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Review

The establishment of plants following long-distance dispersal

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Long-distance dispersal (LDD) beyond the range of a species is an important driver of ecological and evolutionary patterns, but insufficient attention has been given to postdispersal establishment. In this review, we summarize current knowledge of the post-LDD establishment phase in plant colonization, identify six key determinants of establishment success, develop a general quantitative framework for post-LDD establishment, and address the major challenges and opportunities in future research. These include improving detection and understanding of LDD using novel approaches, investigating mechanisms determining post-LDD establishment success using mechanistic modeling and inference, and comparison of establishment between past and present. By addressing current knowledge gaps, we aim to further our understanding of how LDD affects plant distributions, and the long-term consequences of LDD events.

Dispersal shapes the distribution of organisms

Dispersal (see Glossary) is an important movement process shaping the distribution of organisms [1]. In plants, **effective dispersal** reduces inbreeding and competition, shapes local spatial dynamics, and allows tracking of **establishment** opportunities in changing environments [2]. Exceptionally, seeds (Figure 1) may travel hundreds or thousands of kilometers, sometimes founding new populations far outside the species' original range. Such **long-distance dispersal (LDD)** events are rare and difficult to quantify and predict [3], but are profoundly important in biogeography, where they can impact biota assembly, responses to natural and anthropogenic environmental change, and the spread of invasive species [4,5]. In the literature, **within-range LDD** is seldom distinguished from **extra-range LDD**. However, successful **colonization** following extra-range LDD events generally triggers speciation, whereas within-range LDD tends to delay speciation by maintaining occasional gene flow between discrete populations. Here, for simplicity, the term 'LDD' refers only to extra-range LDD (also termed LDD *sensu stricto* in [6]) and we discuss within-range LDD only where it offers potential insights into extra-range LDD.

Dispersal comprises three stages: initiation, transport, and termination [4] (Figure 2), but dispersal is only effective if it is followed by successful establishment. Establishment itself combines three stages (Figure 2). First is arrival, which roughly corresponds to termination of dispersal and the success of which depends on reaching a suitable habitat. Next is recruitment, which, in plants (also fungi, and animals dispersed as eggs or larvae), requires that **propagules** survive postdispersal mortality agents (e.g., seed predators and seedling herbivores) and reach reproductive age [7]. The final stage is viable population build-up, that is, expansion into a self-sustaining population [8]. Both dispersal and establishment are inherently difficult to quantify [3] and are nearly always studied in isolation from each other.

A conceptual synthesis and a general quantitative framework for post-LDD establishment across different taxa and spatiotemporal scales are lacking, reflecting the complexity of the topic, with

Highlights

Dispersal is a central process in the ecology and evolution of living organisms, reducing inbreeding and competition, shaping local spatial dynamics, and allowing tracking of establishment opportunities in changing environments.

Long-distance dispersal (LDD), beyond the range of a species, is rare and cannot be studied directly, but it is a central process in biogeography, contributing to both the assembly of natural biotas over millions of years and the spread of invasive species during the Anthropocene.

Studies of plant LDD at biogeographical scales have focused on the initiation and transport stages but have paid little attention to the subsequent establishment stage, although establishment is necessary for LDD to impact biogeography.

Establishment success is influenced by many factors, including propagule pressure, functional traits, extreme events and anthropogenic disturbances, interactions with predators, competitors and mutualists, niche flexibility, and Allee effects.

We integrate quantitative LDD frameworks with phylogeographic tools to provide a general framework for estimating the probability of colonizing a new site. This integration between biogeography and movement ecology is expected to yield important new tools and insights into the interplay between ecology, evolution, and biogeography in shaping patterns of biodiversity.

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Figure 1. Diversity of seed form and function. Morphological differences among these seeds, including size, shape, color, and external appendages (spines, wings, hairs, etc.), are determinants of the seed dispersal method the seed is adapted for, and the establishment fate of that seed. First row from left to right: *Acer thomsonii*, *Dipteronia dyeriana*, dragon tree (*Paulownia fortunei*), Indian trumpet tree (*Oroxylum indicum*), rose of Sharon (*Hibiscus syriacus*); second row from left to right: *Engelhardia roxburghiana*, hollong (*Dipterocarpus retusus*), yanagi ichigo (*Debregeasia orientalis*), Himalayan yew (*Taxus wallichiana*), marlberry (*Ardisia japonica*), traveller's tree (*Ravenala madagascariensis*), *Aster flaccidus*, *Amberboa turanica*; third row from left to right: hitch hikers (*Bidens pilosa*), nodeweed (*Synedrella nodiflora*), bur forgetmenot (*Lappula squarrosa*), Chinese forget-me-not (*Cynoglossum amabile*), common cocklebur (*Xanthium strumarium*), and wild carrot (*Daucus carota*). Photographs courtesy of Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences.

many interacting factors involved. Here, we review current knowledge of post-LDD establishment in plants and identify the key determinants of establishment success. We then present a general quantitative framework for LDD-mediated colonization, highlight the key challenges, and explore potential opportunities for future research.

