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ARE LONG-DISTANCE DISPERSAL EVENTS IN PLANTS USUALLY CAUSED BY NONSTANDARD MEANS OF DISPERSAL?

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Abstract. It has been argued that nonstandard mechanisms of dispersal are often responsible for long-distance dispersal in plants. For example, plant seeds that appear to be adapted for wind dispersal may occasionally be dispersed long distances by birds, or vice versa. In this paper, we explore whether existing data on dispersal distances, colonization rates, and migration rates support the idea that dispersal processes suggested by the morphology of the dispersal unit are responsible for long distance dispersal. We conclude that the relationship between morphologically defined dispersal syndrome and long-distance dispersal is poor. This relationship is poor because the relationship between the morphology of dispersal units and the multiple processes that move seeds are often complex. We argue that understanding gleaned from the often anecdotal literature on nonstandard and standard means of long distance dispersal is the foundation for both statistical and mechanistic models of long-distance dispersal. Such models hold exciting promise for the development of a quantitative ecology of long-distance dispersal.

Key words: *island colonization; long-distance dispersal; mechanistic dispersal models; mixture models; morphological dispersal syndrome.*

Introduction

Classical works in ecology and biogeography stressed the fundamental importance of long-distance dispersal (LDD) for the distribution and evolution of organisms (e.g., Darwin 1859, Ridley 1930). However, for much of the last 30 years, research on LDD has been regarded by some ecologists as irrelevant and anecdotal (Nathan 2001). Irrelevant, because the advent of vicariance biogeography meant that disjunct species ranges could be explained by vicariance, rather than by LDD. And anecdotal, because the rise of a more quantitative approach to ecology meant that dispersal ecologists focused on local dispersal since it is more readily quantifiable than LDD. However, the recent work that shows how LDD largely defines invasion and migration rates (Wilkinson 1997, Cain et al. 1998, Clark 1998, Higgins and Richardson 1999) has resuscitated ecological interest in LDD.

Despite the ‘‘rediscovery’’ of the importance of LDD, we know relatively little about the processes that generate LDD (Cain et al. 2000). It is known that a great variety of processes can move seeds. These different dispersal processes are often grouped into the ‘‘classic’’ syndromes of dispersal, e.g., anemochory, hydrochory, autochory, ectozoochory, and endozoochory (van der Pijl 1982). Many investigators routinely assume a link between the morphology of a dispersal unit and dispersal syndrome (e.g., fleshy fruits imply endozoochory), hence dispersal syndrome is typically defined by the morphology of the dispersal unit (e.g., Ellner and Shmida 1981, Hughes et al. 1994). In this paper, we refer to these morphological dispersal syndromes (MDS) as the standard means of dispersal of a species; if other dispersal agents are involved, they are considered as nonstandard means of dispersal. Although the MDS concept provides a useful framework for describing local dispersal processes (Hughes et al. 1994), it emphasizes processes that move the majority of seeds rather than the rarer processes that move a small proportion of seeds. The possibility remains that these rarer processes may move seeds long distances.

There are many definitions of LDD, some of which emphasize the scale of dispersal, others emphasize the shape of the distribution of dispersal distances. In practice, of course, the scale and shape of the distribution are not independent. Definitions that emphasize scale are more appropriate for investigating the frequency of dispersal events greater than some ecologically meaningful distance (e.g., proportion of seeds moving further than the typical distance between patches). Whereas, shape definitions are more appropriate for investigating the magnitude of rare dispersal events (e.g., distance of the 99th percentile). In this paper, we examine a variety of case studies, some of which necessitate scale definitions of LDD, some of which necessitate shape definitions.

In the first part of the paper, we argue that LDD is poorly related to MDS. It should be noted at the outset that the lack of a relationship between MDS and LDD

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does not, however, mean that all species are equally likely to have a capacity for LDD; it merely means that MDS is not informative in the context of LDD. The second part of the paper provides suggestions for a quantitative approach for studying LDD. To guide the quantitative study of LDD we review illustrative examples of dispersal mechanisms that may account for LDD and argue that many of these mechanisms operate routinely. We then demonstrate statistical methods for describing empirical dispersal data. Because empirical data on rare events like LDD will always be scarce we also investigate the potential of using mechanistic models to generate predictions of LDD. Two classes of mechanistic models are considered, wind dispersal models and animal-movement–seed-retention models.

RELATIONSHIP BETWEEN MORPHOLOGICAL DISPERSAL SYNDROME AND CORRELATES OF DISPERSAL CAPACITY

Dispersal distance distributions

Willson (1993) and Portnoy and Willson (1993) performed a meta-analysis of the tail (distances $>$ mode) of many seed density vs. distance data sets; these analyses are, as far as we are aware, the most comprehensive attempts to quantitatively synthesize data on seed dispersal distances. Both negative exponential and algebraic distributions were fitted to the data sets. Willson (1993) found large differences between the mean dispersal distances of species with different MDS: wind-dispersed seeds had larger mean dispersal distances than animal-dispersed species, while ballistically dispersed and unassisted seeds had substantially lower mean dispersal distances. The results were strongly influenced by growth form: herbaceous plants had lower mean dispersal distances than trees. The conclusion one reaches from Willson's (1993) analysis is that MDS does influence the tail of the dispersal distribution. However, in the second part of the analysis (Portnoy and Willson 1993) it is shown that dispersal mode is unrelated to the shape (exponential or algebraic) of the tail of the distribution.

There are several important limitations of using these studies to address the question of whether MDS influences LDD. Fundamentally, the mean of dispersal distances that are greater than the mode may not be indicative of the LDD—many dispersal data sets have their modes at the source, hence the analysis may merely be showing that MDS influences local dispersal and not LDD. Moreover, most of the sampling protocols explicitly excluded additional dispersal processes. For example, studies of dispersal units that seem to be morphologically adapted for wind dispersal typically release seeds in controlled conditions or use seed traps to collect seeds. Such practices usually exclude the possibility that some of the dispersal units may be moved (further) by other processes (Chambers and MacMahon 1994). Thus it is not known whether the relationship between MDS and dispersal distance would hold if data that included multiple dispersal processes were collected and analyzed. In addition, the analyses in Willson (1993) and Portnoy and Willson (1993) were not balanced: few animal-dispersed herbaceous, and few unassisted and ballistic dispersed tree data sets were available.

