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The Causes and Consequences of Seed Dispersal

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Keywords

dispersal processes, dispersal syndromes, generalized gravity framework, movement ecology paradigm, seedscape, seed dispersal effectiveness

Abstract

Seed dispersal, or the movement of diaspores away from the parent location, is a multiscale, multipartner process that depends on the interaction of plant life history with vector movement and the environment. Seed dispersal underpins many important plant ecological and evolutionary processes such as gene flow, population dynamics, range expansion, and diversity. We review exciting new directions that the field of seed dispersal ecology and evolution has taken over the past 40 years. We provide an overview of the ultimate causes of dispersal and the consequences of this important process for plant population and community dynamics. We also discuss several emergent unifying frameworks that are being used to study dispersal and describe how they can be integrated to provide a more mechanistic understanding of dispersal.

1. INTRODUCTION

Seedscape: the abiotic and biotic environment surrounding a seed that influences later recruitment stages

Most organisms move at some stage of their life. Dispersal of organisms involves movements of individuals that result in gene flow across space (Ronce 2007). For plants, seed dispersal is a critical life-history stage and the sole opportunity for seeds to move locations, determining the seedscape in which an individual plant spends its life (Beckman & Rogers 2013, Schupp & Fuentes 1995). Therefore, this life-history event sets the spatial template that influences all future interactions with consequences for plant performance, spatial patterns, population dynamics, range expansion, genetic and biological diversity, and ecosystem functions (Beckman et al. 2020b, Levine & Murrell 2003, Rogers et al. 2021b, Schupp & Fuentes 1995). Because seed dispersal influences almost all levels of biological organization, it is a critical issue to study in plant ecology, evolution, and conservation.

It has been four decades since the last significant review of the ecology of seed dispersal (Howe & Smallwood 1982). Since then, there has been an explosion of interest in the topic of seed dispersal (**Figure 1**) and many excellent publications on the topic. Here we broadly review the ultimate and proximate causes of seed dispersal and its ecological consequences, highlighting exciting directions for the field. Throughout, we emphasize research on seed dispersal by both biotic and abiotic dispersal vectors, two often disparate subfields of dispersal ecology. We begin with a summary of the basics followed by an overview of the adaptive advantages of seed dispersal. Next, we describe complementary frameworks that are used to study the processes, mechanisms, and outcomes of seed dispersal and discuss how they can be integrated to obtain a synthetic understanding of seed dispersal ecology. We end by discussing higher-level consequences of seed dispersal for populations and communities. Throughout this review, we are intentional in the terminology we use in an effort to make seed dispersal ecology more inclusive (Cheng et al. 2023) (see the sidebar titled Toward More Inclusive Terminology).

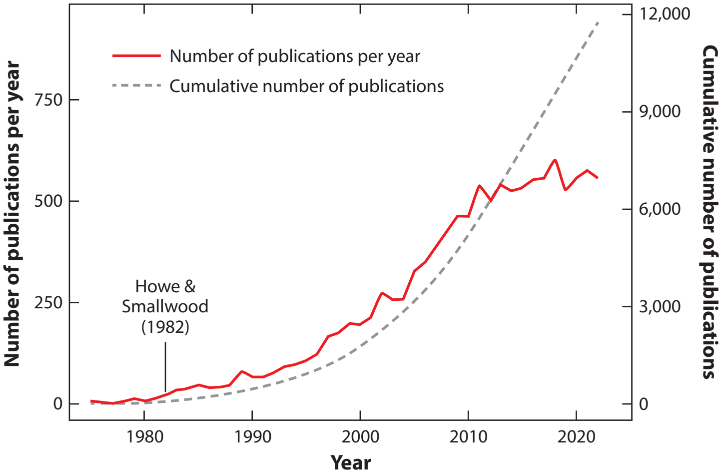


Figure 1

Number of publications per year from 1975 to 2022 on the topic of seed dispersal (total publications = 11,779). The solid red line represents the number of publications per year, and the dashed gray line represents the cumulative number of publications. We searched SCOPUS using the search term "seed dispers*" in the article title, abstract, or keywords. From 1975 to 2022, there were 10,596 articles, 594 reviews, 221 book chapters, 182 conference papers, 61 notes, 47 letters, 28 short surveys, 21 erratum, 19 editorials, 15 books, 6 reports, 6 data papers, and 2 retracted papers.

TOWARD MORE INCLUSIVE TERMINOLOGY

We intentionally avoid using terms that are exclusionary or associated with negative experiences for members of marginalized communities (Cheng et al. 2023). For example, we avoid using the terms colonization and settlement (associated with settler colonialism; alternatives include arrival, establishment, destination), invasive or exotic species (exclusionary; alternatives include nonendemic species, introduced species), and invasion (associated with militarism; Larson 2005).