Determinants of post-LDD establishment success

(i) Propagule pressure

The post-LDD establishment phase begins when at least one propagule arrives at a site outside the range of the species (Figure 2). Plant propagules are passively dispersed by various vectors, and arrival rates to distant sites depend on the **source strength** of the original population(s) and the **LDD capacity** of the propagules. Six main mechanisms facilitating LDD may be distinguished: (i) **open landscapes**; (ii) large vertebrates; (iii) migratory animals; (iv) extreme meteorological events; (v) ocean currents; and (vi) human transportation [4]. Of these, LDD by migratory animals and especially by humans is more likely to be directional. Conversely, open landscapes, large foraging vertebrates, extreme meteorological events, and ocean currents, even if acting in a particular direction, will ultimately deposit propagules at random locations, making arrival of multiple individuals at the same place unlikely.

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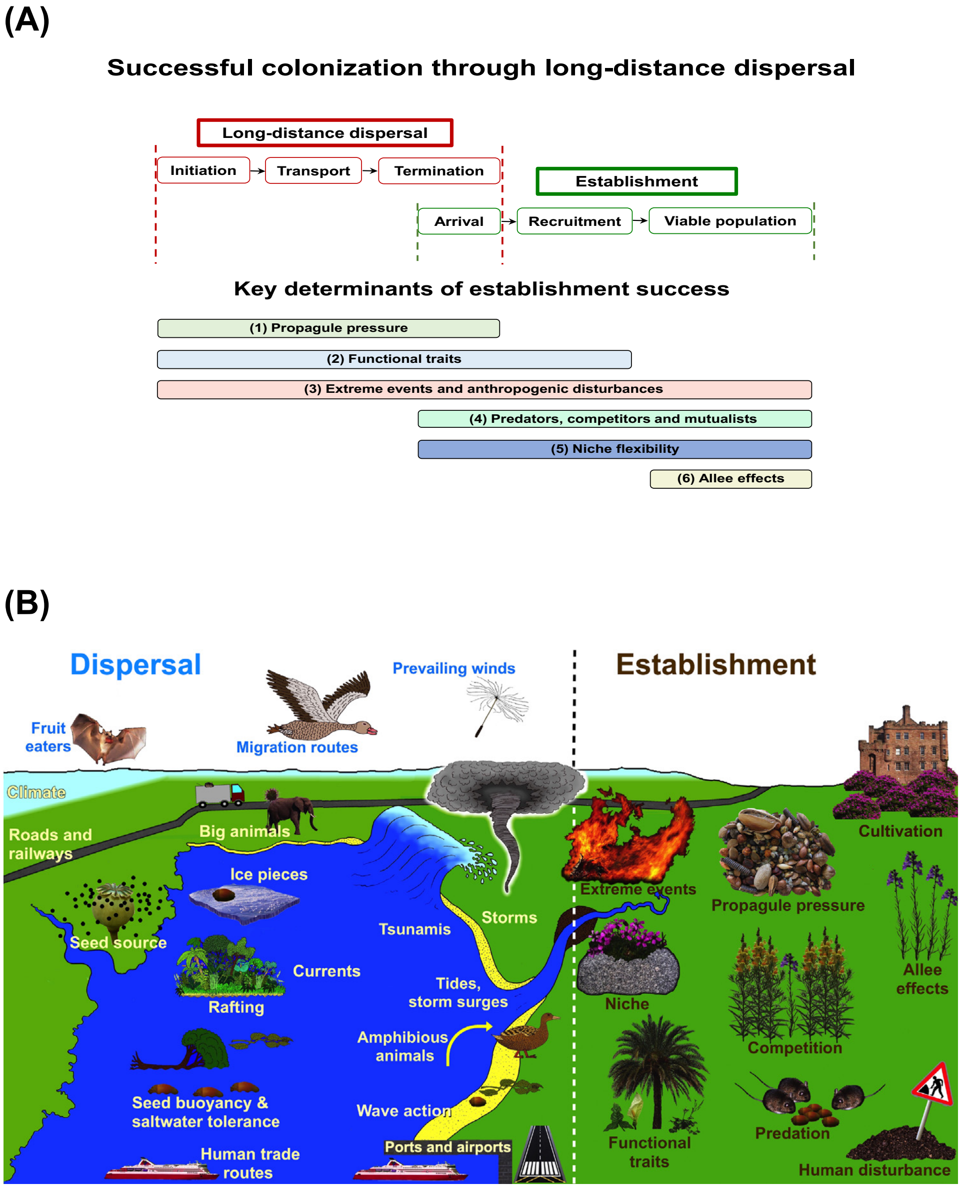

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Figure 2. Factors determining the success of plant long-distance dispersal (LDD) and subsequent establishment. (A) Schematic diagram, showing the LDD and establishment phases, each of which comprises three main stages, with the final stage of LDD overlapping the first of establishment. The six major determinants of successful establishment are shown in the order in which their effects would apply during the combined LDD and establishment process. (B) Conceptual view, showing factors determining plant LDD and subsequent establishment. The dispersal phase ends when dispersed propagules arrive at a new site, where the establishment phase begins.

