Review

Mechanisms of long-distance seed dispersal

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Growing recognition of the importance of long-distance dispersal (LDD) of plant seeds for various ecological and evolutionary processes has led to an upsurge of research into the mechanisms underlying LDD. We summarize these findings by formulating six generalizations stating that LDD is generally more common in open terrestrial landscapes, and is typically driven by large and migratory animals, extreme meteorological phenomena, ocean currents and human transportation, each transporting a variety of seed morphologies. LDD is often associated with unusual behavior of the standard vector inferred from plant dispersal morphology, or mediated by nonstandard vectors. To advance our understanding of LDD, we advocate a vector-based research approach that identifies the significant LDD vectors and quantifies how environmental conditions modify their actions.

The scope and importance of long-distance seed dispersal

Dispersal is the movement of individuals from their source location (e.g. birth or breeding site) to another location where they might establish and reproduce [1,2]. In plants, adults are sessile and dispersal typically occurs as vector-mediated transport of seeds or other dispersal units (hereafter simply seeds). In most plant species, the majority of seeds are dispersed relatively short distances from the source, rarely exceeding a few dozen meters [3]. The bulk of locally dispersed seeds generate a spatial template that often molds the local dynamics of populations and communities [4–8]. Long-distance dispersal (LDD) events are typically rare, yet play a major role in determining large-scale processes such as population spread, the flow of individuals between populations, the colonization of unoccupied habitats and the assembly of local communities from the metacommunity [7–9]. Hence, LDD, rather than local dispersal, determines large-scale phenomena of greatest conservation concern, such as the spread of invasive plants, range shifts following climate change and the persistence of species in fragmented landscapes [10]. Consequently, and despite immense difficulty in measurement and prediction [11–13], LDD research is currently experiencing an upsurge of general interest [14], especially in plant ecology [8,15–18].

Approaches to define, understand and predict LDD

Two general approaches are typically used to define LDD [14]. The proportional definition considers LDD events as a certain small proportion (e.g. 1%) of all dispersed seeds that traveled the farthest distances. According to the alternative absolute definition, LDD events are longer than a specified distance (e.g. 1 km). These two complementary aspects of LDD definition can be combined by using one component to set a threshold and reporting the corresponding value of the other component [14]. Studies reporting the absolute distance associated with a certain threshold selected according to the proportional definition reveal an important shortcoming of the proportional approach: the farthest dispersal events identified by this definition are not necessarily plausible LDD events. For instance, for 108 out of 190 wind-dispersed species examined by Soons and Ozinga [19], the estimated 99th

Glossary

Dispersal kernel: a probability density function characterizing the spatial distribution of dispersal units originating from a common source. The 'dispersal distance kernel' describes the probability of seed deposition at a certain distance, whereas the 'dispersal density kernel' describes the same probability per unit area. We use the former type throughout this review.
Dispersal vector: an agent transporting seeds or other dispersal units. Dispersal vectors can be biotic (e.g. birds) or abiotic (e.g. wind).
Fat-tailed dispersal kernel: a highly leptokurtic dispersal kernel, indicating relatively high levels of LDD, formally defined as a kernel with a tail that drops off more slowly than that of any negative exponential kernel.
Generalized dispersal: a dispersal system in which a plant is dispersed by one or more vectors, although it shows no traits that traditionally are interpreted as adaptations for dispersal by these vectors [27].
Generalized dispersal vector: a vector dispersing a large variety of plant species, including species with no apparent adaptation for dispersal by this vector.
Haplochory: seed dispersal by a single dispersal vector.
Nonstandard dispersal vector: a dispersal vector different from the one that can be inferred from the phenotypic characters of the plant [23].
Polychory: seed dispersal by multiple dispersal vectors.
Seed: in a strict sense, the fertilized ovule of spermatophytes consisting of embryo, endosperm and testa. We follow here the typical use of this term in the plant dispersal literature as a synonym for a reproductive propagule.
Seed dispersal: the process in which seeds move away from the mother plant, most commonly by a dispersal vector.
Specialized dispersal: a dispersal system in which the plant exhibits phenotypic characters that are interpreted as adaptations for dispersal by a particular vector [27]. This vector is also called the 'standard dispersal vector.'
Standard dispersal vector: a dispersal vector inferred from the phenotypic characters of the plant (e.g. the morphology of the dispersal unit) [23]. Typically, this is the vector dispersing most seeds.
Total dispersal kernel: in the context of this review, the dispersal kernel generated by all vectors dispersing a certain plant species [24].

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Table 1. Summary of the six major generalizations of LDD mechanisms in plants

Generalization number	LDD-promoting state or conditions	Relative effect on[a]			Spatial scale of LDD events[b] ($\log_{10}$ meters)	Refs
		Vector seed load (Q)	Vector displacement velocity (V)	Seed passage time (P)		
G1	Open terrestrial landscapes	Low-intermediate	Intermediate	High	2–5	[29,39]
G2	Large animals	Intermediate-high	High	Intermediate-high	2–5	[18,45]
G3	Migratory animals	Intermediate-high	High	Low-intermediate	3–6	[50,52]
G4	Extreme meteorological events	Intermediate-high	High	Intermediate	3–6	[53,54]
G5	Ocean currents	High	Low-intermediate	High	3–6	[55,56]
G6	Human transportation	High	High	High	3–7	[58,59]

[a] Relative effects on the three basic components of the general model for passive dispersal (Figure 1).