2. THE BASICS OF SEED DISPERSAL

Seed dispersal is the movement of a diaspore outside of a parent plant's location (for an overview of dispersal processes, see **Figure 2**). Dispersal of seeds is ubiquitous across extant seed-bearing plants (i.e., gymnosperms, angiosperms). Flowering plants (angiosperms) have evolved a diversity of adaptations to disperse their seeds by various dispersal modes (see the sidebar titled What Are Fruit?). A plant's dispersal mode is typically inferred from direct observations or dispersal syndromes (for a comprehensive list of dispersal modes and corresponding syndromes, see **Supplemental Table 1**). Fruit and seed characteristics of dispersal syndromes are hypothesized to reflect past selection pressures from dispersal vectors (see the sidebar titled Fruit Dispersal Syndromes), though these syndromes may not align with extant dispersal vectors or current environmental conditions (Howe 2016). Some species exhibit fruit adaptations for more than one dispersal mode, such as through heterocarpy (e.g., Cheptou et al. 2008) or diplochory (Vander Wall & Longland 2004) (**Figure 2**). More frequently, fruit without specific adaptations for multiple modes of dispersal are dispersed by more than one vector. Finally, some plant species do

Diaspore: the plant part being dispersed; what constitutes a diaspore varies by species and dispersal mode

Dispersal mode: category of dispersal method or vector

Supplemental Material >

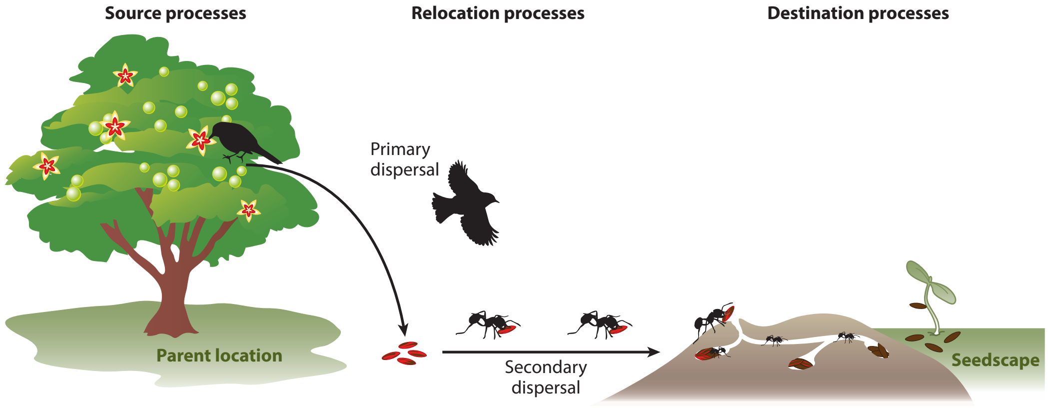


Figure 2

Seed dispersal consists of source processes (e.g., seed production, seed departure), relocation processes that result in the spatial movement of seeds, and destination processes (e.g., seed deposition, postdispersal establishment). Source processes affect source limitation and quantitatively restricted seed dispersal. The initial phase of relocation occurs when diaspores are dispersed from the plant location, either directly from the plant or from the ground under the parent plant, termed primary dispersal. After contacting a surface, such as a branch or the ground, dispersal vectors can move diaspores one or more times, resulting in secondary or higher-order phases of dispersal. Relocation processes affect distance-restricted seed dispersal and spatially contagious seed dispersal. The parent's location (*green ground*, *left*) encompasses the parent's crown, trunk or stem, and root system, and the seedscape (*green ground*, *right*) is the abiotic and biotic environment surrounding a seed that influences later recruitment stages. The figure shows an example of diplochory with dispersal of an arillate diaspore by a bird and subsequent dispersal by ants to their nests. Animal silhouettes adapted from **https://www.phylopic.org** (CC0 1.0).

WHAT ARE FRUIT?

Fruit are the mature ovaries of flowering plants that contain seeds. The pericarp of fruit consists of three layers: endocarp (inner), mesocarp (middle), and exocarp (outer). The two main categories of fruit are fleshy and dry. Fleshy fruit have higher water content in the mesocarp relative to dry fruit. Fleshy fruit include blueberries and apples; dry fruit include rice, peanuts (including the shell), and maple seeds. With the origin of fruit, flowering plants rapidly diversified, and, across major angiosperm lineages, there is little phylogenetic signal in fruit types (fleshy, dry dehiscent, and dry indehiscent fruit) (Lorts et al. 2008). By the nineteenth century, fruit and their characteristics were assumed to have an adaptive function in dispersal (van der Pijl 1982). In the twentieth century, these views were criticized as overly simplistic and adaptationist; thus, views shifted toward fruit as nonadaptive in the context of dispersal (van der Pijl 1982). In the last two decades, the adaptive function of fruit and the role of fruit traits in mediating interactions with mutualistic and antagonistic frugivores have been an active area of research resulting in significant scientific advances.