Source strength and LDD capacity jointly increase the **propagule pressure** on a new range, increasing the likelihood of successful establishment; these are often considered the most consistent predictors of successful colonization [9–11]. LDD should be more likely in monoecious and self-compatible plants than in dioecious or self-incompatible species (Baker's law [12]). Therefore, if only one propagule is needed to establish a population, variation in propagule

Glossary

Allee effect: positive relationship between individual fitness and population size or density. Newly arrived plant species may experience negative Allee effects due to difficulty in finding a mate, inbreeding, or lack of facilitation among conspecifics.

Colonization: process of effective dispersal to a site not previously occupied by a species, which combines a movement (dispersal) phase and subsequent establishment phase in a site of final propagule arrival.

Dispersal: unidirectional movement of propagules away from their source (birth or breeding site), with potential implications for gene flow and colonization. The dispersal process is divided into three consecutive stages: initiation, transport, and termination (Figure 2).

Dispersal kernel: probability density function characterizing the spatial distribution of propagules in relation to the distance from a common source. The total dispersal kernel reflects the joint contribution of all vectors dispersing a particular species.

Dispersal syndrome: suite of propagule traits associated with a particular dispersal mode.

Effective dispersal: dispersal followed by population establishment.

Enemy release effect: idea that colonizing species benefit from leaving their coevolved natural enemies behind when dispersed outside their native ranges.

Establishment: at the individual level, refers to the transition from a dispersed propagule to a reproductive individual; at the population level, refers to the formation of a viable population. Altogether, the establishment process comprises three consecutive stages: arrival, recruitment, and viable population build-up (Figure 2).

Extra-range long-distance dispersal (LDD): LDD events that extend beyond the original geographical range of a species.

Long-distance dispersal (LDD): dispersal beyond a certain (long) absolute distance and/or a certain (low) proportion of all dispersal events.

LDD capacity: probability of a propagule arriving at a site of potential establishment by LDD.

Movement ecology: discipline that aims to understand movements of any type of organism in the context of the pressure might linearly predict, albeit with substantial uncertainty, the probability of a successful colonization event. However, establishment from one propagule involves a severe founder effect, while genetic diversity may be correlated with successful establishment [13]. Conversely, high propagule pressure generated by propagules arriving from multiple parts of a species range would promote genetic diversity and enhance establishment. This is one way to overcome the obstacle of requiring at least two individuals to found a population of self-incompatible or dioecious plants, the other being to disperse multiple propagules in a group, such as on dead plant matter [14] or an animal.

(ii) Functional traits

Evidence is accumulating that LDD is often not mediated by the standard dispersal mechanism inferred from the morphology of the propagule [15], implying little or no relationship between LDD and **dispersal syndromes** [16,17]. Therefore, LDD for a species is often not restricted to the vector identified from its propagule morphology (Figure 1) but can be mediated by multiple vectors. This suggests that LDD is more frequent than previously assumed, especially over long periods [3], and, hence, that the role of post-LDD establishment might have been underestimated. A global comparison of genetic diversity in plant populations found that wind-dispersed species can achieve higher diversity on islands than in mainland populations, suggesting an advantage for this syndrome [18]. On the newly emerged volcanic island of Surtsey, species adapted for water dispersal constituted only 20% of arrivals via water, but 40% of the successful colonizers, suggesting that traits facilitating establishment in coastal habitats form a significant aspect of adaptation for oceanic transport [15]. Fruiting phenology can be a key trait for directed LDD via migratory animals; for example, poleward LDD via migratory birds requires fruit ripeness to coincide with the spring migration [5]. Other traits unrelated to dispersal can also have a large influence on establishment success [10,11]; for example, the global success of the grasses might be partly due to the precocious embryo and large starch reserves aiding establishment [19]. Rates of establishment and seedling survival generally increase with seed size [20]. In invasive species, traits related to higher competitive ability also enhance establishment success [11]. Overall, however, plant traits are relatively poor predictors of colonization success in general, although they could be useful in specific contexts [21].