Migration rate

All other things being equal, we would expect LDD capacity to be positively related to migration rate (Wilkinson 1997). We therefore ask: is MDS related to observed migration rates? We used published estimates of postglacial migration rates for tree taxa from North America, the United Kingdom, and Europe (summarized by MacDonald [1993]). The MDS of these taxa were assigned as either animal dispersed or wind dispersed. We used published floras, Ridley (1930), Grime et al. (1988), and Bonn et al. (2001) to assign MDS categories to species. The mean migration rates of the wind and animal MDS groups did not differ significantly (Fig. 1A, $F_{1,40} = 0.371$, $P = 0.543$, $n = 42$). This result is in agreement with Wilkinson (1997) who performed a similar analysis, albeit with a smaller sample size ($n = 8$). Although this result is consistent with the idea that MDS does not influence migration rate and by implication LDD, there are reasons why this result is not convincing. First, the reliability of the pollen record, as well as the assumptions and the techniques used to reconstruct migration rates, have been questioned (Macdonald 1993, Stewart and Lister 2001). Second, plant life history and the suitability of the environmental can strongly influence migration rates (Higgins and Richardson 1999).

Colonization rate

Tvärminne.—Thousands of rocky islands surround the Hanko peninsula, southern Finland. Continuing uplift of the Baltic sea floor, initiated some 7000 years ago, means that new islands are still appearing and that existing islands are increasing in size. New islands are not particularly hospitable: the substrate is typically rocky, the elevation is low, and plants must survive exposure to winds and inundation. Despite their inhospitability, these islands provide a wonderful opportunity to study colonization. In 1900, Hayren started to study succession on islands in the Tvärminne area. Between 1907 and 1913, he conducted complete floral surveys of 19 islands (Hayren 1914). Luther followed up on Hayren's work by surveying the flora of 22 islands between 1933 and 1960 (Luther 1961). Luther's islands included 18 of those surveyed by Hayren (the 19th island could not be found because its name is no longer used). Luther surveyed five islands in 1933–1934, 19 islands in 1948–1949, and all 22 in 1960. The islands are between 0.2 and 7 km from the mainland.

Luthers's (1961) meticulous synthesis of Hayren's and his own surveys allows one to identify 516 colo-

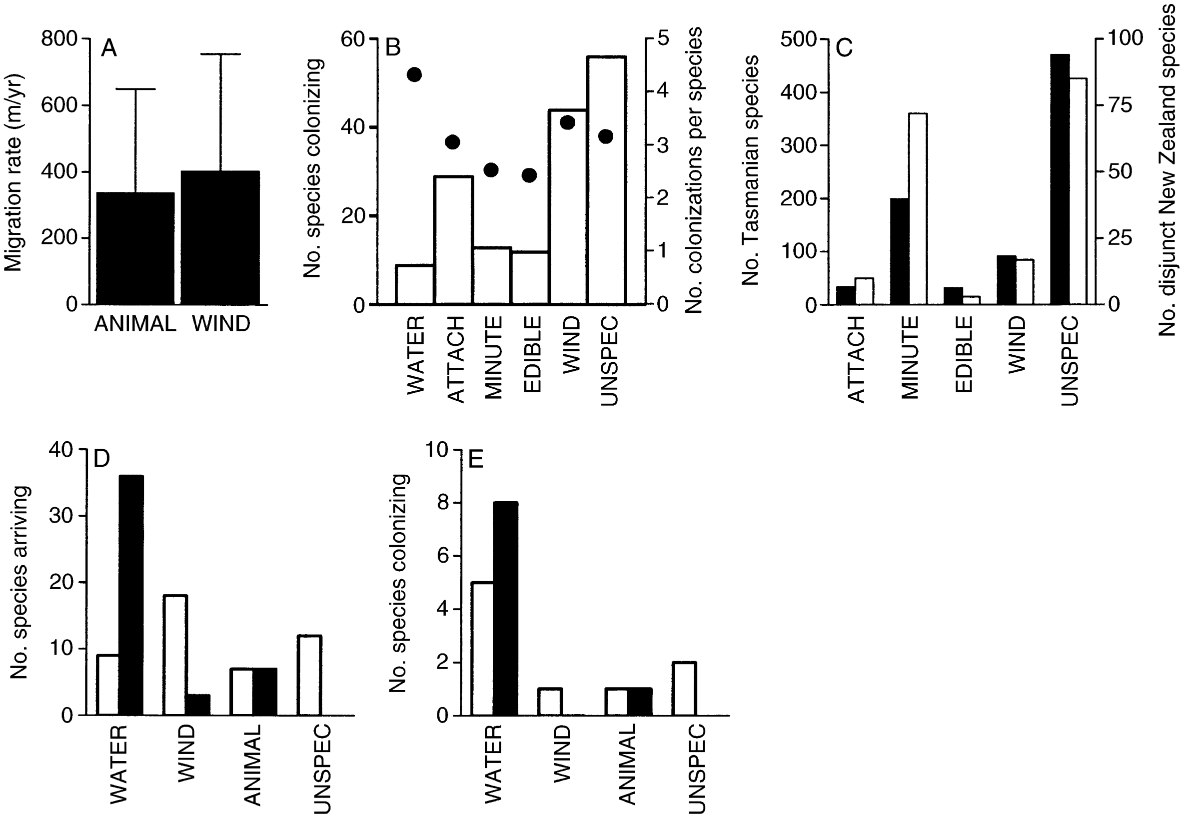

FIG. 1. Tests of the relationship between correlates of long-distance dispersal (LDD) and morphological dispersal syndrome (MDS). (A) The mean (bars indicate one standard deviation) postglacial migration rates for trees with different MDS's estimated from pollen records in North America and Europe (data are from MacDonald [1993]). (B) The number of colonizing species (bars) and mean colonization frequency per species (circles) recorded on 22 islands in the Tvärminne archipelago by MDS (data from Luther [1961]). (C) The number of Tasmanian species (black bars) and number of Tasmanian species also found in New Zealand (white bars) by MDS (data from Jordan [2001]). (D and E) The number of arriving and colonizing species on Surtsey island classified by MDS (white bars) and actual means of dispersal (black bars) (data are from Fridriksson [1975]). The MDS categories are: wind, dispersal units with wings or plumes; attach, dispersal units with hooks, barbs, or other attachment devices; edible, edible (e.g., fruits, nuts) dispersal units; minute, small (<0.05 mg for Tvärminne, <1 mm diameter for New Zealand) dispersal units; water, dispersal units with airspaces; unspec, dispersal units with no apparent morphological features. The edible and attach MDS's are often lumped into an animal MDS.