[b] The order of magnitude estimate for the dispersal distances of seeds transported by each LDD mechanism within ecological timescales (years to decades). The lower value refers to the typical modal dispersal distance related to this LDD mechanism; the higher value indicates the scale of extreme cases.

percentile of all dispersal events was shorter than 1 m, a distance typically considered 'short' rather than 'long.' Applying the proportional definition is thus useful only when the farthest (but not necessarily long) dispersal events are of interest. For all other cases, including all matters discussed in this review, we recommend applying the absolute definition. In particular, we recommend the *a priori* setting of a question-specific threshold distance, whenever a meaningful scale can be identified. For example, in an experimentally fragmented landscape, the distance between habitat patches (150 m) was used to define LDD because it represents the minimum distance seeds must travel to reach the nearest neighboring patch [20]. Studies applying an absolute definition to set a threshold should report not only whether dispersal exceeds the LDD threshold or not but also the proportion of LDD (i.e. above-threshold) events. Because this review encompasses LDD processes operating at different scales, ranging from landscape (10^2–10^3 m) to regional (10^3–10^5 m) and biogeographical (10^5–10^7 m) scales, we specify, for each LDD mechanism highlighted here, the range of spatial scales over which it typically operates (Table 1).

For most plant species, LDD events relevant at these landscape-to-biogeographical scales correspond to the

Box 1. Berg's principles of LDD mechanisms

In an insightful summary of the 'General Principles and Basic Modes of Plant Dispersal' published a quarter of a century ago, botanist Rolf Y. Berg [27] identified three basic principles that can guide the study of LDD mechanisms in plants. He first distinguished specialized from generalized dispersal, identified by the presence or absence, respectively, of characters interpreted as adaptations for dispersal by a particular vector. According to recent terminology, specialized dispersal is mediated by the 'standard' vector, the one inferred from the seed morphology (e.g. dispersal by wind inferred from the presence of a wing), whereas generalized dispersal is mediated by 'nonstandard' vectors [23]. Berg's emphasis on the likely co-occurrence of both specialized and generalized dispersal for any plant species is equivalent to the recent emphasis on the importance of dispersal by multiple vectors (polychory) [18,24,29,32,42,45]. The term 'generalized' aptly indicates that many plant species can have the same nonstandard dispersal vectors [24].

Berg's second principle highlights the importance of 'chance dispersal' for LDD. He argued that chance dispersal occurs in two different forms. The first form involves 'an unusually favorable combination of the regular dispersal factors, whether specialized or generalized.' The second form is 'an unusual coincidence involving a dispersal factor not normally operating together with the taxon in question.' The key distinction between these two forms is whether LDD results from an unusual behavior of a regular (standard or nonstandard) dispersal vector (such as extremely turbulent wind conditions [35]), or an unusual involvement of an irregular nonstandard dispersal vector (such as an escaped circus elephant). Berg's distinction is important, because it marks the boundary between LDD events that might in principle be predicted (the first form) and truly unpredictable chance events (the second form).

Berg's third principle combines the two previous principles. He argued that although morphological dispersal adaptations determine local dispersal of a plant species, they play a subordinate role in LDD. Correspondingly, nonstandard vectors (involved in generalized dispersal) have a higher tendency to generate LDD than the standard vector (involved in specialized dispersal) [23,24].

An illustration of Berg's principles (Figure I) shows that nonstandard vectors generating fat-tailed kernels will dominate LDD even if they disperse a very small proportion of seeds (see also Box 2). This illustration is likely to work well for the majority of plant species, but will not fit some particular cases. For instance, coconuts dispersed by ocean currents [56] and large-seeded pines dispersed by nutcrackers [74] are exceptional examples of LDD by standard vectors.

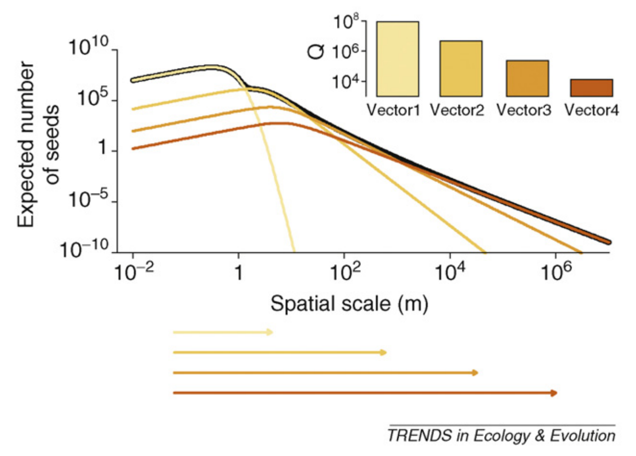

Figure I. The importance of four different dispersal vectors (different orange tints) for different parts of the total dispersal kernel (thick black line), the overall distribution of distances traveled by all seeds dispersed by all vectors, of a hypothetical plant. Vector 1 is a standard vector generating a thin-tailed dispersal kernel. Vectors 2–4 represent three nonstandard vectors, generating dispersal kernels with increasingly fatter tails indicating LDD mechanisms that operate over larger spatial scales. Although vector 4 transports 10^4 times fewer seeds than vector 1 (see inset for the distribution of vector seed loads [Q, Figure 1]), the range of dispersal distances (horizontal arrows at the bottom) is far greater for vector 4 than for vector 1. Thus, nonstandard dispersal vectors can dominate LDD, even if they disperse only a very small fraction of all seeds.

tail of the dispersal distance kernel (i.e. the statistical distribution of dispersal distances). Attempts to resolve Reid's paradox of the surprisingly rapid postglacial expansion of trees in the Northern Hemisphere [21] have highlighted the importance of 'fat-tailed' dispersal distance kernels, defined as those having a tail that drops off more slowly (i.e. LDD is more likely) than that of a negative exponential distribution. The introduction of new fat-tailed functional forms [21,22] has provided a major thrust to LDD research but also highlighted our limited quantitative understanding of LDD. Because LDD is difficult to observe and because dispersal kernels fitted to small-scale dispersal observations conflate the contribution of different dispersal vectors and cannot necessarily be extrapolated to longer distances [13,17] (Box 1), such a quantitative understanding requires investigation of LDD mechanisms.

The mechanistic approach to LDD research [6,8] encompasses two steps. First, we need to identify the relevant vectors dominating LDD of the focal plant species [23,24]. Second, we need to identify the mechanisms involved in dispersal by each relevant vector, keeping in mind that LDD might emerge from mechanisms very different from those determining local dispersal.