(iii) Extreme events and anthropogenic disturbance

Agents of sudden, widespread destruction, such as fires, cyclones, volcanic eruptions, tsunamis, and humans, can impact all stages of LDD and establishment (Figure 2), aiding arrival of seeds from the ocean [14] or escape from cultivation. Although extreme events can eliminate new colonists, a more common effect is to disturb the arrival site, reducing competition [22]. Severe disruption can influence colonization whether it is natural (e.g., volcanic eruptions [23]) or anthropogenic (e.g., farming, hunting, and urbanization [24,25]). However, relative to natural extreme events, anthropogenic disturbances are more likely to cause long-lasting or permanent changes. Given that native floras are likely to be adapted to the existing local environment, major disturbances are, on balance, more likely to aid the colonizer, especially one capable of a **niche shift**. For example, road construction drastically increased the invasion success of common ragweed (*Ambrosia*) in Germany [26].

Disturbance can affect native and alien plants at the same time, and these contrary effects may sometimes cancel each other out, leaving no net change in species number [10]. For example, roads can facilitate distribution shifts of both native and non-native plant species [27]. Anthropogenic reductions in animal populations can likewise affect both native and colonizing plant species, harming those that rely on them for seed dispersal or pollination [25] but benefitting those they predate, whereas the addition of non-native animals may have the opposite effects.

traits, internal state, motion and navigation constraints of an individual, and its interactions with other organisms and the environment.

Niche conservatism: tendency of species or lineages to colonize environments that are similar to their original habitat.

Niche shift: any change in the characteristics of the niche occupied by a species or lineage.

Open landscapes: areas lacking dense vegetation; occur naturally in arid and semi-arid regions and artificially in urban and agricultural areas. Such landscapes enhance the efficiency of LDD by wind and some animals.

Priority effects: influence upon establishment success of the order in which species arrive at a new site. Typically, earlier arrivals acquire a higher competitive advantage because they have time to both adapt to local conditions and increase in number.

Propagule: any structure capable of being propagated or acting as an agent of reproduction; a general term for all dispersal units.

Propagule pressure: number of propagules arriving at a region outside the native range of a species; considered the most consistent predictor of colonization success.

Source strength: number of propagules originating from one or more potential source populations, estimated as the product of the effective population size (N_e, size of the population that participates in producing the next generation) and the average number of propagules produced by a propagule-producing individual in a certain time period (fecundity).

Within-range LDD: LDD events in which the dispersed propagules arrive at sites within the original geographic range of a species.

(iv) Predators, competitors, and mutualists

The fundamental niche concept integrates all biotic and abiotic factors enabling individuals to survive and reproduce, and populations to persist [28]. However, we followed Soberón and Nakamura [29] in separating the realized niche from the effects of biotic interactions in studies of geographical distributions, in part because (see also [30]) predators and competitors essentially affect only the recruitment stage of establishment [9,31], whereas niche effects also impact the arrival and viable population build-up stages (Figure 2). Seed predators contribute substantially to seed loss in many ecosystems [32], and in some cases, such as black mangroves (*Avicennia germinans*) [8], predation might strongly restrict colonization success. Conversely, seeds have physical or chemical defenses [33,34], which local predators may have evolved to evade, but LDD can place the seed among nonadapted predators, generating an **enemy release effect** that might promote establishment [35,36].

Competition is also a major determinant of seed or seedling survival, but unlike predation, enemy release does not apply. Instead, in addition to the initial numerical disadvantage of the few colonists, biotic resistance by native species may evolve on millennial timescales [37]. Ecological competitiveness includes not only usurping resources from other species, but also sometimes transforming the environment biotically [38]. Although any species that establishes following LDD must overcome competition, transforming species force native species to adapt to their presence. For example, invading grass species can render habitats more hostile for other plants, especially woody species, via feedback mediated by fire or herbivory [19]. Therefore, species that can cope well with novel competitors are expected to achieve greater establishment success. Furthermore, competition also occurs among new colonists, resulting in **priority effects** [39], whereby earlier arrivals acquire a twofold competitive advantage because they have time to both increase in number and adapt to the local conditions [40], often quickly enough to prevent preadapted but later-arriving species from colonizing (the monopolization effect [2]).

Mutualists may impact establishment success at multiple stages. The ‘dust’ seeds of orchids can be dispersed long distances by wind but lack endosperm and depend on fungi for germination and establishment [41]. For some orchids, establishment in the wild may be difficult or impossible without the correct fungus. Orchids are an extreme case, but there is evidence that elements of the local microbiome can strongly impact growth in other plants [42]. Specialist pollination is also common in orchids [43] and species of figs (*Ficus*, Moraceae) cultivated outside their natural ranges cannot reproduce unless the species-specific pollinator is introduced [44]. These biotic dependencies might help explain why the Hawaiian Islands have only three native orchids and no native figs. Seed dispersal mutualisms are generally less specialized than pollination mutualisms [45], making it less likely that a plant species that has achieved LDD will fail to find local dispersal agents after arrival.