nization events by 163 vascular plant species. We assigned these species to six MDS categories (see Fig. 1B) using the sources described in *Migration rate.* This procedure probably underestimates the number of species with morphologies suited for flotation, since whether a dispersal unit has air spaces within is often not illustrated or not known. Plotting the number of species that colonize makes it clear that the unspecialized and wind MDS are the most common colonists. However, this does not mean that species with these MDSs are the best colonists—it may be that these MDSs are the most common in the pool of potential source species. Unfortunately, the distribution of the MDS in the potential source pool is not known. We can, however, ask whether the frequency of colonization per species differs with MDS. A log-likelihood ratio for contingency tables (Zar 1999) shows that although species with MDS for water had, on a per species basis, higher colonization frequencies, that colonization frequency was not influenced by MDS (Fig. 1B, $G = 8.651$, $P = 0.8762$). The Tvärminne analysis therefore suggests that MDS is unrelated to colonization ability.

New Zealand.—Excluding orchids, there are 187 angiosperm species native to both Tasmania and New Zealand. A vicariant explanation for these disjunct populations would require that allopatric populations remained in evolutionary stasis for the 80 million years that Tasmania and New Zealand have been separated (Jordan 2001). Since stasis for such a long periods is unlikely, it is accepted that these species dispersed across the 1500–2000 km Tasman Sea more recently (Jordan 2001). Analysis of which of the Tasmanian flora (excluding orchids) colonized New Zealand shows that species with minute seeds (<1 mm propagule diameter) were more likely to colonize New Zealand (Fig. 1C, $G = 22.82$, $P = 0.0001$, Jordan 2001). Hence, the evidence from New Zealand suggests that over long time scales and large dispersal distances, small seeded species are more likely to colonize. The MDS minute is, however, an unspecialized syndrome—small seeds can be moved by wind, attachment, and ingestion (Ridley 1930).

Surtsey.—Surtsey is a volcanic island that emerged between 1963 and 1967. Surtsey lies 33 km south of Iceland and 20 km southwest of Heimaey Island. The colonization of this island (the area has shrunk from 2.7 km^2 in 1967 to 1.5 km^2 in 1998) has been studied in remarkable detail. The Surtsey study is exceptional in that it follows a true primary succession, by recording both the arrival of dispersal units and the subsequent colonization of plants on the island (Fridriksson 1975). The means of arrival of seeds were assigned by regularly searching netted birds, bird droppings, the island, and its shoreline for seeds. These unusual data provide a unique opportunity to examine some of the principal questions addressed in our paper. First, we examine whether the actual (observed) means of dispersal could have been predicted based on knowledge of the MDS. Second, we compare species arrivals with species colonizations; this comparison allows us to assess the biases associated with the common practice of inferring dispersal patterns from colonization data.

Fifty-one taxa of higher plants were recorded arriving on Surtsey between 1963 and 1972 (Fridriksson 1975). We excluded three taxa that were identified at the genus level and could have been confused with a species of the same genus. For all species, Fridriksson (1975) specifies the actual means of dispersal; we specified the MDS as described in *Migration rate.* For simplification, we grouped the species in four dispersal categories (Fig. 1D).

Most (78%) plant taxa arrived by sea currents, although only one quarter of those taxa are morphologically adapted for water dispersal (Fig. 1D). Goodman and Kruskal's (1954) τ shows that knowledge of the MDS leads to a small (7%) and insignificant reduction of the error in predicting the actual means of dispersal ($\tau_{actual} = 0.071$; $P = 0.35$). Only 10 of the 48 higher plant taxa observed arriving between 1963 and 1972 colonized during this period (Fig. 1E). For these colonizing species, knowledge of MDS leads to a greater (44%) albeit insignificant ($\tau_{actual} = 0.438$; $P = 0.32$) reduction of the error in predicting the actual means of dispersal. Water was both the MDS and actual means of dispersal for 50% of the 10 colonizing species. In contrast, water was both the MDS and actual means of dispersal for only 20% of the entire suite of 48 arriving species. These data suggest (albeit with insufficient statistical power) that species with water MDS have adaptations not only for flotation, but also for the colonization of barren islands. It therefore seems that the ability to predict a species' actual means of dispersal from its MDS is better for colonizing species than for species that arrive but do not colonize.

MECHANISMS OF LONG-DISTANCE DISPERSAL

Plant seeds can move long distances by a rich variety of mechanisms. LDD in plants can be facilitated by dispersal adaptations, as exemplified by seeds with burrs or other structures that attach to animals. While morphological adaptations can lead to LDD, it is also clear that seeds can move long distances by other, nonstandard means (Ridley 1930). For example, Carlquist (1967) concluded that 4–35% of the species that colonized 16 sets of islands in the Pacific reached the islands by two nonstandard means: rare rafting events and transport in mud on the feet of birds.

Mechanisms of LDD can be grouped into three nonexclusive conceptual categories. In the first category, LDD dispersal events result from rare or exceptional behavior of the (standard) dispersal vector. For example, strong vertical updrafts might move wind-dispersed seeds long distances (see *Mechanistic models for dispersal distance: Mechanistic models for long-distance dispersal by wind*). The second, but related, possibility is that variability in a property of the dispersal unit, for instance seed mass, may be responsible for LDD events. A third possibility is that a nonstandard dispersal vector is responsible for LDD. Below, we review examples of each of these three types of mechanisms, placing special emphasis on nonstandard means of dispersal. Our brief review indicates that there are many nonstandard mechanisms of dispersal and that these mechanisms can lead to LDD on a regular basis; extensive reviews in Darwin (1859), Ridley (1930), and Carlquist (1967) reach the same conclusion.

Variation in the behavior of a standard dispersal vector

Exceptional behavior of a standard dispersal vector, as seen in interannual variation in seed dispersal by rodents (Hoshizaki et al. 1999; see *Statistical description of dispersal distance: Variation in behavior of a standard dispersal vector*) and in interseasonal variation in wind conditions (Nathan et al. 2000), can cause some seeds to move relatively long distances. A third example is provided by the work of Shilton et al. (1999) on bat dispersal of small-seeded plant species. Because they consume vast quantities of fruit, bats are usually thought to retain plant seeds for short periods only (<30 min). Hence, bats are commonly thought to disperse seeds relatively short distances. However, Shilton et al. indicate that bats can retain seed for much longer periods (12–18 h) and hence on occasion may disperse seed for hundreds of kilometers.

