic deviations generated by extreme events or generalized LDD vectors (see text) may raise the probability of LDD to levels that may be sufficient for LDD to be realized and detected even by contemporary ecological and genetic methods.

all, as we accumulate data and refine our models, we usually reinforce Darwin's (*14*) contention that across species and over time, LDD is a widespread phenomenon of great importance (*5*, *8*, *10*, *11*). In the following, I outline the recent achievements and the further research needed to quantify and understand the patterns, mechanisms, causes (evolution), and consequences of LDD.

Patterns of LDD: Pursue Better Data or Better Analyze Obtainable Data?

A variety of new methods provide better data for LDD of plant diaspores (*5*, *9*). The great potential ascribed to genetic methods to unveil LDD of seeds is beginning to show (*18*), but such studies are still uncommon and are limited in their spatial scale to a few hundred meters or less. Studies estimating effective dispersal kernels from genetic material taken from seedlings have been able to detect effective LDD events at scales of several kilometers (*19*). Genetic methods have also been used to assess the relative contributions of dispersal to gene flow by pollen versus by seed. Although the only way to colonize a distant location is through LDD by seeds, a common generalization asserts that LDD by pollen occurs over much larger spatial scales and hence is more important for interpopulation genetic structure. Yet some recent studies [e.g., (*19*)] of effective seed versus pollen LDD revealed that the opposite is true.

The above studies illustrate important attempts to provide more accurate data for depicting LDD. However, the hierarchical Bayesian (HB) approach better exploits existing data to infer the fundamental relationships that constitute the complex processes (see below) that give rise to LDD events (*20*). More accurate information is still necessary to guide HB models of LDD, so efforts to pursue better data complement attempts to develop better methods to analyze obtainable data.

Mechanisms of LDD: Should We Look Beyond "Standard" Dispersal?

LDD has long been considered to be "chance dispersal" (*7*), but for every passively dispersed diaspore there must be some vector, hence some mechanism, that takes it from one place to another. The past 5 years have seen active research into the mechanisms of LDD, and we now better understand the factors affecting LDD across plant populations and species. For example, the recognition that prolonged turbulent updrafts are critically important for LDD of forest tree seeds by wind (*21*) allows prediction of LDD from input data on wind attributes, seed terminal velocity (falling rate in still air), and height of seed release. A better understanding of the mechanisms also opens new directions for studying LDD evolution. For example, seed abscission is a plant-controlled trait that is likely to have much greater effect on LDD than seed terminal velocity, a property long considered to be the major determinant of dispersal capacity of wind-dispersed species (*22*).

An emerging generalization in LDD research asserts that morphological adaptations of the diaspore, typically used to identify the "standard" dispersal vector, determine short-distance dispersal but often do not constitute the main mechanism responsible for LDD (*23*, *24*). A single plant species may be dispersed by multiple dispersal vectors, including vectors that have traditionally been considered efficient for LDD (e.g., wind, water, birds, bats, and large mammals; Fig. 1), even in the absence of specific adaptations for each (*24*–*26*). Total dispersal kernels, which incorporate the contribution of multiple dispersal vectors, are important to consider when different vectors act differently at different scales (*24*). Large herbivores, for example, disperse viable seeds of multiple plant species with diverse diaspore types over large distances (*25*, *26*). The same holds for dispersal by strong updrafts (*21*) and streams (*27*). Such generalized LDD vectors, which routinely disperse a variety of species and diaspore types over long distances, may drastically increase the probability of LDD relative to the "standard" dispersal vectors.

Extreme events are another potential explanation for LDD. A longstanding hypothesis proposes that tropical cyclones can disperse diverse life forms over very long distances (*28*), but quantitative investigation of such extreme events has not yet been conducted. Extreme events include weather events of unusual power that occur irregularly yet are not necessarily rare; for example, hurricanes, typhoons, and tornadoes occur rather frequently in ecological time scales. Intentional or accidental human-mediated LDD—probably not a new phenomenon (*28*)—can also be considered an extreme event, although, given the current all-inclusive anthropogenic impact on Earth, people might be better considered a generalized LDD vector. Human-mediated LDD is almost certainly now the single most important mechanism of LDD of plants and animals.

Causes of LDD: What Drives LDD Evolution?

Theoretical studies have been instrumental in elucidating the general causes and conditions for the evolution of dispersal, emphasizing the role of spatial and temporal heterogeneity, kin competition, and inbreeding depression (*1*, *10*). Recent theoretical studies have shown that dispersal kernels of different shapes with correspondingly different LDD levels are favored under different sets of conditions (*10*, *29*). Thus, LDD in particular, and not only dispersal in general, may have adaptive value and hence can be favored by natural selection. Furthermore, it has been shown that spatially explicit models incorporating realistic dispersal kernels can elucidate ecological and evolutionary dynamics such as the interplay between relative abundance and the strength of selection for LDD (*29*) and between local population dynamics and LDD (*13*) that cannot be explained by models that treat dispersal simplistically.