(v) Niche flexibility

Niches are crucial for understanding biogeographical patterns and the effects of speciation, climate change, and biological invasions [46]. LDD events are likely to bring propagules to sites dissimilar to the site of origin and, hence, less suitable for establishment [3]. This might reduce colonization success for species displaying **niche conservatism**, which can only establish following LDD into similar environments [47]. Conversely, where environmental differences exist, establishment requires a niche shift, which widens the range of suitable conditions and, hence, the areas where a species could establish. Niche shifts are often detectable in invasive species following human-mediated LDD [48] and in responses to climate change (e.g., [49]); species that move to track one climate variable may still need to adapt to changes in others. Greater niche flexibility increases the chance of successful establishment following LDD and

Box 1. Differences between human-mediated and natural long-distance dispersal (LDD)

LDD caused directly or indirectly by humans or by their activities (e.g., commercial transportation and travelling) is significantly different from natural LDD in seven aspects: these differences could potentially lead to greater success rates for human-mediated dispersal events than for natural ones.

(i) Timing: human-mediated LDD is a recent phenomenon, starting in the early Holocene and accelerating over the past 2000 years [54], whereas natural LDD has occurred throughout plant evolutionary history.
(ii) Frequency: tens of thousands of species have been transported by humans to new ranges over the past 2000 years, leading to numerous, simultaneous biological invasions, and making human-mediated LDD more frequent than natural LDD [55]. In the Urticaceae, for example, one natural LDD event resulting in establishment has occurred on average approximately once every million years on a global scale [14].
(iii) Quantity: human-mediated LDD will commonly carry large numbers of individuals at the same time, often from multiple sources [56], hence avoiding or minimizing negative Allee effects and founder effects.
(iv) Targeting: plants can be accidentally dispersed by humans to random sites, but intentional human-mediated LDD tends to bring seeds to sites (and especially climates) highly suitable for establishment, whereas natural LDD tends to be a random process, usually delivering propagules to sites of lower suitability for establishment [3,4].
(v) Disturbance: human activities that alter habitats tend to favor new arrivals over local floras that are adapted to the prehuman conditions. Given that this tends to coincide in both space and time with anthropogenic introductions, it provides an advantage that plants arriving naturally mostly lacked [57].
(vi) Cradling: plants introduced by humans often complete many generations in cultivation, increasing numbers and allowing adaptation to local conditions while, unlike naturally dispersed plants, being shielded from predation and competition [54]. Many species only naturalize after a significant lag phase in cultivation, indicating a clear benefit from this period.
(vii) Impact: the effects of simultaneous invasions [26], aided by other factors that favor the invader [58,59], mean that human-mediated LDD can have a greater impact on local ecosystems compared with rare natural LDD events.

might promote rapid radiation in a new environment [46,50]. However, it remains unclear what proportion of LDD events involve niche shifts.

Niche shifts are most easily examined following anthropogenic introductions, but these shifts are always within centuries of introduction, whereas most natural LDD events occurred on millennial timescales (Box 1). Natural LDD and niche flexibility have rarely been studied together (but see [46,50–53]), and no study has yet used genomic data, limiting the accuracy of evolutionary inference and how closely niche shifts can be linked to LDD events. Therefore, the role of niche dynamics in establishment following LDD remains poorly understood.

(vi) Allee effects

Once a generation has been completed following LDD (i.e., dispersed individuals become reproductive), the challenge shifts from individual survival to population maintenance, because very small populations are likely to go extinct. Disadvantages for small populations, collectively termed negative **Allee effects,** can have profound effects on colonization success following LDD, such as in outcrossing species through the difficulty of finding a mate [60] (Figure 2). Anything that reduces population size, such as predation and competition, will enhance these effects. Consequently, strategies for strengthening negative Allee effects might be useful for managing biological invasions [61]. However, species can adapt to small population sizes through self-fertilization, clonal reproduction, or other mechanisms [62]. Newly arrived species with these traits may withstand negative Allee effects, either permanently or until their effective populations achieve a larger size.

Challenges and opportunities for future research

Improved detection and understanding of LDD

Darwin [63] advocated using biogeographical data to infer dispersal events. Phylogenetic and phylogenomic methods [64], ancestral distribution reconstruction, and fossil calibration now provide increasing explanatory power for this approach. Increasing speed, accuracy, and genome coverage allows the incorporation of thousands of species into dated phylogenies and permits analytical approaches to ancestral distribution reconstruction that use parametric models (e.g., dispersal–extinction–cladogenesis), rather than narrative dispersal accounts [65]. Increasingly dense sampling of both taxa (ideally, including fossils) and genomes continues to improve phylogenetic resolution and, hence, detection of historical LDD events. From this, likely LDD modes may be inferred, such as seawater in Urticaceae [14], and seawater or birds in pearlsedge, *Scleria* [50], and also major ecological transitions associated with LDD, such as biome switching in sandalwood, *Pterocarpus* [46].