Improving our understanding of these two components would help to reduce, respectively, two types of uncertainty (*sensu* [25]) involved in LDD predictions: the model uncertainty (can we identify all important LDD vectors?) and the parameter uncertainty (can we quantify the factors affecting dispersal by each vector?). It would also help us to formulate general guidelines (hereafter 'generalizations') on the major mechanisms promoting LDD, which are compulsory for setting the mechanistic foundations of LDD research. However, the search for generalizations of LDD mechanisms is particularly challenging, given that LDD research has traditionally been based on anecdotal observations, and has lacked rigorous theoretical background.

Here we use a general mechanistic model of passive dispersal to distill a comprehensive literature review into six generalizations of LDD mechanisms (Table 1). We then discuss the consequences of these generalizations for our understanding of the large-scale ecological and evolutionary dynamics of plants, and outline directions for future research. Overall, we highlight the role of a set of environmental conditions and generalized dispersal vectors that often differ from those inferred from seed morphology, and that cause LDD of many plant species. Focusing research on these generalized vectors and conditions is crucial for better understanding and predicting plant LDD.

Principles of seed dispersal across multiple scales

Specific morphological attributes of the dispersal unit (e.g. a wing-like structure that increases the time a seed remains aloft) have traditionally been used to infer the 'standard' dispersal vector (e.g. wind) of a plant species [23,26]. Because seed morphology often suggests a particular dispersal vector, the notion of haplochory (i.e. dispersal mediated by a single standard dispersal vector) has long dominated plant dispersal research [26]. This strong association between a plant species and its standard dispersal vector has also been described as 'specialized dispersal' [27]. If haplochory and specialized dispersal prevail, the LDD potential of a given species should be predictable from the identity of the standard dispersal vector. For example, it has commonly been assumed that LDD requires morphological adaptations for dispersal by birds, water or wind, but is extremely unlikely for species exhibiting morphological adaptations for dispersal by ants, ballistic dispersal (explosive discharge of seeds) or for species lacking obvious dispersal adaptations [26–28].

Calls to reconsider this traditional focus on specialized dispersal by the standard vector have abounded in recent years but are not new. In particular, Berg [27] has compellingly suggested shifting the focus of dispersal research to polychory (i.e. dispersal by multiple vectors), generalized

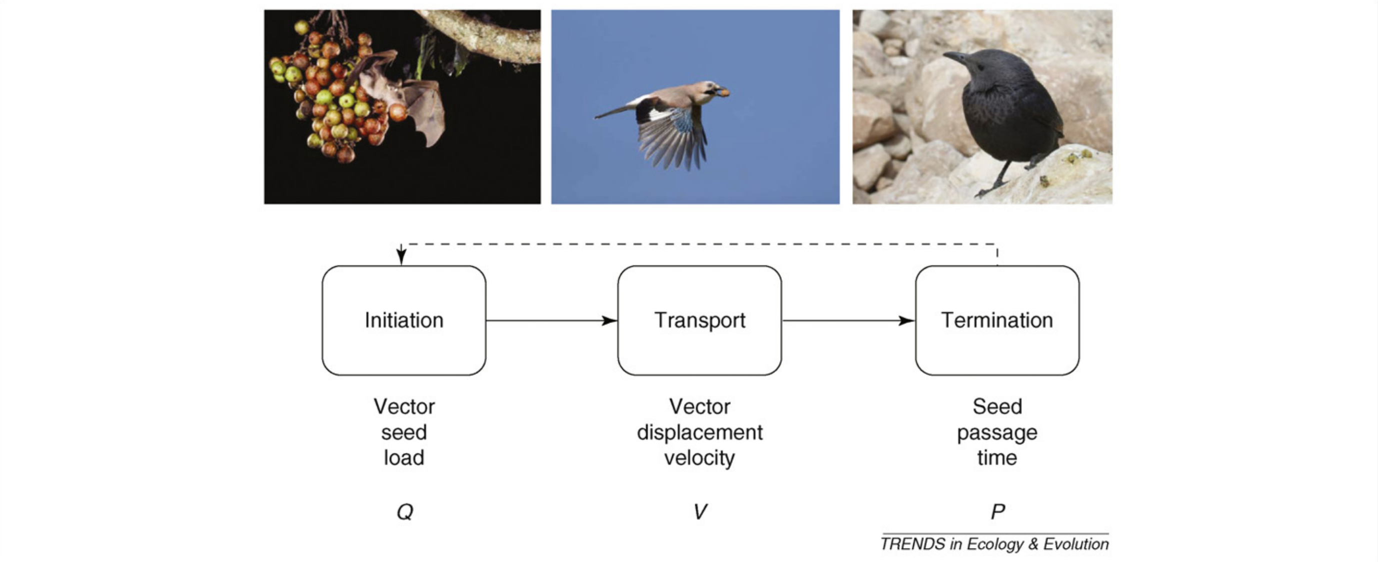

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Figure 1. A general mechanistic model of passive dispersal (adapted from Ref. [73]), describing three phases of dispersal (boxes) which depend on three key parameters (text below boxes). Photos show (from left to right): a fruit bat *Epomophorus sp.* departing from a fig cluster (© Merlin D. Tuttle, Bat Conservation International); a European jay *Garrulus glandarius* carrying an acorn (© Ran Schols, http://www.pbase.com/ranschols); and a Tristram's grackle *Onychognathus tristramii* perching near defecated *Ochradenus baccatus* seeds (© Orr Spiegel).

dispersal by nonstandard vectors and chance events (Box 1). Berg's principles, which correspond well with recent findings, can guide the investigation of the mechanisms of plant dispersal across multiple scales (Box 1). This framework emphasizes that seeds of a given species are usually dispersed by multiple vectors [24,29], including LDD vectors that tend to be different from the standard vector which disperses the vast majority of seeds locally [23]. For example, seeds with morphological adaptations for dispersal by ants can be dispersed long distances by deer (*Odocoileus virginianus*) [30] and emu (*Dromaius novaehollandiae*) [31], and seeds with adaptations for bird dispersal can be transported by floods [32]. Although the dandelion (*Taraxacum officinale*) is arguably the most popular textbook example for a wind-dispersed species with a hairy structure aiding aerial transport, the vast majority (99%) of wind-dispersed seeds are predicted to travel less than 2.15 m [19]. Yet, the hairy seed of the dandelion has a half-time buoyancy of 2.5 days in water [33] and a relatively high potential for long-term retention in furs [34]. This implies that hydrochory (dispersal by water) and epizoochory (externally by animals) have much

Box 2. What makes for an LDD vector?

