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21 **Abstract**

22 Long-distance dispersal (LDD) beyond the range of a species is an important driver of
23 ecological and evolutionary patterns, but insufficient attention has been given to post-
24 dispersal establishment. We summarize current knowledge of the post-LDD
25 establishment phase in plant colonization, identify six key determinants of
26 establishment success, develop a general quantitative framework for post-LDD
27 establishment, and address the major challenges and opportunities in future research.
28 These include improving detection and understanding of LDD using novel
29 approaches, investigating mechanisms determining post-LDD establishment success
30 using mechanistic modeling and inference, and comparison of establishment between
31 past and present. By addressing current knowledge gaps, we aim to further our
32 understanding of how LDD affects plant distributions, and the long-term consequences
33 of LDD events.
34

35 **Key words** Biogeography, establishment, long-distance dispersal, mechanistic models,
36 movement ecology

37

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 original species' 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 leads to 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 whose success 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 post-dispersal mortality agents (e.g., seed predators and seedling herbivores) and reach reproductive age [7]. The final stage is *viable population buildup,* i.e., 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 spatial-temporal scales is currently lacking, reflecting the complexity of the topic, with 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

(1) Propagule pressure

The post-LDD establishment phase begins when at least one propagule arrives at a site outside the species' range (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: (1) open landscapes, (2) large vertebrates, (3)

78   migratory animals, (4) extreme meteorological events, (5) ocean currents, and (6)
79   human transportation [4]. Of these, LDD by migratory animals and, especially, by
80   humans is more likely to be directional. Conversely, open landscapes, large foraging
81   vertebrates, extreme meteorological events, and ocean currents, even if acting in a
82   particular direction, will ultimately deposit propagules at random locations, making
83   arrival of multiple individuals at the same place unlikely.
84   Source strength and LDD capacity jointly increase the **propagule pressure** on a
85   new range, increasing the likelihood of successful establishment; these are often
86   considered the most consistent predictors of successful colonization [9-11]. According
87   to Baker's law, monoecious and self-compatible plants should be more likely to
88   undergo LDD than dioecious or self-incompatible (SI) species [12]. Therefore, if just
89   one propagule is needed to establish a population, variation in propagule pressure might
90   linearly predict, albeit with substantial uncertainty, the probability of a successful
91   colonization event. However, establishment from one propagule involves a severe
92   founder effect, while genetic diversity may be correlated with successful establishment
93   [13]. High propagule pressure generated by propagules arriving from multiple parts of
94   a species range, in contrast, would promote genetic diversity and enhance establishment.
95   This is one way to overcome the obstacle of requiring at least two individuals to found
96   a population of self-incompatible or dioecious plants, the other being to disperse
97   multiple propagules in a group, e.g., on dead plant matter [14] or via an animal.

98   **(2) Functional traits**

99   Evidence is accumulating that LDD is often not mediated by the standard dispersal
100   mechanism inferred from the propagule's morphology [15] – implying little or no
101   relationship between LDD and **dispersal syndromes** [16,17]. Therefore, LDD for a
102   species is often not restricted to the vector identified from its propagule morphology
103   (Figure 1) but can be mediated by multiple vectors. This suggests that LDD might be
104   more frequent than previously perceived, especially over long periods [3], and hence
105   that the role of post-LDD establishment might have been underestimated. A global
106   comparison of genetic diversity in plant populations found that wind-dispersed species
107   can achieve higher diversity on islands than in mainland populations, suggesting an
108   advantage for this syndrome [18]. Species adapted for water dispersal constituted only
109   20% of arrivals through water to the newly emerged volcanic island of Surtsey, but they
110   comprised 40% of the successful colonizers, suggesting that traits that facilitate
111   establishment in coastal habitats form a significant aspect of adaptation for oceanic
112   transport [15]. Fruiting phenology can be a key trait for directed long-distance dispersal
113   via migratory animals [5]. For example, directed long-distance dispersal via migratory
114   birds towards northern latitudes is only possible for species whose fruiting period
115   overlaps the spring migration [5]. Other traits unrelated to dispersal can also have a
116   large influence on establishment success [10,11]. For example, the global success of
117   the grasses might be partly due to the precocious embryo and large starch reserves
118   aiding establishment [19]. In general, rates of establishment and seedling survival
119   increase with seed size [20]. In invasive species, traits related to higher competitive
120   ability also enhance establishment success [11]. Overall, however, plant traits are

121 relatively poor predictors of colonization success in general, although they could be
122 useful in specific contexts [21].