Given the large uncertainty around LDD processes and the high stochasticity of LDD events, many biogeographical studies implicitly assume that extra-range LDD and within-range LDD are generated by similar processes, even though these differ profoundly in their consequences. Evidence is lacking for differences in the dispersal processes underlying these two LDD types. Differences might exist but, based on current knowledge, we assume that the same **dispersal kernel** can be applied to both within- and extra-range LDD events. Where periodic within-range LDD events permit gene flow between populations, the frequency and typical scale of these events can be estimated [66]. Phylogeographic analysis across populations of a widespread but fragmented species could determine the approximate time and route of each within-range LDD event, as can be done for extra-range LDD at closely related species levels. Furthermore, phylogeography can be used to test hypotheses about paleoecological history and the viability of dispersal routes over time. For example, this approach revealed that the Australian seagrass *Heterozostera nigricaulis* crossed the Pacific Ocean to colonize South American by rare LDD events [67], and that migrating frugivorous birds profoundly affected the population genetic structure of the fleshy fruited shrub *Pistacia lentiscus* around the Mediterranean Basin [68]. Moreover, if within-range LDD enhances population genetic diversity and individual fitness, LDD-associated traits should be positively selected, implying that species inhabiting naturally fragmented habitats might be more prone to extra-range LDD. Although population genetic diversity is affected by various biological and environmental factors [18], the immediate outcome of extra-range LDD will usually be a strong founder effect, leading to very low genetic diversity even if the source population was genetically diverse [69]. In some cases, this disparity in diversity might allow the direction of extra-range LDD to be determined.

Thus far, biogeographic analyses have rarely gone beyond determining the route, direction, and timing of LDD events (but see [14]), with the underlying mechanisms rarely examined. Meanwhile, simulations of dispersal from empirical data have generally only covered recent timescales (Anthropocene) and short to intermediate spatial scales, without considering LDD and related mechanisms occurring in evolutionary/geological history. Experimental control at large temporal and spatial scales is impossible, but mechanistic simulation models [70], combining **movement ecology** with detection of within-range LDD via phylogeographic analysis of fragmented species ranges, might provide a more powerful predictor of LDD than either approach alone (Figure 3).

Movement ecology has contributed greatly, through both theoretical and empirical studies, to our understanding of LDD mechanisms [71–73], and empirical studies of within-range LDD can be used to test the accuracy of dispersal kernels as descriptors of the dispersal phase. One such kernel, WALD, incorporates the effects of key factors affecting LDD [74], such as using wind dynamics and related plant traits to estimate the colonization, competitive, and establishment abilities of wind-dispersed grassland species, and to predict their succession dynamics [75]. More complicated wind-dispersal models were used to assess the effects of landscape structure on LDD and establishment of plants in a large-scale landscape experiment [76]. LDD through the ocean can be modeled using ocean current simulations [14,77], without enforcing a particular dispersal kernel. Such mechanistic approaches can also incorporate knowledge about animal

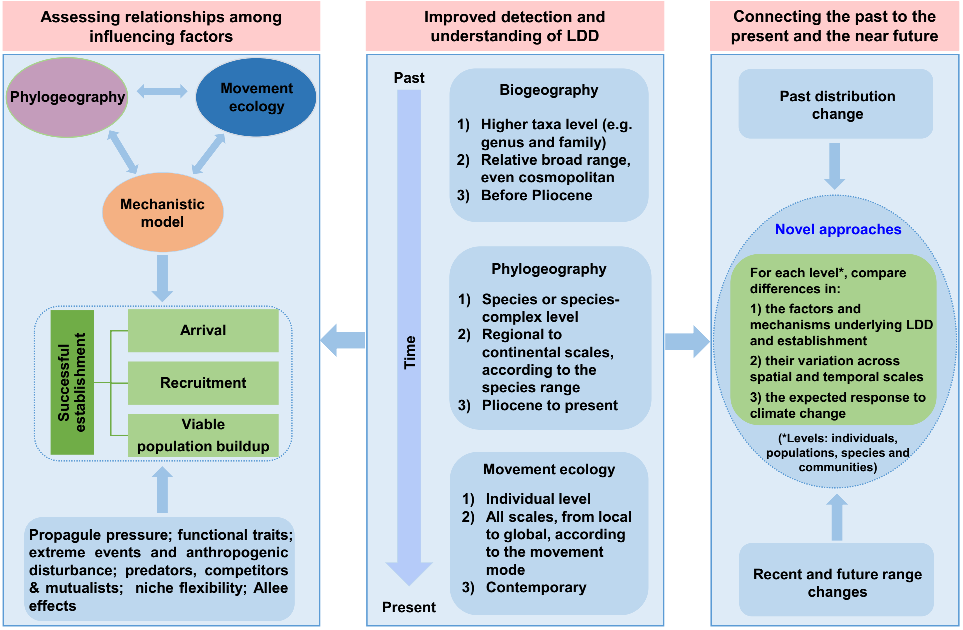

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Figure 3. A conceptual framework explaining challenges and potential directions for future research about plant long-distance dispersal (LDD) and subsequent establishment.