The general model for passive dispersal (Figure 1 in main text) helps to identify likely LDD vectors for a given plant species. Recall that the dispersal distance of a seed is the product of its retention time at the vector (*P*) and the vector displacement velocity during this time (*V*) (Figure 1 in main text). For a set of seeds dispersed by the same vector, both *V* and *P* are likely to vary, producing a set of dispersal distances. Thus, multiplying *V* and *P* as two random variates, we obtain the dispersal distance kernel, portraying the per-seed probability to be dispersed to different distances. The area under the dispersal kernel to the right of a predefined threshold distance gives the per-seed probability of LDD. Note that a vector characterized by relatively high mean values of *V* and/or *P* does not necessarily generate higher per-seed LDD probability (Figure Ia). A vector with lower mean values might generate higher per-seed LDD probability if unusual incidents of relatively high *V* and/or long *P* are relatively more common for this vector (Figure Ia). To assess the vector's potential contribution to LDD, we therefore need to consult the *entire distribution* of *V* and *P*, not only the mean values. More specifically, we need to pay special attention to the tail of these distributions, reflecting, for example, an unusually fast displacement by a migratory bird (G3) or an exceptionally long passage time on a raft carried by ocean currents (G5). Consequently, we also need to pay special attention to the tail of the resulting dispersal kernel.

A dispersal kernel is said to have a fat tail if it drops off more slowly than the tail of a negative exponential kernel (Figure Ib). A dispersal vector generating a fat-tailed kernel is thus expected to produce more LDD events than a vector generating an exponential kernel with the same mean dispersal distance, assuming the same vector seed load (*Q*). But what if *Q* differs? To examine how seed load and tail fatness interact, we calculate the expected number of LDD events as the product of the per-seed probability of LDD and *Q* (Figure Ic). If the per-seed probability of LDD is small (thin-tailed kernels), the expected number of LDD events increases only slowly with *Q*. However, if the per-seed probability of LDD is high (fat-tailed kernels), the expected number of LDD events increases steeply with *Q*. Thus, vectors that produce fat-tailed dispersal kernels – because *V*, *P* or both are at least occasionally high – can contribute considerably to LDD even if their *Q* is relatively small. On the contrary, vectors with thin-tailed kernels might contribute very little to LDD even if *Q* is very large.

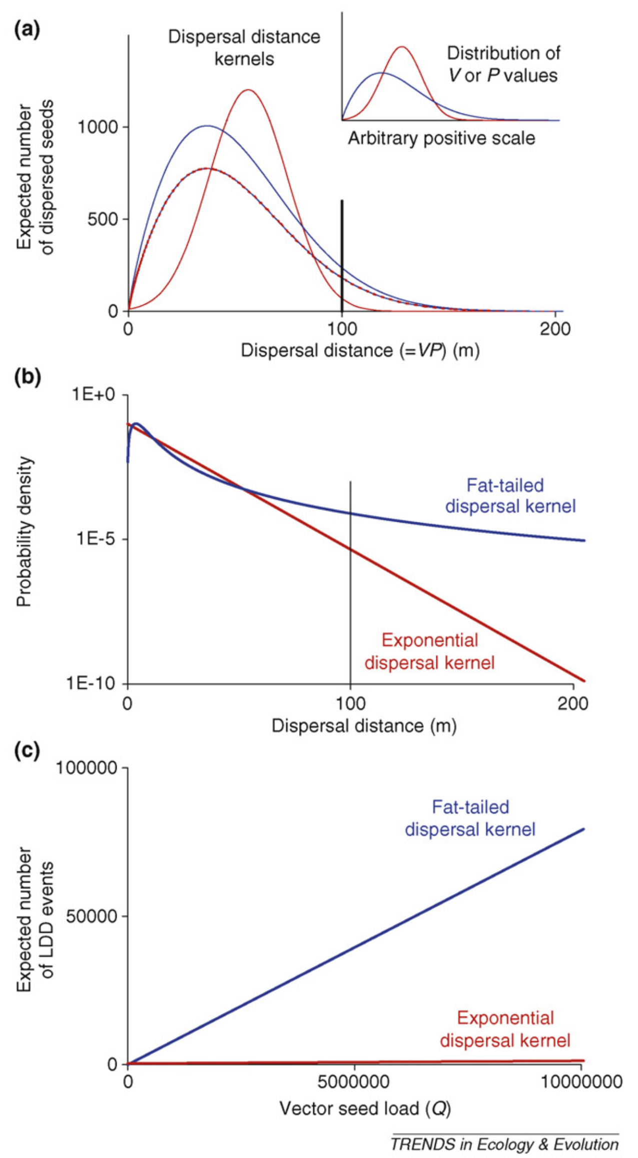

Figure I. Effects of vector seed load (*Q*), displacement velocity (*V*) and retention time (*P*) on the expected number of LDD events. The dispersal distance of a seed is the product of *V* and *P*, and thereby the distributions of *V* and *P* values determine the distribution of dispersal distances. In **(a)**, we compare a vector characterized by normally distributed *V* and *P* (red line in the inset) with higher mean values than a vector characterized by right-skewed distribution of *V* and *P* (blue line in the inset). Despite lower mean values of *V* and *P*, the dispersal kernels estimated for a combination of two right-skewed distributions (blue line in the main figure) are expected to yield more LDD events beyond a predefined absolute LDD threshold (black line in the main figure). Note that a third vector (red and blue line) characterized by normally distributed *V* and right-skewed *P* (or vice versa) also produces a relatively large number of LDD events, illustrating the importance of extreme *V* and/or *P* values for LDD. In **(b)** and **(c)**, we compare a dispersal vector generating a negative exponential kernel (red line) and a vector generating a fat-tailed kernel (blue line; represented here by the 2Dt kernel [22]). (b) The mean dispersal distance of two kernels is identical (10 m) and is much shorter than the LDD threshold (black line). (c) For the vector generating a fat-tailed kernel (blue line), the expected number of LDD events increases much more steeply with vector seed load (*Q*) than for a vector generating an exponential kernel (red line).