Variability in the properties of the dispersal unit

Continuous variation in a property of the dispersal unit can cause some seeds to travel considerably farther than other seeds (Augspurger and Franson 1987; see *Statistical description of dispersal distance: Variation in properties of the dispersal unit*). Seed characteristics that vary in a discrete manner also can lead to variation in how far seeds are dispersed. For example, in very dry years the desert annual *Gymnarrhena micrantha* produces one to three large ‘‘nondisperser’’ seeds in belowground flowers (Koller and Roth 1964). In wet years, the plant continues to produce a small number of nondisperser seeds, but it also produces many small, wind-dispersed seeds in aboveground flowers; these wind-dispersed seeds have the potential to be dispersed long distances by wind either due to uplifting (see *Mechanistic models for dispersal distance: Mechanistic models for long-distance dispersal by wind*) or by tumbling along the soil surface (see *Statistical description of dispersal distance: Nonstandard mechanisms of dispersal*).

Nonstandard mechanisms of dispersal

Although it is common to label, based on MDS, one mode of dispersal as ‘‘standard’’ for a particular species, the seed of many—perhaps most—plant species are dispersed by multiple mechanisms (Ridley 1930, Chambers and MacMahon 1994). For a given plant species, a dispersal mechanism other than its standard one may be a ‘‘classic’’ dispersal mechanism (e.g., wind, water, animal) that is well described (for instance by van der Pijl 1982) or it may be a more unusual dispersal mechanism that is not commonly reported in the literature.

Seeds of many species often are dispersed by combinations of well-described dispersal mechanisms. For example, apparently wind-dispersed seed frequently float and remain viable in rain wash, streams, rivers, and even sea currents (Ridley 1930, Carlquist 1967); in such instances, it may be typical that seed are dispersed longer distances by water than by wind. In addition, ant-dispersed seed, wind-dispersed seed, and seeds that lack a known dispersal mechanism often attach easily to the fur or feathers of vertebrates (Ridley 1930, Bonn and Poschlod 1998). For instance, results in Berthoud (1892) indicate that buffalo may have been effective LDD agents for a wide range of plant species, and Kiviniemi and Eriksson (1999) show that seed from both wind- and ant-dispersed species attach readily to the hair of cattle and thus could be transported long distances (up to 120–780 m, depending on the species). The ease with which wind-dispersed seed attach to the bodies of vertebrates suggests that nonstandard means of seed dispersal may often be facilitated by the same features of the seed that govern the standard mode of dispersal. Finally, humans provide an extremely effective (nonstandard) means of dispersal for many plant species with a wide variety of MDSs (Hodkinson and Thompson 1997, Bonn and Poschlod 1998).

The additional or nonstandard means of dispersal may also be a dispersal syndrome that is not commonly described in the literature. For example, plant parts (including seed) of wind-dispersed plant species can be transported by birds 3 km or more and used to build nests. Although Ridley (1930) reported this practice, more recent studies have reported seed morphologies that appear to be designed to attract the attention of nest building birds (Dean et al. 1990). Hence, the dispersal of seeds as nesting material may be the standard MDS for some species and a nonstandard means of dispersal for other species. Ridley (1930) also describes how seed, thought to be ant dispersed, were found attached to the bodies of *Helix asperata* snails that had removed (and eaten) the elaiosomes from the seed (elaiosomes are fat- and protein-rich bodies that attract ants). Ridley (1930) argued that these snails could move seeds long distances. Similarly, predators often serve as nonstandard seed dispersal agents when they eat fruits (Hickey et al. 1999) or eat herbivores that have previously eaten seed (this and other types of indirect dispersal are described in the closing paragraph of this section). As discussed by Ridley, Darwin, Carlquist, and others, seemingly novel dispersal mechanisms actually occur on a regular basis, thus providing effective means for LDD.

Other nonstandard mechanisms of dispersal can be thought of as accidental. For instance seed can be transported accidentally in the feet of vertebrates, often for long distances (Darwin 1859, Ridley 1930). Carlquist (1967), for example, estimated that 21.4% of the plant species that dispersed to Easter Island (6 of 28 species) and 21% of the species that dispersed to the Juan Fernandez Islands (21 of 100 species) did so in mud on the feet of birds. For small-seeded plant species, large herbivores frequently eat seeds by accident as they consume foliage (Ridley 1930, Janzen 1984). The seed of such plants typically remain viable when passing through animal digestive tracts, thus enabling LDD. Even more unusually, Fridriksson (1975) found 131 viable seed of five plant species attached to a sample of 23 ‘‘mermaids purses’’ (the egg casing of the skate, *Raja batis*) on the shores of the volcanic island, Surtsey. The MDS of these five species does not suggest either attachment or flotation.

Finally, nonstandard dispersal vectors can achieve LDD of plant seed in an indirect manner. In particular, many different types of predators, including jaguars that eat tapirs, falcons that eat sparrows, and fish that eat other fish, can serve as regular, indirect, dispersal vectors of plant seeds (Ridley 1930). Indirect seed dispersal by predators is especially important in cases where the predator is likely to move seeds longer distances than does the typical dispersal vector. For example, Nogales et al. (1998) recovered viable plant seeds from the pellets of shrikes (which disperse relatively long distances) that had eaten lizards (which disperse relatively short distances) that had eaten seeds.

STATISTICAL DESCRIPTION OF DISPERSAL DISTANCE

The implicit argument in the previous section was that if we understand the multiple dispersal processes