foraging [73], yielding new insights into how landscape structure and resource predictability affect seed dispersal [78]. Furthermore, incorporating mechanistic links between the functional traits of organisms and their environments into species distribution models permits more robust predictions of range shifts in novel or nonequilibrium contexts, such as invasions, translocations, climate change, and evolutionary shifts [79]. Moreover, recent advances in biotelemetry have enabled the direct tracking of numerous individual seed-dispersing animals, even on a global scale, generating high-resolution movement data [80] that can further advance the incorporation of multiple LDD vectors. For local dispersal, DNA barcoding can be used to identify the species of the dispersed seeds and the animal vector [81], and narrow down their sources within the ranges of the species, thereby estimating the degree of propagule pressure per species [82]. From this, the contribution of each frugivore to within-range LDD, community establishment, and plant population dynamics can be examined [83], and their potential for extra-range LDD can then be inferred. To foster integration between movement ecology and phylogeography, we present a general quantitative framework for colonization success that combines concepts and tools developed in the two disciplines (see Table I in Box 2).

Assessing relationships among factors that influence establishment

Permanent population establishment after LDD requires adaptation to local biotic and abiotic conditions. The many individual factors influencing establishment success are interrelated and while most have been studied, two key questions remain. First, which factors have most influence on colonization success in natural populations? And second, how do these factors interact to affect establishment success? These questions are critical for understanding both past biogeographical history and future responses to global environmental change.

Assessing the ultimate factors influencing the success of establishment in natural populations requires a mechanistic, ecoevolutionary, and modeling approach (Figure 3). For example, a

Box 2. A simple quantitative framework for estimating the probability of colonizing a new site

Here, we integrate quantitative long-distance dispersal (LDD) frameworks [3,4,85,86] with phylogeographic tools [87] to provide a general framework for estimating the probability of colonizing a new site.

Using phylogeographic and niche modeling tools, we first map the geographical distribution of a species during time period t (e.g., [88]) and distinguish between the Y_t occupied sites $\{y_i\}$ and the Z_t suitable-but-unoccupied sties $\{z_j\}$ (e.g., [89]), disregarding sites that are clearly unsuitable. To estimate the colonization probability ($C_{j,t}$) that the species will colonize a new site j during period t, we consider occupied (Y_t) and unoccupied (Z_t) suitable sites at the start of the period, as the baseline.

To estimate $C_{j,t}$, we need to estimate the four basic components of a successful colonization process: the source strength ($S_{i,\, t}$) (e.g., [3,4,85,90]), the total dispersal kernel ($D_{x_{ij},\, k,\, t}$) generated by k dispersal vectors (where x_{ij} is the distance between sites i and j) (e.g., [3,4,86]), the probability of recruitment of a reproductive individual ($R_{j,t}$) in a new site j (e.g., 'post-dispersal seed-to-adult survival' in [3,72]), and the transition probability from a single colonizing individual to a viable population ($V_{j,t}$) (e.g., [91]).

The product of the first two components corresponds to the propagule pressure ($P_{j,t}$) in a potential colonization site j (i.e., the expected number of propagules that arrive to that site). To estimate $P_{j,t}$, we first estimate the source strength as the product of individual fecundity (e.g., [3,85]) and population size in each site (e.g., [90]). We then estimate the fraction of the source strength that each dispersal vector k transports from an occupied site i, denoted as $S_{i,k,t}$, such that $\sum_{k=1}^{K} S_{i,k,t} = S_{i,t}$. Thus, summing across all possible source sites (Y) and all possible vectors (K), we get Equation I:

$$P_{j,t} = \sum_{i=1}^{Y} \sum_{k=1}^{K} \left(S_{i,k,t} * D_{x_{ij},k,t}\right) \qquad [I]$$

The product of the last two basic colonization components (recruitment and viable population) is the establishment probability ($E_{j,t}$) at a new site j after propagule arrival, such that $E_{j,t} \equiv R_{j,t} \times V_{j,t}$. Assuming for simplicity that all of LDD, establishment processes, and the four basic components are independent, we can estimate the probability that a single colonization attempt (i.e., the arrival of one propagule) would fail, as $1 - E_{j,t}$. With $P_{j,t}$ representing the number of attempts, the colonization probability $C_{j,t}$ of at least one successful colonization in site j can be estimated using Equation II:

$$C_{j,t} = 1 - \left(1 - E_{j,t}\right)^{P_{j,t}} \qquad [II]$$

Table I. Explanatory details for how to measure the components of LDD and establishment