greater potential for LDD of dandelion seeds than anemochory (dispersal by wind). LDD can also result from unusual behavior of the standard dispersal vector as one form of a chance event (Box 1). For example, studies on LDD by wind have revealed the importance of infrequent prolonged turbulent updrafts [35]. Likewise, LDD by animals can result from specific behaviors such as rapid early-morning foraging movements of frugivorous monkeys [36].

If LDD is not necessarily driven by standard vectors and regular events, how can we then identify those other vectors and/or chance events that matter for LDD? A general mechanistic model of passive dispersal (Figure 1) can help us to assess the LDD potential of candidate vectors. This model describes three main phases of vector-mediated dispersal: the initiation phase, in which the dispersal vector removes seeds from the mother plant; the transport phase, in which the vector moves seeds away from the source; and the termination phase, in which seeds are deposited. This chain of events can be repeated, possibly involving different vectors transporting the same single seed [37].

The key parameter of the initiation phase is the *vector seed load* (Q), the number of seeds dispersed by a certain vector. Q depends on plant fecundity, fruiting schedule in relation to the behavior of the vector and the loading ability of the vector. The *vector displacement velocity* (V) is the key parameter of the transport phase. It depends primarily on the movement properties of the vector, such as its travel velocity, directionality and intermittence. The key parameter of the termination phase is the *seed passage time* (P), the duration of seed transport by the vector, which depends on both seed and vector traits and their interactions. All three key parameters can also be affected by environmental conditions such as landscape structure and climatic conditions. The dispersal distance is calculated as V times P. Dispersal vectors can disperse seeds long distances if they, at least occasionally, have high V, long P or both (Box 2). Such vectors can have a considerable contribution to LDD even if their Q is small. On the contrary, vectors with consistently low V and short P can hardly contribute to LDD even if their Q is huge (Box 2).

Six major generalizations of LDD mechanisms in plants

Guided by the general model of passive dispersal and the basic principles highlighted in the previous section, we reviewed the seed dispersal literature in search of the major proximate mechanisms promoting LDD. We did not attempt to cover exhaustively all possible mechanisms driving LDD. Rather, we searched for the mechanisms for which we have sufficient information in the literature and/or those that are characterized by mechanistic features that are likely to make them important for LDD of many plant species. We identified six major generalizations about mechanisms promoting LDD in plants. Arranged by the spatial scale for which they are most relevant (Table 1), the six generalizations state that LDD is more likely to occur in open terrestrial landscapes (G1), and to be mediated by large animals (G2), migratory animals (G3), extreme meteorological events (G4), ocean currents (G5) and human transportation (G6). In the following sections, we summarize the mechanistic reasoning and the evidence for each generalization. We then highlight relationships among the different generalizations, their consequences and directions for future research.

G1: open terrestrial landscapes

Open terrestrial landscapes – defined here as regions of no, sparse or very short vegetation, such as grassland meadows and arid steppes, as opposed to more closed landscapes such as forests and woodlands – provide favorable conditions for LDD, chiefly owing to the relative lack of obstacles to movements of seeds and their vectors. Therefore, all else being equal, vectors moving through open landscapes should have higher vector displacement velocity (V) and especially long seed passage time (P), but not necessarily larger vector seed load (Q).

Mechanistic models strongly suggest that seeds dispersed by wind have higher LDD in more open landscapes (e.g. [38]). Over smooth playa surfaces [39] and snow [40], dispersal distances of wind-dispersed seeds are much longer than in closed landscapes. Cleared channelized streams and relatively wide rivers provide highways for LDD of seeds and vegetative fragments of many plant species [33]. Furthermore, an analysis of potential LDD vectors for 123 plant communities (mostly grasslands) in The Netherlands showed a clear positive correlation between the potential for LDD and light availability as an index for landscape openness [29].

G2: large animals

Within taxonomic and/or dietary groups, animals with larger body mass tend to favor LDD because of their larger home ranges and higher travel velocity (implying higher V), as well as larger gut capacity and longer seed retention time (implying higher P) [41]. The relationship between animal body mass and Q is less clear cut: whereas the higher intake rate of large animals means that they are likely to have higher Q per individual animal, smaller animals might compensate by visiting fruiting plants more frequently or by having denser local populations (e.g. [42]).

The recent literature abounds with quantitative examples of relatively large animals dispersing seeds over long distances (e.g. [30,31,36,42,43]). Moreover, large animals have been shown to act as generalized vectors transporting seeds of a large variety of plant species, irrespective of their dispersal morphology (e.g. [43,44]). So far, studies comparing the relative contribution to LDD of animal species of different body sizes have focused chiefly on internal (endozoochory) rather than external (epizoochory) seed dispersal by animals (e.g. [18,42,45]).

G3: migratory animals

Migratory animals, specifically birds and mammals, can transport seeds both externally and internally over long distances because they move relatively fast and in a directional manner, thereby having considerably higher V compared to equivalent nonmigratory animals. Furthermore, migratory animals are more likely to transport seeds across dispersal barriers.