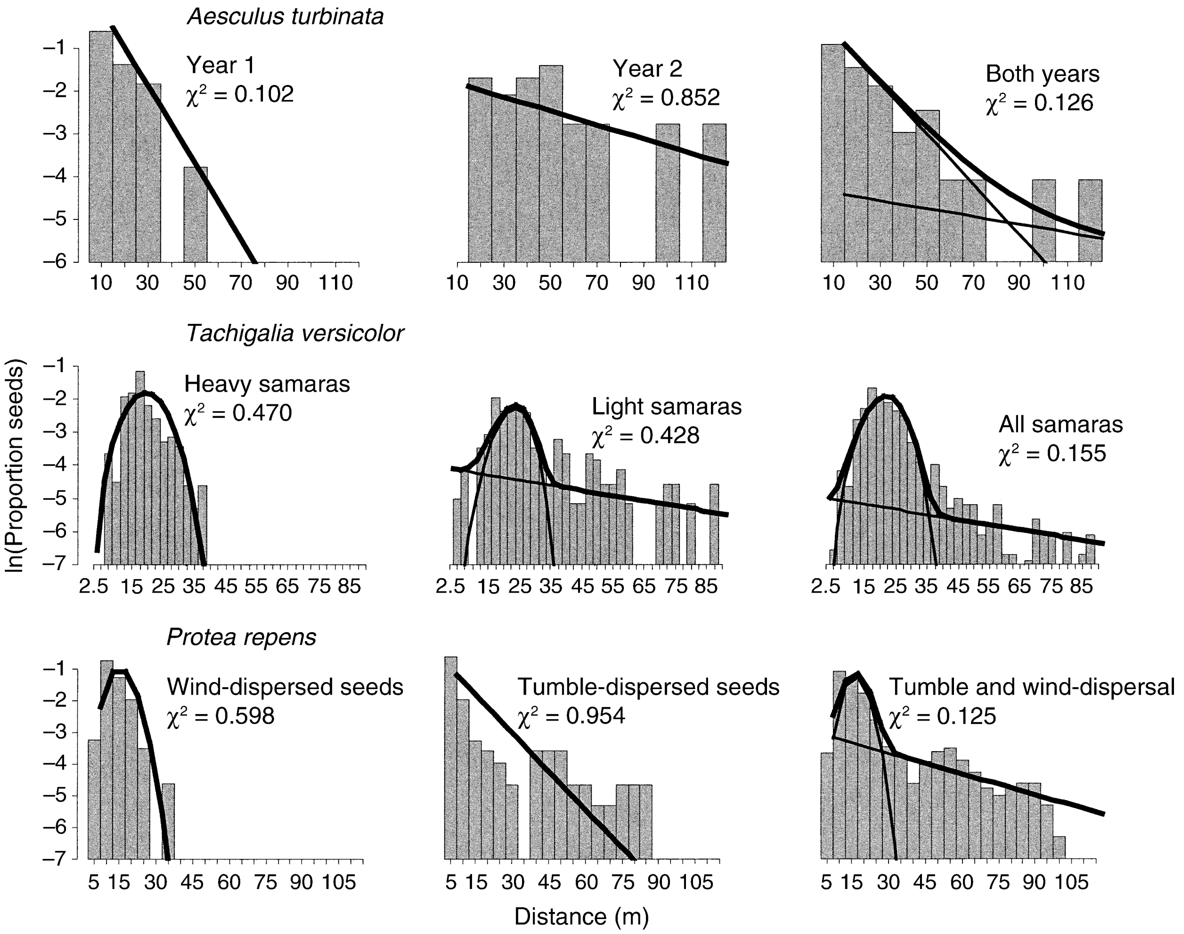

FIG. 2. Statistical fit of the mixture model (Eq. 2) to three different dispersal data sets illustrating how different sources of variation increase LDD. The *Aesculus turbinata* example shows between-year variation in the distance rodents moved seeds (Hoshizaki et al. 1999). The *Tachigalia versicolor* example shows that variation in samara mass creates variance in dispersal distances (Augspurger and Franson 1987). The *Protea repens* example shows how a standard (wind) and nonstandard (tumble) dispersal process can be combined to yield a composite dispersal distribution (Bond 1988). Pearson's χ^2 indicate the goodness of fit (lower values indicate a better fit).

involved in moving seeds, then we can design a sampling strategy that is capable of detecting these dispersal processes. Here we show that mixture distributions can statistically describe data produced by multiple dispersal processes. Mixture distributions are attractive because they provide a formal, yet flexible way to describe data from a population that is a mixture of component populations. In general, we can represent $g(x)$, the probability density function for distance x of a mixture of k component densities, as

$$g(x) = p_1 f_1(x) + \ldots + p_k f_k(x) \qquad (1)$$

where p_i is the proportion of dispersal units that move according to the ith probability density function, $f_i(x)$. The component distributions $f_i(x)$ can be any probability density function. In the examples that follow we use a mixture between a Weibull and an exponential distribution:

$$g(x) = p\alpha\beta_1^{-\alpha}x^{\alpha-1}\exp[-(x/\beta_1)^{\alpha}] + (1-p)\frac{1}{\beta_2}\exp\left(-\frac{x}{\beta_2}\right) \qquad (2)$$

where α, β_1, and β_2 are parameters of the component Weibull and exponential distributions (note that Weibull simplifies to the exponential when $\alpha = 1$) and p is the proportion of seeds in the first component distribution. In the examples described in the next three subsections, we use maximum likelihood techniques (assuming a Poisson likelihood) to estimate the parameters of the mixture distribution. We report the mean, coefficient of variation, 99th percentiles and Pearson's χ^2 (a goodness of fit measure) of the fitted models (Fig. 2). See Titterington et al. (1985) for a general overview of mixture distributions, Venables and Ripley (1999) for a practical guide to fitting mixtures using maximum likelihood methods, and Higgins and Richardson

(1999) for an example of fitting mixtures of Weibull distributions to dispersal data.

A rationale for using mixture distributions is to combine sampling techniques that capture the variance in the distances that seeds move with statistical techniques that describe this variance. In the following three examples we show how mixture distributions can be used to quantify how (1) variation in behavior of a standard dispersal vector, (2) variation in the properties of the dispersal unit, and (3) additional (nonstandard) dispersal processes can influence dispersal distances.

Variation in behavior of a standard dispersal vector

Variation in site conditions or temporal variation in conditions, can capture variance in the behavior of the standard dispersal vector. For example, Hoshizaki et al. (1999) examined the dispersal of *Aesculus turbinata*, a temperate forest species that is dispersed by rodents. They monitored dispersal distance by relocating marked seeds over two years; the between-year variation was staggering. We attempted to fit a mixture of two exponential distributions (Eq. 2, with $\alpha = 1$) to each year's data set and to the combined data set. It was only possible to fit the mixture distribution to the combined data, a single exponential distribution was fitted to each year's data. The fitted models yielded a mean dispersal distance of 11 m for the first year, and 59 m for the second year (the CV for the exponential distribution is 100). Combining the data sets yielded an overall mean dispersal distance of 29 m and a CV of 177. This mixture distribution predicts that most seeds (87%) move relatively short distances (mean 17 m) but that a small proportion (13%) move longer distances (mean 106 m). The 99th percentiles were 51 m for the first year, 281 m for the second year, and 275 m for the combined sample. Hoshizaki et al. (1999) could find no obvious reason for the large between-year differences.