Phase	Initiation		Transport	Termination	
Component	Source strength		Total dispersal kernel	Establishment	
Subcomponents	Individual fecundity	Population size	K dispersal vectors	Recruitment	Viable population
Direct estimation methods	Fruit/seed count correlations with plant traits (e.g., diameter at breast height, height)	Density sampling, population demographic analysis	Genetic-based models; mechanistic models based on vector movement data; random walk models	Germination tests; seedling survival count; quadrat dynamic monitoring	Adaptation, genomic diversity, genomic load, effective population size (Ne) and inbreeding estimates
Examples	[3,4,85,90]	[90]	[3,4,86,92]	[31,71,93,94]	[91,95,96]

physiology-based mechanistic landscape model was used to study the interactions among climate change, disturbance, and competition in determining expansion rates of trees in the northeastern USA [84], while an individual-based mechanistic model demonstrated that propagule pressure and invasion traits are the most important factors in invasion success [10]. Future research should incorporate a mechanistic understanding of the processes underlying successful colonization, advancing predictive frameworks for colonization dynamics, and revealing the relationships among influencing factors.

Bridging disciplines and connecting the past to the present

The biota of the world is being profoundly affected by biological invasions and climate change [24]. Research placing anthropogenic distribution changes in the context of natural ones over geological time is critically needed. A rare example showed that contemporary invading populations of *Pinus* belong to lineages that were particularly successful colonizers in the evolutionary past, with accelerated niche evolution detected, but not niche shifts [51]. In an animal example, comparisons of evolutionary and contemporary responses to climate change showed that the joint effects of biological invasions and climate changes have caused a breakdown of past biogeographical barriers in terrestrial gastropods [97]. Data from recent within-range LDD events and movement ecology can be applied to past LDD events. Moreover, movement ecology and allometric scaling [98] could be combined to assess the 'movement paleoecology' of extinct animals and, hence, reconstruct their role in past plant LDD [99].

Ambitious integrative and transdisciplinary efforts are needed to bridge existing gaps between biogeography, phylogeography, and movement ecology in the context of post-LDD establishment (Figure 3). This integration was advocated a decade ago [100], but recent advances in genetics and genomics have made it more feasible. Evolutionary history can inform the present, and vice versa, especially concerning the mechanisms underlying LDD and establishment. General quantitative frameworks (e.g., Box 2), which integrate all basic components of successful colonization, could guide a new generation of multidisciplinary research combining the strengths of phylogeography and movement ecology. Mechanistic simulation models should be used to investigate different spatiotemporal patterns across multiple levels of ecological organization (i.e., individuals, populations, and communities). A major goal should be to link LDD with macroevolution, and both with as many influencing factors as possible.

Concluding remarks

The lack of conceptual and quantitative frameworks linking LDD and subsequent establishment has hampered predictions and understanding of the ecological and evolutionary causes and consequences of plant colonization. Understanding these processes in the context of biogeographical, evolutionary, and ecological data can provide insights into how LDD affects plant distributions, and the long-term consequences of LDD events. Major challenges include combining findings from multiple disciplines and identifying major factors and mechanisms of colonization at different spatiotemporal scales (see Outstanding questions). Movement ecology should be integrated with mechanistic ecoevolutionary modeling, phylogenomics, and phylogeography to assess the mechanisms of colonization. This review provides conceptual and quantitative baselines for filling current knowledge gaps concerning establishment and advancing our understanding of the processes that shape global biota dynamics. An improved understanding of establishment after LDD will help us make sense of the past and predict the future in a period of rapid anthropogenic global changes. It may also help us to mitigate some of the adverse impacts of these changes, by reducing biological invasions and assisting plant movements in response to climate change.

Outstanding questions

How can LDD events at different spatial and temporal scales be detected?

Which factors have most influence on establishment success after LDD in natural populations? How do these factors interact to determine establishment? How do they interact with factors determining the success of the preceding LDD phase?

How variable are the LDD and the establishment phases across spatial and temporal scales? Can we map the major spatial hotspots of LDD and establishment at different periods in the past? How variable are these phases across individuals, populations, species, and communities?

What proportion of LDD events are followed by successful establishment? Might LDD be relatively common, but successful establishment afterwards rare?

How does establishment of alien species during the Anthropocene differ from establishment following natural LDD before human influence? In what ways can successful Anthropocene invasions inform us about the outcomes of natural LDD events?

Conversely, what can we learn from successful past LDD events that can be used to understand modern invasions?

Can we develop mechanistic models of LDD plus establishment that are accurate enough to realistically describe past events and, hence, to predict both plant invasions and plant responses to anthropogenic climate change? What factors must be incorporated into such models and how best should they be quantified?

Can the increasing number of successes and failures of establishment following plant reintroductions to the wild after extirpation teach us anything about establishment after LDD?

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Declaration of interests

No interests are declared.

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