Evidence for this generalization comes from a large set of anecdotal observations (e.g. [46]) reported since Darwin

[47] highlighted this particular LDD mechanism. LDD by migratory animals should be especially important for plants fruiting during peak migration periods [48]. Migratory passerines typically disperse fleshy-fruited plants, whereas waterfowl typically disperse small-seeded (semi)aquatic plants. Despite a recent upsurge in research on plants dispersed internally by migratory waterfowl (e.g. [49–52]), we have almost no quantitative information on other plants, other dispersal modes and other migratory birds or mammals. The assumption that V can be estimated from observed migratory flight speeds (e.g. [50]) very likely overestimates LDD, because delays and local movements in stopover sites are ignored [52]. Moreover, laboratory estimates of P and Q from captive animals might fail to represent effects of premigratory fasting and reduction of the digestive system ([50], but see Ref. [52]). Although Q could be very high given the large number of migrating animals, general conclusions about the number of seeds dispersed during animal migration are still premature.

G4: extreme meteorological events

Extreme meteorological events, defined here as meteorological phenomena which cause exceptionally energetic flows of wind or water (e.g. tropical cyclones, tornadoes, dust devils, thunderstorms and floods induced by heavy precipitation), can produce LDD because of their exceptionally high V for plant seeds and other, even much larger, dispersal units. Extreme events are also likely to exhibit relatively long P (storms and floods carry seeds for longer periods than normal conditions) and high Q (storms and floods induce mass release of seeds).

Plants are probably dispersed by meteorological extreme events irrespective of their taxonomy and dispersal morphology (Box 3), but species occupying habitats and

Box 3. Extreme meteorological events: an example of tornado power

We are not aware of any published quantitative analysis of plant LDD induced by extreme meteorological events. Yet, some inspiration and insight can be drawn from a unique long-term (1871–1990) compilation of 163 reports on various objects – ranging in size from bank checks through books to an airplane wing and even a cow – that have been lifted by tornadoes, transported long distances by thunderstorms and found as fallout debris with sufficient information to identify the source location [75]. The resulting histogram (Figure I) resembles the right-skewed leptokurtic dispersal distance kernel typical of plant seeds, but the scale of the distances is roughly three orders of magnitude larger than any measured seed dispersal kernel. As expected, transport distances were shorter for objects classified as ‘heavy’ (>450 g) compared to ‘light,’ whereas ‘paper’ items were transported the longest distances (Figure I). The paper category is presumably the one resembling seeds of most plant species; heavy seeds, vegetative fragments and whole plants might also fit into the light and heavy categories.

A more detailed analysis of debris objects transported by a particular tornadic thunderstorm showed no correlation between terminal velocity (the constant falling velocity in still air) of 31 traceable objects (0.5–3.6 m s^{-1}, a typical range for wind-dispersed seeds) and their transport distance [76], suggesting that terminal velocity of seeds is unlikely to be a good predictor for tornado-mediated dispersal distances. The complex transport processes in tornadoes thus need to be investigated in more detail [76] to roughly estimate the scale of tornado-driven plant LDD.