(3) Extreme events and anthropogenic disturbance

124 Agents of sudden, widespread destruction such as fires, cyclones, volcanic eruptions,
125 tsunamis, and humans, can impact all stages of LDD and establishment (Figure 2),
126 aiding arrival of seeds from the ocean [14] or escape from cultivation. Although
127 extreme events can eliminate new colonists, a more common effect is to disturb the
128 arrival site, reducing competition [22]. Severe disruption can influence colonization
129 whether it is natural (e.g., volcanic eruptions [23]) or anthropogenic (e.g., farming,
130 hunting, and urbanization [24,25]). However, relative to natural extreme events,
131 anthropogenic disturbances are more likely to cause long-lasting or permanent changes.
132 Because native floras are likely to be adapted to the existing local environment, major
133 disturbances are, on balance, more likely to aid the colonizer, especially one capable of
134 a niche shift. For example, road construction drastically increased the invasion success
135 of common ragweed (*Ambrosia*) in Germany [26].
136   Disturbance can affect native and alien plants at the same time, and these two
137 contrary effects may sometimes cancel each other out, leaving no net change in species
138 number [10]. For example, roads can facilitate distribution shifts of both native and
139 non-native plant species [27]. Anthropogenic reductions in animal populations can
140 likewise affect both native and colonizing plant species, harming those that rely on them
141 for seed dispersal or pollination [25] but benefitting those they predate, whereas the
142 addition of non-native animals may have the opposite effects.

(4) Predators, competitors, and mutualists

144 The fundamental niche concept integrates all biotic and abiotic factors enabling
145 individuals to survive and reproduce, and populations to persist [28]. However, we
146 followed [29] in separating the realized niche from the effects of biotic interactions in
147 studies of geographical distributions, in part because (see also [30]) predators and
148 competitors essentially affect only the recruitment stage of establishment [9,31],
149 whereas niche effects also impact the arrival and viable population buildup stages
150 (Figure 2). Seed predators contribute substantially to seed loss in many ecosystems [32],
151 and in some cases, such as black mangroves (*Avicennia germinans*) [8], predation might
152 strongly restrict colonization success. Conversely, seeds have physical or chemical
153 defenses [33,34], which local predators may have evolved to evade, but LDD can place
154 the seed among non-adapted predators, generating an **enemy release effect** that might
155 promote establishment [35,36].
156   Competition is also a major determinant of seed or seedling survival, but unlike
157 predation, enemy release does not apply. Instead, in addition to the initial numerical
158 disadvantage of the few colonists, biotic resistance by native species may evolve on
159 millennial timescales [37]. Ecological competitiveness includes not only usurping
160 resources from other species, but also, in some cases, transforming the environment
161 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 feedbacks 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 doing so fast 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]. In some cases, 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 [45], so it is less likely that a plant species that has achieved long-distance dispersal will fail to find local dispersal agents after arrival.

(5) 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, 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 can potentially 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 both increases the chances of successful establishment following LDD and 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 can only identify shifts within centuries of introduction, whereas most natural LDD events occurred millions of years ago (Box 1). Natural LDD and niche flexibility have rarely been studied together (but see [46,50-53]), and no study has employed genomic data, limiting the accuracy of evolutionary inference and how closely niche shifts can be linked to LDD events. The role of niche dynamics in establishment following LDD is therefore still poorly understood.

Box 1 Differences between human-mediated and natural long-distance dispersal

Long-distance dispersal (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 natural ones.

(1) <u>Timing.</u> Human-mediated LDD is a recent phenomenon, starting in the early Holocene and accelerating over the last 2000 years [54], whereas natural LDD has occurred throughout plant evolutionary history.

(2) <u>Frequency.</u> Tens of thousands of species have been transported by humans to new ranges over the last 2000 years, leading to numerous, simultaneous biological invasions, and making human-mediated LDD much more frequent than natural LDD [55]. In the Urticaceae for example, one natural LDD event resulting in establishment has occurred on average roughly once every million years at a global scale [14].

(3) <u>Quantity.</u> 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.

(4) <u>Targeting.</u> Plants can be accidently 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].

(5) <u>Disturbance.</u> Human activities that alter habitats tend to favor new arrivals over local floras that are adapted to the pre-human conditions. Because this tends to coincide in both space and time with anthropogenic introductions, it provides an advantage that plants arriving naturally mostly lacked [57].

(6) <u>Cradling.</u> 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.

(7) <u>Impact.</u> 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 than rare natural LDD events.

(6) 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, as 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 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 in 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 employ parametric models (e.g., dispersal-extinction-cladogenesis (DEC)), 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, e.g., seawater in Urticaceae [14], and seawater or birds in *Scleria* [50], and also major ecological transitions associated with LDD, such as biome-switching in *Pterocarpus* [46].