At present, given advances in theoretical techniques and computing power, understanding of LDD evolution is limited mostly by the dearth of empirical data on the costs and benefits of LDD (*10*, *29*), and even how it occurs. The key questions about LDD evolution are still fairly fundamental: Which traits and conditions promote (or deter) LDD de facto? What are their tradeoffs with short-distance dispersal and with other fitness components? To what extent can they be controlled, directly or indirectly, by the plant? If generalized LDD vectors and extreme events determine LDD irrespective of the diaspore morphology, it is likely that the diaspore morphology is molded by natural selection for the benefits of short-distance dispersal by "standard" vectors, regardless of the benefits of LDD. The question is then whether LDD is a process over which plants have little or no control, or whether it influences the evolution of traits other than the diaspore morphology (e.g., palatability to large herbivores). LDD evolution studies should be redirected to the mechanisms that actually drive LDD.

Consequences of LDD: How Does LDD Affect Populations and Communities?

LDD can clearly play a major role in shaping a variety of ecological and evolutionary processes. However, this role has been thoroughly investigated only for population spread (invasive species and postglacial expansion), for which the importance of the dispersal kernel shape and the actual level of LDD have been forcefully demonstrated (*6*, *10*, *15*). To explore the consequences of LDD for other population-level processes and for all metapopulation-, community-, metacommunity-, and ecosystem-level processes, our simplistic assumptions about dispersal should be relaxed and LDD should be incorporated realistically (*10*, *30*).

A prime example is Hubbell's (*31*) unified neutral theory, which controversially assumes that all individuals of all species are equivalent and assigns a critical role for dispersal limitation (i.e., very low LDD) in shaping communities. This theory folds all dispersal dynamics into a single parameter m, the probability that an unoccupied site will be colonized by an immigrant. Recent theoretical studies that did incorporate realistic dispersal kernels in spatial models show that the scale of dispersal (or the level of LDD) can strongly influence community patterns in both neutral and non-neutral models (*32*). It should be emphasized, however, that all these studies have applied the same dispersal kernel for all species; incorporating between-species variation in dispersal is likely to provide new insights into the study of community dynamics. The key problem is that we often lack knowledge of the dispersal kernel of even a single species in a community.

Synthesis

LDD research is severely constrained by data limitations. Although our progress in recent years is encouraging, we must seek further improvements in our ability to estimate the probabilities of LDD. Estimating the "mean trend" of dispersal is challenging yet important; however, estimating the deviations from the mean trend is even more challenging and even more important (Fig. 2). Practically speaking, it will always be impossible to predict a single LDD event or to estimate the probability of seed arrival to a specific location far away from the seed source. Yet reliable estimates of the distribution of the deviations are within reach, and deeper understanding of the underlying mechanisms is the best way to accomplish this goal.

To better understand LDD, we should take several steps. First, we need to develop better methods to quantify LDD and to better integrate existing methods, including genetic and ecological techniques, telemetry tracking of diaspores and dispersers, and models of different kinds. We should also further develop the statistical methods to extract information from more readily obtainable data. Second, we need to consider dispersal by multiple vectors, probably the rule rather than the exception (*24*), and accommodate differences in the spatial and temporal scales within which different vectors act. Third, we need to develop mechanistic models of LDD by animals and by abiotic factors other than wind, to use spatially explicit models with stochasticity and realistic dispersal kernels in all aspects of LDD research, and to test them rigorously through field manipulations or observations. Fourth, to better investigate the role of landscape structure, generalized LDD vectors, and extreme events, our research must encompass the multiple spatial and temporal scales over which LDD operates [e.g., (*33*)]. This calls for closer integration among ecologists, environmental scientists, population geneticists, paleontologists, and biogeographers. Finally, we should not isolate dispersal from the general context. Dispersal studies should be coupled with investigations of pre- and postdispersal factors affecting fecundity, population size, survival, and establishment.

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ERRATUM

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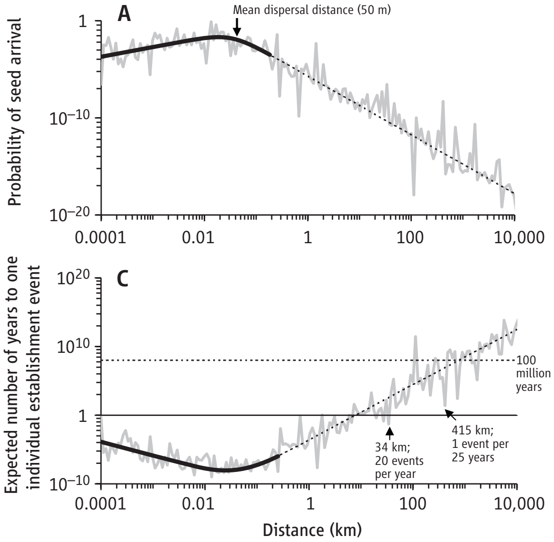
Perspectives: "Long-distance dispersal of plants" by R. Nathan (11 Aug. 2006, p. 786). There was an error in the formula used to create Fig. 2, panels A and C. The corrected panels are shown here. The figure caption is correct, but the error affects two sentences in the text. On page 786, second column, first line, the text beginning with "In the hypothetical case shown in Fig. 2…" should read "In the hypothetical case shown in Fig. 2, the expected time for a single effective dispersal event to occur is longer than one million years beyond 250 km. Nevertheless, an effective LDD event 415 km from the source, expected to occur once in almost 10 million years under the mean trend, may occur once in 25 years as a result of processes or events that 'break the rules.'"



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