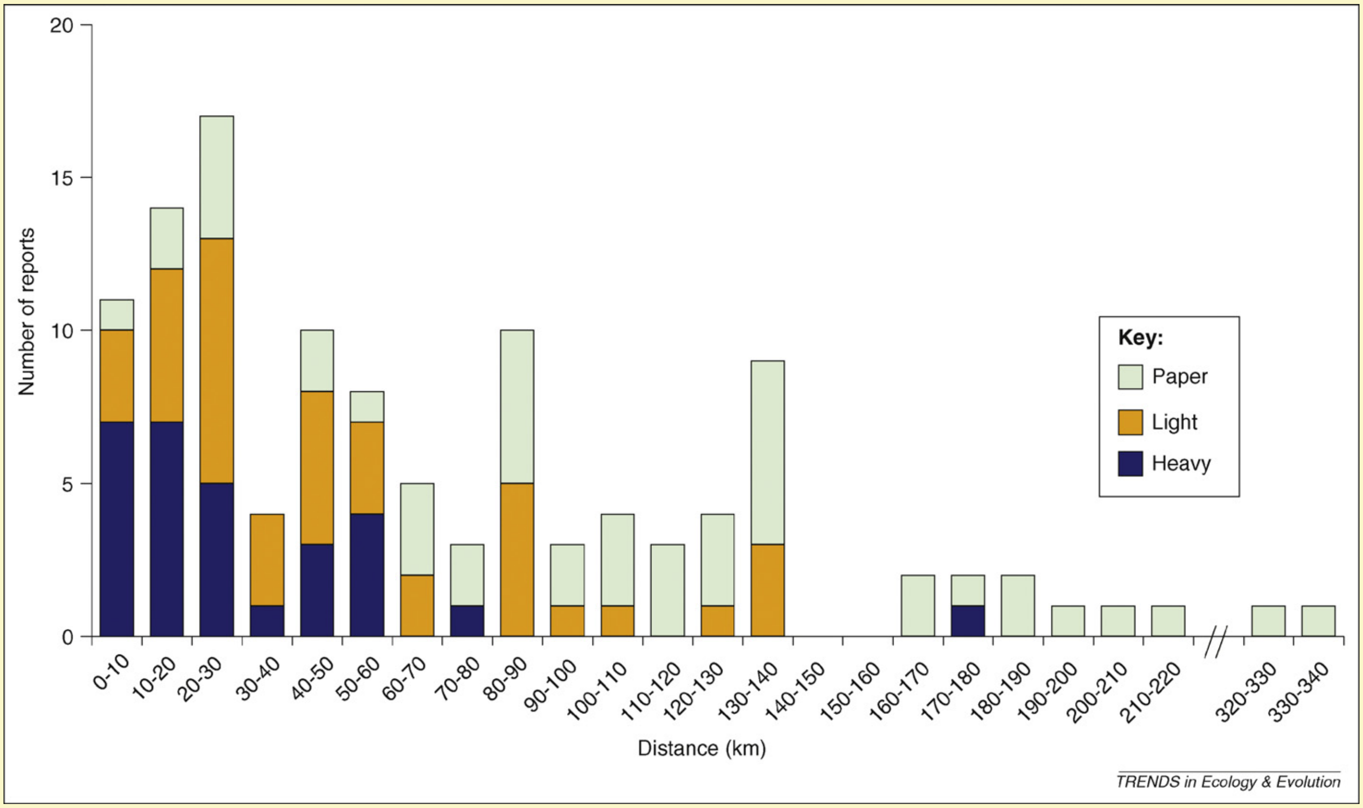

Figure I. The frequency distribution of distances traveled by tornado debris objects classified by Snow and colleagues [75] as ‘heavy’ (>450 g), ‘light’ (<450 g) and ‘paper’ items. These categories might represent entire herbaceous plants, vegetative fragments and seeds, respectively. Thus, the spatial scale over which plants can be dispersed by tornadoes is roughly three orders of magnitude greater than the spatial scale of dispersal by regular vectors. Reproduced, with permission, from Ref. [75].

regions prone to extreme events (e.g. coasts, river banks and islands) are more likely to be transported by this LDD mechanism. Dispersal biogeographers have long considered the potential of extreme meteorological events to facilitate LDD, even at intercontinental scales (e.g. [53]). Indirect evidence from studies of plant recruitment or genetic analyses suggests a causal relationship between extreme events and LDD. For example, a high frequency of kelp (*Pterygophora californica*) recruitment events at relatively long distances (up to 4 km) from the nearest zoospore source was documented after severe winter storms [54]. However, quantitative analyses that directly link extreme events to plant LDD are critically missing (Box 3).

G5: ocean currents

Ocean currents serve as efficient LDD vectors for floating fruits and for rafts transporting seeds. Ocean currents are relatively slow (mean $V = 0.1\text{–}0.3\ \mathrm{m\ s^{-1}}$), but their Q is essentially limitless. Moreover, fruits adapted for floating typically have a high P of tens of days (exceptionally extending to 19 years), and for rafting, P is typically one order of magnitude longer [55].

Only a few hundred species of higher plants have clear adaptations for prolonged floating, but a much wider range of species has been recorded as rafting. These species mostly originate from islands and coastal habitats (e.g. estuaries and salt marshes) [55,56]. A plethora of floating and rafting records suggest frequent transoceanic LDD of land plants at macroevolutionary timescales [28,46,47,55,56]. But even at ecological timescales, ocean currents can transport plant propagules of various nonspecialized dispersal morphologies over tens and even hundreds of kilometers. For example, of all plant species colonizing the volcanic island Surtsey (35 km from Iceland) in the first decade after its emergence, 78% were recorded as arriving by ocean currents, although only 25% had apparent morphological adaptations for dispersal by water [23].

G6: human transportation

Compared to non-human dispersal vectors, global trade and transportation by humans have higher Q, and most notably much higher V and longer P, thereby acting as a paramount LDD vector. Human transportation also increases the probability of seeds to disperse over natural barriers.

This generalization probably holds for most plants, especially those closely associated with human activities (e.g. crop and ornamental plants, weeds and ruderals). The rapid spread of agricultural crops across Eurasia after 8500 BC is evidence of early human-mediated LDD [57]. Over the last centuries, massive human-mediated plant LDD is evident in the large number of plant species that have become naturalized in regions outside their native range [58,59]. In most cases, human-mediated transport is given as the most plausible explanation for the unprecedented scale and frequency of dispersal over very broad barriers [60]. At smaller scales, the identification of human-mediated dispersal mechanisms is even clearer: it has been shown that LDD of seeds is caused, for example, by agricultural machinery [61] and livestock herds [62].

Relationships among generalizations

The literature provides ample evidence for interactions between the six generalizations. Such interactions can be positive so that the joint operation of two LDD mechanisms reinforces LDD. For example, tropical storms (G4) can sweep large amounts of plant debris (including seeds and other dispersal units) from continents and islands to oceans and vice versa (G5) [55]. Particularly good examples for such positive interactions are those between open terrestrial landscapes (G1) and all other mechanisms: large generalist herbivores (G2), migratory animals (G3), extreme meteorological events (G4) and human transportation (G6) are generally more frequent in more open landscapes (G1). Furthermore, for seeds or other dispersal units that float or raft on ocean currents (G5), the marine environment is obstacle free, analogous to open terrestrial landscapes (G1). Because all LDD vectors highlighted here (G2–G6) can – for most plant species – be considered as nonstandard vectors or unusual conditions of the standard vector, G1 and the general notions of nonstandard LDD vectors and chance events might be the ‘central nodes’ in the complex network of interactions among LDD mechanisms.

Other interactions between the six generalizations might be negative. Notable exceptions from several generalizations tend to be explained by the opposing effect of another generalization. For example, LDD in closed forests (i.e. an exception to G1) can be mediated by relatively large animals (G2) such as cassowaries (*Casuarius casuarius*) [43] and spider monkeys (*Ateles paniscus*) [36]. Furthermore, small migratory birds might disperse seeds farther than larger resident species (i.e. an exception to G2 is explained by G3).

Consequences of the generalizations

The six generalizations highlighted above would hopefully contribute to the development of a general mechanistic foundation for LDD research. In the following three sections, we highlight the implications of these generalizations for studying the potential ecological consequences and the ultimate evolutionary causes of LDD.

Response to environmental changes

Habitat fragmentation, climatic changes and other environmental changes, especially those occurring rapidly over relatively large spatial scales, emphasize the importance of LDD for the persistence of populations and the dynamics of communities [10]. Identification of the vectors responsible for LDD is important for predicting and understanding large-scale dynamics of plants, because different LDD vectors might be of differential importance for plant responses to environmental change. For instance, many northern temperate plants produce ripe seeds in autumn when birds migrate southward [63], suggesting that migrating birds are unlikely to play an important role in northward expansion under climate change. Thus, the directionality of the dispersal process, and not only the dispersal distance, should be considered in evaluating plant response to environmental change and other consequences of LDD.