Given the large uncertainty around LDD processes and the high stochasticity of LDD events, many biogeographic studies implicitly assume that extra-range LDD and within-range LDD are generated by similar processes. Although this might not always be the case, we are not aware of any evidence of distinctions in the underlying dispersal processes between these two LDD types, which generally differ markedly in their consequences. Thus, at the current state of inquiry, we assume that the same **dispersal kernel** can be applied to both within- and extra-range LDD. 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 higher taxonomic levels. Furthermore, phylogeography can be used to test hypotheses

about paleoecological history and the viability of dispersal routes over time. This approach, for example, revealed that the Australian sea grass *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, although gene flow may eventually erase this signature.

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 time scales (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 far 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 emperical 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], e.g. 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 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 non-equilibrium 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 mutliple LDD vectors. For local dispersal, DNA barcoding can be

330 used to identify the species of the dispersed seeds and the animal-vector [81], and
331 narrow down their sources within the species' ranges, and thereby estimate the degree
332 of propagule pressure per species [82]. From this, the contribution of each frugivore to
333 within-range LDD, community establishment, and plant population dynamics can be
334 examined [83], and their potential for extra-range LDD can then be inferred. To foster
335 integration between movement ecology and phylogeography we present a general
336 quantitative framework for colonization success that combines concepts and tools
337 developed in the two disciplines (Box 2).

Assessing relationships among factors that influence establishment

339 Permanent population establishment after LDD requires adaptation to local biotic and
340 abiotic conditions. The many individual factors influencing establishment success are
341 interrelated and, while most have been studied, two key questions remain largely
342 unanswered. First, which factors have most influence on colonization success in natural
343 populations? And second, how do these factors interact to affect establishment success?
344 These questions are critical for understanding both past biogeographic history and
345 future responses to global environmental change.
346 Assessing the ultimate factors influencing the success of establishment in natural
347 populations requires a mechanistic, eco-evolutionary, and modeling approach (Figure
348 3). For example, a physiology based mechanistic landscape model was used to study
349 the interactions among climate change, disturbance, and competition in determining
350 expansion rates of trees in the northeastern USA [84], while an individual-based
351 mechanistic model demonstrated that propagule pressure and invasion traits are the
352 most important factors in invasion success [10]. Future research should incorporate a
353 mechanistic understanding of the processes underlying successful colonization,
354 advancing predictive frameworks for colonization dynamics, and revealing the
355 relationships among influencing factors.

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 ones $\{z_j$ (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] and [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

$$P_{j,t} = \sum_{i=1}^{Y} \sum_{k=1}^{K} (S_{i,k,t} * D_{x_{ij},k,t}).$$

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 $E_{j,t} \equiv R_{j,t} * V_{j,t}$. 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 as

$$C_{j,t} = 1 - \left(1 - E_{j,t}\right)^{P_{j,t}}.$$

Table 1. Explanatory details for how to measure the components.

Phase	Initiation		Transport	Termination	
Component	Source strength		Total dispersal kernel	Establishment	
Sub-components	Individual fecundity	Population size	K dispersal vectors	Recruitment	Viable population
Direct estimation methods	Fruit/Seed counts Correlations with plant traits (e.g., DBH, height)	Density sampling, genetic markers	Genetic-based models; Mechanistic models based on vector movement data; Random walk models;	Germination tests; seedling survival plots;	Genetic data
Examples	[3,4,85,90]	[90]	[3,4,86,92]	[31,71,93,94]	[91,95,96]

Bridging disciplines and connecting the past to the present

The world's biota 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 the 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 easier. 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 eco-evolutionary modeling, phylogenomics, and phylogeography in order 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 adverse impacts of these changes,

441 by reducing biological invasions and assisting plant movements in response to climate
442 change.
443
444

Glossary

Allee effect: a 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: the 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: The 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: A 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: a suite of propagule traits associated with a particular dispersal mode.

Effective dispersal: dispersal followed by establishment.

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

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

Extra-range LDD: LDD events that extend beyond the 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: the probability of a propagule arriving at a site of potential establishment by **long-distance dispersal**.

Movement ecology: A discipline that aims to understand movements of any type of

organism in the context of an individual's traits, internal state, motion and navigation constraints, and its interactions with other organisms and the environment.

Niche conservatism: the 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.

Priority effects: the 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: the number of propagules arriving at a region outside the native range of a species. Considered the most consistent predictor of colonization success.

Source strength: the number of propagules originating from one or more potential source populations, estimated as the product of *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 geographic range of a species.

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757

758 **Figure legends**

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

773

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

782

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

786