Variation in properties of the dispersal unit

A polymorphism, such as the size and color of a vertebrate dispersed fleshy fruit or the wing-loading of a wind-dispersed plume, is another source of variation in dispersal distance. Augspurger and Franson (1987) investigated variation in seed morphology of wind dispersed dispersal units by creating artificial dispersal units, modeled on the samaras of *Tachigalia versicolor*, of varying mass and area. They explored several kinds of morphological variation, but we concentrate on their mass experiment because the variation in samara mass investigated was consistent with natural variation. The samara mass experiment used five artificial populations of increasing mass. Samaras were released in moderate and even winds and the distance that each dispersal unit moved was directly observed. The fitting mixtures showed that the population with lightest samaras had the highest mean dispersal distance (39 m), 99th percentile (236 m), and a large CV (118). The population with the heaviest samaras had a mean dispersal distance of 17 m, a 99th percentile of 31 m, and a small CV (34). Fits using data from all populations (assuming an equal proportion of samaras in the five weight categories) generated a mean dispersal distance of 27 m, a 99th percentile of 184 m, and a large CV (119). The lightest samaras inflate the mean dispersal distance and increase the amount of LDD, conversely, sampling a population with heavy samaras would underestimate the amount of LDD.

Nonstandard mechanisms of dispersal

Mixture distributions also provide a convenient way to integrate dispersal data when multiple dispersal mechanisms or dispersal vectors move seeds. Obvious examples are fleshy fruits, most of which fall close to the tree canopy, but a small proportion of which are dispersed further by frugivores. We use the slightly more complicated case of secondary dispersal, using Bond's (1988) data on *Protea repens* dispersal. Here, primary dispersal is from the canopy to the soil surface by wind and secondary dispersal is by tumbling along the soil surface. The MDS of *Protea repens* suggests that it is adapted for wind and not tumble dispersal. Bond directly observed primary (wind) and secondary (tumble) dispersal distances. For wind dispersal, only a one-component Weibull distribution could be fitted: the mean dispersal distance was 11 m, the 99th percentile was 24 m, and the CV was only 45, indicating low variance in dispersal distance. For tumble dispersal, only a one component exponential distribution could be fitted: the mean was 12 m and the 99th percentile was 56 m (the CV of the exponential is 100); this exponential provides a conspicuously poor fit. For the model combining wind and tumble dispersal processes 62% of seeds travel an average of 12 m and 38% travel an average of 47 m. The overall mean dispersal distance was 26 m, the 99th percentile was 170 m, and the CV was 134.

MECHANISTIC MODELS FOR DISPERSAL DISTANCE

Statistical models require only data on dispersal distances, i.e., they require no information on the underlying dispersal processes. While this could be regarded as an advantage, the disadvantage is that for LDD such data will remain rare. For LDD, mechanistic models are therefore very appealing because they use information on the underlying dispersal processes to independently predict dispersal distances. Of course, mechanistic models are not without empirical data requirements: mechanistic models need empirical data for model parameterization and validation. The challenge in developing useful mechanistic models of dispersal, however, lies in including the appropriate dispersal processes. In the next two subsections, we examine LDD models for wind and animal dispersal.

TABLE 1. Statistics of dispersal distances for *Acer rubrum* (maple) and *Carya glabra* (hickory) dispersal units simulated using the Nathan et al. (2002) wind dispersal model.

u^* (m/s)†	Cumulative frequency observed ≤ u^* (%)‡	Median (m)		99th percentile (m)		Maximum (m)		Fraction uplifted (%)§	
		Maple	Hickory	Maple	Hickory	Maple	Hickory	Maple	Hickory
0.1	38.12	2.8	0.1	10.0	0.2	12.4	0.4	0.0	0.0
0.2	57.01	6.3	0.4	20.4	0.9	24.7	1.3	0.0	0.0
0.5	94.13	18.4	0.9	53.1	2.3	67.4	3.2	0.0	0.0
1.0	99.89	39.4	1.4	136.0	3.8	180.0	27.1	0.0	0.0
2.0	99.98	83.3	2.5	314.3	140.0	11 371	646.8	1.0	0.5

Notes: Statistics are presented for different friction velocities (u^*). The simulations are based on parameters estimated at the Duke forest. The simulations (each 10 000 dispersal events) were repeated for the different u^* values recorded. These u^* values represent a range of wind conditions from calm winds ($u^* = 0.1$) to strong and turbulent winds associated with storms ($u^* = 2.0$). The vertical profile of the leaf area density, the leaf area index (2.8), and the height of the canopy top (33 m) were measured at the Blackwood division of Duke Forest. The height of release is 20 m, and terminal velocity is randomly selected from a normal distribution (mean ± 1 SD: 0.66 ± 0.12 m/s for *A. rubrum* [Green 1980], 7.84 ± 0.43 m/s for *C. glabra* [our measurements]). Each dispersal event is terminated either when the seed hits the ground surface or after it reaches an elevation greater than six times the canopy height.

† The friction velocity (u^*) scales the vertical transfer of the horizontal momentum flux.

‡ The cumulative frequency of wind measurements with increasing u^*, based on wind measurements taken within the canopy at the Blackwood division of Duke Forest during 65 days (2985 0.5-h means).

§ An uplifting event is determined if seed elevation exceeds canopy height and remains above the canopy at least two time-steps (to maintain some coherency of the flight trajectory).

Mechanistic models for long-distance dispersal by wind

The factors that influence the dispersal of seeds by wind can be categorized as either atmospheric or biological factors. Important biological factors are the terminal velocity of the dispersal unit, release height, and timing of release. Important atmospheric factors are the spatial and temporal statistics of the wind velocity field (vertical, longitudinal, and latitudinal), their covariance structure and their integral time scale properties. The scale at which the dispersal model makes predictions will influence which factors are included in the model. For instance Nathan et al. (2001) showed that knowledge of the average wind velocities is sufficient to predict local dispersal. However, to predict LDD additional information on updrafts and strong gusts is needed.