Environmental change can also affect the mechanisms promoting LDD: climate change might increase the frequency and intensity of hurricanes [64] and rising levels of atmospheric CO_2 might increase tree fecundity [65], both potentially leading to an increase in LDD. Yet the loss or decline of large (G2) and migratory (G3) animals can substantially reduce LDD of many plant species. Certain drivers of environmental change might have complex effects on LDD: for example, habitat loss and fragmentation can either enhance LDD by making landscapes more open (G1) or reduce it by preventing the movement of large animals (G2) [66].

Population and community dynamics

To understand the consequences of LDD for population and community dynamics, an understanding of LDD mechanisms has to be combined with knowledge on post-LDD establishment [17], including an assessment of how LDD vectors (G2–G6) affect the establishment of individuals and populations. For example, extreme meteorological events (G4) do not only transport seeds over very long distances but also generate establishment opportunities by removing competitors and seed predators, thereby augmenting the importance of LDD for population spread, colonization and range dynamics. Extreme events might also have negative effects by damaging plant seeds, which lowers effective seed load (Q) and reduces the establishment probability of transported seeds.

Even with good understanding of LDD and post-LDD establishment, the stochasticity inherent in LDD can severely limit our ability to forecast the spread of a single population [12]. At larger scales, however, detailed information about LDD mechanisms can explain a substantial proportion of interspecific variation in biogeographical distributions [67], suggesting that mechanistic forecasts of range dynamics are within reach [68]. Further research on interspecific variation in LDD will also contribute to quantitative community ecology. For example, it will help to assess to what extent the immigration rate from the metacommunity to local communities is indeed constant across species, as assumed by the neutral theory of biodiversity [9].

LDD evolution

LDD clearly is exposed to selection pressures: it can be selected for to avoid kin competition [69] or to colonize new sites at the expanding front of species ranges [70]. These benefits are balanced by costs such as the failure to reach suitable establishment sites [71], which might increase with dispersal distance owing to spatial autocorrelation in habitat quality [17].

But can LDD actually respond to these selection pressures? The unpredictable occurrence of extreme meteorological events (G4) and the uncertain fate of transport by ocean currents (G5) are presumably the prime reasons for the traditional perception of LDD as an unpredictable phenomenon [27,46] which has very low heritability and cannot respond to natural selection [27,46]. However, the more predictable nature of LDD in open landscapes (G1), by large (G2) and migratory (G3) animals and by human transportation (G6) suggests that LDD can evolve through changes in hitherto unstudied phenotypic traits. Instead of a narrow focus on seed traits that predominantly affect seed passage time (P), we should thus search more broadly for traits influencing the two other basic parameters (vector displacement velocity V and vector seed load Q) of the general passive dispersal model (Box 2). For example, changes in fruiting phenology can increase the probability of seeds being dispersed by LDD vectors such as migrating animals or prolonged turbulent updrafts [72]. The identification of such 'unconventional' dispersal traits opens new avenues for the study of LDD evolution.

Concluding remarks

LDD is extremely important for the large-scale dynamics of plant populations and communities. Unfortunately, LDD research has long been limited by difficulties arising from the rarity and unpredictability of LDD and from the complexity of seed dispersal systems which often involve multiple vectors operating at different scales (Box 1). An emerging mechanistic vector-based approach promises to, at least partly, overcome these difficulties and to make

Box 4. Directions for future research

Three major lessons from this review promise to make LDD research more efficient than before. First, traditional seed-centered research approaches are unlikely to reveal LDD mechanisms. Focusing on the usual behavior of the standard vector and/or the vector dispersing most of the seeds is likely to miss chance events and generalized nonstandard vectors that drive LDD. We also need to keep in mind the limited ability of small-scale studies to detect LDD vectors, and the fallacy of extrapolating from the small-scale behavior of the standard vector to LDD (Box 1).

Second, a mechanistic vector-centered approach is needed to identify the vectors most likely to transport seeds at the scales of interest and the environmental conditions promoting LDD by these vectors. In this review, we have highlighted a set of potentially important candidate vectors (G2–G6). For example, to understand LDD of a terrestrial plant species at the regional scale, we recommend assessing the landscape structure (G1), the abundance and foraging habits of large animals (G2), the proximity to migratory routes and stopover sites of migrants (G3), the occurrence of extreme meteorological events (G4), proximity to the ocean (G5) and the intensity of human transportation (G6).

Third, once a set of relevant LDD vectors has been identified, we need to quantify the vector seed load (Q), displacement velocity (V) and passage time (P) of seeds dispersed by each vector. Each of these three basic components entails a cluster of specific parameters that need to be quantified to construct a mechanistic model for each vector. Advances in modeling seed dispersal by wind [77,78] and animals [36] in heterogeneous environments set the stage for understanding LDD in open versus closed terrestrial landscapes (G1). The quantification of allometric relationships between dispersal distance and the body size of seed-dispersing animals will provide tools for assessing LDD by animals of different size (G2). The study of LDD by both resident and migratory animals (G3) will benefit from technological advances in biotelemetry that allow us to track large-scale foraging and migration trajectories. Models and measurement devices developed by atmospheric scientists and oceanographers can be used to predict plant LDD by extreme meteorological events such as tornadoes (G4) and ocean currents (G5). Finally, data on traffic and commodity flows lend themselves to models of human-mediated LDD (G6). Better empirical data on LDD will come from linking regional-scale genetic [18] and biogeographical [15] patterns with information on LDD mechanisms, and from regional-scale field measurement campaigns [79]. The combination of all these quantitative tools will add further momentum to the already dynamic field of research on LDD in plants.

LDD research more effective (Box 4). Perhaps the greatest future challenge is to link LDD with successive stages of establishment, to quantify its consequences for fitness and for the large-scale dynamics of plants.

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