The problem of simulating updrafts has been addressed by Tackenberg (2003) who developed a flight trajectory model of seed dispersal. Tackenberg's model simulates turbulence by using high-resolution measurements of the horizontal and vertical wind vector to drive the simulation of the flight trajectory of the dispersal units. The model also considers the effects of topography on the wind vector. The model's performance was compared to existing flight trajectory (Andersen 1991) and two diffusion (Greene and Johnson 1989; D. Greene, *personal communication*) models for wind, topographic, dispersal unit type, and release height conditions typical of European agricultural fields. All models performed relatively well at the local scale: however, only the models of Tackenberg and Greene were capable of predicting LDD (seeds moving more than 150 m). These models generated LDD because they capture the turbulent structure and coherency of vertical wind excursions. Tackenberg's analysis also showed that gentle winds (horizontal wind velocity <2 m/s) were best at moving dispersal units long distances as they were often associated with thermal updrafts; strong winds were often characterized by downdrafts and consequently did not yield LDD.

A more numerically advanced approach to the updraft problem has been developed by Nathan et al. (2002). Rather than using the observed wind data directly, this model computes the first and second moments of the wind velocity statistics within and above the forest canopy by using higher-order Eulerian closure principles. These statistics are then preserved in three-dimensional stochastic Lagrangian simulations, which in turn simulate the flight trajectories of each individual dispersal unit within and above a forest at fine spatial and temporal resolutions. The model has shown to provide a reliable description of the observed vertical distribution (up to 45 m) of seeds for five wind dispersed species in 33 m tall deciduous forest (Nathan et al. 2002). Uplifted seeds are predicted to travel long distances (>1000 m); in fact, the model predicts a clear bimodal distribution of dispersal distances, with uplifted seed forming a distinct second mode, ~1000 m from the first mode (Nathan et al. 2002). This result suggests that, for wind dispersal, there may be a objective distinction between short-distance (not uplifted) and long-distance (uplifted) dispersal.

The Nathan et al. model, initiated with parameters estimated for *Acer rubrum* dispersing in deciduous forest, shows that seeds are expected to travel rather short distances under common wind conditions, but may reach several kilometers in extremely strong and turbulent winds (Table 1). Interestingly, in the open landscapes where Tackenberg worked, thermal updrafts dominated, while in the forests where Nathan and colleagues worked, shear-induced updrafts dominated.

The former disappear when winds are too strong, the latter are generated by strong winds; these system-specific effects of strong winds on updrafts explains why strong winds inhibit LDD in Tackenberg's study but facilitate LDD in Nathan et al.'s study.

If the Nathan et al. model is run for *Carya glabra*, which has a 7.8 g nut (the *A. rubrum* samara is 14 mg) it is shown, as expected, that wind dispersal is limited ($<$3.2 m) under most wind conditions. However, under the wind conditions of the strongest winds recorded during a 65-d period, nuts were uplifted and moved hundreds of meters (Table 1). Hence, both the *A. rubrum* and *C. glabra* simulations show that uplift can generate LDD, but that uplifting only occurs under extremely strong and turbulent winds. The implication is that winds capable of uplifting dispersal units with wind MDS may also be capable of uplifting dispersal units without wind MDS. However, fundamental differences in the wind dispersal potential of these species do exist, exemplified by the large differences in the median dispersal distances for all wind conditions (Table 1). Tackenberg (Tackenberg et al. 2003) also used his flight trajectory model to examine the relationship between MDS and the wind dispersal potential of 335 vascular plant species (mostly European herbs). Although Tackenberg's results show that the wind dispersal potential (indexed by the proportion of seeds dispersed $>$100 m) of wind-MDS species was typically higher than non-wind-MDS species, his results also show that many non-wind-MDS species nonetheless had nontrivial wind-dispersal potentials ($>$1% seeds dispersed $>$100 m by winds characterized by thermal uplift).

Mechanistic model for long-distances dispersal by animals

A second class of mechanistic model combines information on animal movement and seed retention to yield seed-dispersal distributions. Data on retention times in an animal's gut or on an animal's body are relatively easy to obtain. Animal movement data, however, requires more careful treatment. This is because animal movement is influenced by both habitat and behavioral responses. Moreover, as a computational convenience, animal-movement studies often use movement steps as the currency of analyzing movement, rather than time steps (Turchin 1998); this obviously makes integration with retention time data problematic.

Only a handful of studies have combined movement data with seed-retention data to generate seed-dispersal distributions. Studies of this type that we reviewed all involved the dispersal of tropical plant species by frugivorous vertebrates, but all used quite different techniques to generate dispersal distributions. Although these methodological differences prohibit formal comparison, all these animal-movement–seed-retention studies report relatively large dispersal distances. For example, Sun et al. (1997) report mean dispersal distances of 119–304 m; Yumoto et al. (1999) report mean dispersal distances of 218–440 m and maximal distances of 288–637 m; Holbrook and Smith (2000) report mean distances of 1127–1947 m and maximal distances of 3558–6919 m.

To facilitate comparison among studies, resampling techniques could be used to generate dispersal distributions. Such an empirically based approach makes no assumptions about how the data are distributed, and is consequently likely to be appropriate in many situations. A resampling algorithm would be (1) Produce an empirical distribution of retention times (Fig. 3A). (2) Produce many time series of net displacement (Fig. 3B shows two time series, 30 were used for the calculations). Note that the net displacement could incorporate the three-dimensional movement of the dispersers in relation to the seed source. (3) Sample, with replacement, a large number (e.g., 10 000) of retention times from the empirical distribution of retention times (Fig. 3A). For each retention time sampled, select a time series (Fig. 3B) and record the net displacement. (4) Summarize the recorded net displacement data using a frequency distribution of dispersal distances (Fig. 3C).

The most difficult step of the procedure we propose will be to produce the time series of net displacement, as this requires high-resolution movement-path data. In addition, net displacement data is often highly variable. However, the popularity and advances in telemetry mean that such data are now more commonly collected (Turchin 1998). Another option for generating time series is to use simulation models of animal movement to generate net-displacement time series. These simulation models are useful because they allow the extrapolation from fine scale movement observations to coarser scale movement patterns (Turchin 1998). However, such models include many assumptions, some of which may bias estimates of dispersal distances. This is particularly important when retention times are longer than the available time series of movement data.

DISCUSSION

Ideal data sets for testing for a link between LDD and MDS are rare. The analysis of dispersal-distance data suggests that dispersal capacity is related to MDS (Willson 1993). In contrast, the shape of the tail of the dispersal distribution is not related to MDS (Portnoy and Willson 1993). Similarly, migration rate data reveals no relationship between MDS and migration rate (MacDonald 1993).

Although the studies of Willson (1993), Portnoy and Willson (1993), and MacDonald (1993) are the best data sets of their kind, there are good reasons to be skeptical about the value of these results for exploring relationships between LDD and MDS (see *Relationship between morphological dispersal syndrome and cor-*

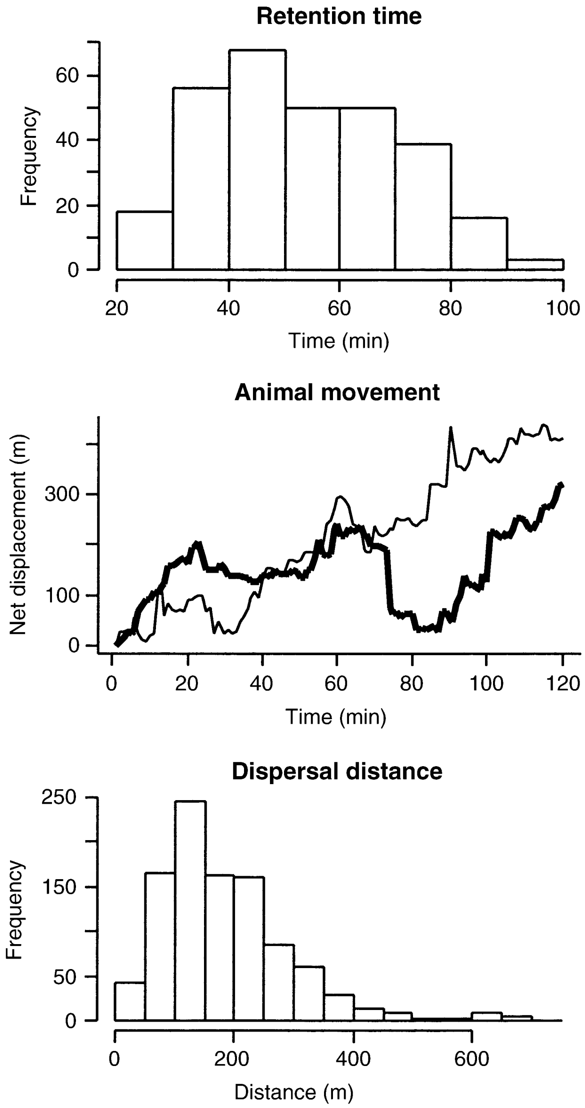

FIG. 3. An illustration of a procedure for combining data on the retention times of dispersal units and data on net displacement of dispersal vectors to yield dispersal distance distributions. The procedure involves first sampling (with replacement) a retention time and then using this retention time to sample a distance from the net displacement data; this distance is then an estimated dispersal distance. This procedure is repeated many times to yield a frequency distribution of dispersal distances. The data are simulated.

relates of dispersal capacity). However, the island colonization data from Tvärminne (Luther 1961) and Surtsey (Fridriksson 1975) provide stronger evidence that MDS is poorly related to LDD. In both cases, we found that knowledge of MDS did not improve our capacity to predict arrivals (in the case of Surtsey) and colonizations (in the case of Tvärminne). The Surtsey data revealed that most species arrived by ocean currents, in spite of the fact that only one-quarter of them have a water MDS. The data on the colonization of New Zealand from Tasmania (Jordan 2001) revealed that small-seeded species were more frequent colonists. Small seed species are dispersed by a variety of processes and appear specialized for none.

Our review of nonstandard mechanisms of dispersal showed that they are many ways that seeds can move and that the morphology of the dispersal unit is not necessarily informative of which seeds have access to which mechanisms (see *Mechanisms of long-distance dispersal*). The purpose of the review was to draw attention to the diversity of processes that move seeds. The implication is that empirical studies of LDD need to design sampling strategies that detect populations of dispersal units that have been moved by multiple processes. This is not merely a matter of increasing sampling effort. It also involves developing techniques to sample seeds being moved by different processes and to sample at sites or at times that represent unusual conditions. In effect, we are advocating sampling to increase variance in the sample, in contradiction to the statistical mantra of reducing variance in samples to increase statistical power for hypothesis testing. Our statistical analyses of data that included variance in sample conditions yielded higher estimates of LDD (see *Statistical description of dispersal distance*).

Because data on LDD will always be rare, mechanistic models provide an appealing approach for describing LDD. Recent advances in wind dispersal models allow the effects of updrafts on dispersal distance to be simulated, thus providing a way to describe exceptional behavior of a standard dispersal mechanism. Furthermore, these new wind-dispersal models suggest that dispersal units without MDS for wind can also be uplifted (Ridley 1930; *Mechanistic models for dispersal distance: Mechanistic models for long-distance dispersal by wind*), hence wind may also be a nonstandard means of LDD for some species. A second class of mechanistic models simulates LDD by animals. Seed dispersal by animals has always been difficult to study, because animals can be hard to track and their movement patterns are influenced by many factors. The increasing availability of telemetry methods has made it easier to study animal movements. Animal-telemetry data combined with seed-retention or seed-attachment data represents a revolution for our capacity to quantitatively describe seed dispersal by animals. Some of the dispersal units moved by animals in these studies have animal MDS but for others animals are a nonstandard means of dispersal. Hence both classes of mechanistic models we review predict exceptional dispersal distances due to both standard and nonstandard mechanisms. The challenge is to compare the large dispersal distances predicted by both classes of mechanistic models with field data (see *Mechanistic models for dispersal distance*).

CONCLUSION

Our analyses and review indicate that long-distance seed dispersal in plants can be caused by both standard and nonstandard mechanisms of dispersal. Unfortunately, LDD in plants remains too poorly characterized to provide a definitive answer to the question posed in the title of this paper. However, given the low predictive power of morphological dispersal syndromes and the rich variety of nonstandard mechanisms of dispersal, we suspect that as additional data become available, the answer will prove to be ''yes.''

Some of the processes that cause LDD are amenable to formal investigation (e.g., seeds dispersed as nest material, or seeds caught in updrafts), while others seem inherently untractable (e.g., the occasional seed dispersed on an oceanic raft). The multitude of mechanisms of LDD means that it is difficult to exclude the possibility that a species has access to an undetected LDD mechanism. However, the fact that the world's flora is not cosmopolitan reminds us that, although exceptional dispersal events do occur, not every species ends up realizing its potential for the exceptional. Perhaps more importantly, it reminds us that dispersal is not the only biogeographical barrier.

Can we predict which species will be long distance dispersers? We believe that this question will only be resolved once we have better empirical data on the phenomena involved in long-distance dispersal. Opening our minds to the possibilities is the first step towards capturing the data.

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