FRUIT DISPERSAL SYNDROMES

Fruit dispersal syndromes have been hypothesized for more than a century. However, whether frugivore mutualists select for fruit and seed traits has been debated (Valenta & Nevo 2020). Over the past two decades, evidence has supported frugivore selection on fruit and seed traits, specifically fruit/seed size, scent, and color, that match the morphology, behavior, and preferences of frugivores (Valenta & Nevo 2020). While color, scent, and morphological traits tend to show little phylogenetic signal, there may be mechanical, physiological, or biochemical constraints on their evolution (Valenta & Nevo 2020). For example, the prevalence of cryptic colored fruit associated with mammal dispersal in the tropics may be due to the higher relative prevalence of mammal versus bird dispersers or greater metabolic costs in producing pigments to color larger fruit, as cryptically colored fruit tend to be larger than fruit with contrastive colors associated with bird dispersal (Sinnott-Armstrong et al. 2021). In addition, diaspores experience diverse selection pressures while progressing through the phases of dispersal that can complement or oppose selection from frugivore mutualists. Elucidating the traits that constitute fruit dispersal syndromes, their functions (e.g., dispersal, defense, tolerance), and their effect on dispersal is an exciting future area of research.

not disperse seeds at all, with seeds germinating directly on or under the plant (**Supplemental Table 1**).

Supplemental Material >

In contrast to animals, which tend to be active dispersers, most plants are passive dispersers, relying on biotic and abiotic dispersal vectors for movement. More than half of seed-bearing plants are dispersed by animals (Rogers et al. 2021b), such as birds, mammals, ants, fish, and reptiles. Fleshy fruits consumed and dispersed by frugivores through regurgitation or excretion offer rewards to attract animals (endozoochory). Fruit dispersal syndromes of plant species that are mammal dispersed tend to be large fruit that have an odor and are cryptically colored (e.g., green, yellow) against green foliage, while those of bird-dispersed plant species are typically smaller fruit that are contrastively colored (e.g., black, blue, red) against green foliage (Valenta & Nevo 2020). For vision-oriented vectors, such as birds, and olfaction-oriented vectors, such as bats and primates, color and scent can act as a signal indicating fruit ripeness (Nevo et al. 2018), location (Leiser-Miller et al. 2020), and nutritional content (Sinnott-Armstrong et al. 2020). Gut passage by a wide variety of vertebrates tends to increase the probability of germination, explained mainly by deinhibitory effects of pulp removal (Rogers et al. 2021a). Fruit syndromes of diaspores moved by ants (myrmecochory) and hornets (vespicochory) contain lipid- and protein-rich structures

Dispersal syndrome: covariation of traits associated with dispersal; these can be morphological, chemical, visual, phenological, behavioral, or life-history traits

Heterocarpy: production of two or more distinct diaspores that differ in dispersal ability in the form of eliasomes (Jules 1996, Lengyel et al. 2010). Diaspores may also attach to animal fur, feathers, and so forth via hooks or hairs (ectozoochory). Some diaspores are moved by animals typically thought of as seed predators to seed caches suitable for seedling establishment (synzoochory) and may escape predation if the animal forgets them, becomes satiated, or dies before consuming them (Gómez et al. 2019). Because of the conflicting selective pressures exerted by seed-caching seed predators, fruit syndromes for synzoochory remain elusive (Gómez et al. 2019). Fruits without obvious adaptations for animal dispersal can be consumed and dispersed by vertebrate herbivores such as large ungulates or waterfowl while they consume other vegetative structures of the plant; this phenomenon is known as "foliage is the fruit" (Janzen 1984). Diaspores can even be dispersed secondarily after a carnivore eats a frugivore that ingested diaspores (diploendozoochory; Hämäläinen et al. 2017). Some plant species disperse their seeds via abiotic means, such as wind (anemochory) and water (hydrochory). The fruit syndromes of wind-dispersed species include structures that influence the release of a diaspore and appendages that aid in dispersal by decreasing a seed's falling speed (i.e., terminal velocity), such as wings on maple seeds or the hairs that form the pappus on dandelion seeds (Seale & Nakayama 2020). Fruit syndromes of species adapted to water dispersal include traits such as seed buoyancy and falling velocity in water (Soons et al. 2017). Some plant species disperse their seeds through ballistic or explosive means, in which diaspores are ejected from the plant through the release of tension as the fruit capsule opens. Humans disperse seeds via vehicles or trade (Auffret et al. 2014).

Diplochory: seed dispersal by a sequence of two phases, each involving a different dispersal agent

Frugivore: any animal that eats fruit, including seed predators, pulp feeders, and seed dispersers

Spatially contagious seed dispersal: deposition of seeds in clumps independent of distance

The relative frequency of dispersal modes varies with latitude, biome, climate, and availability of dispersers. Most plants are dispersed by animals in tropical regions, and the proportion of animal-mediated dispersal decreases with latitude (Rogers et al. 2021b) and increases with precipitation (e.g., Correa et al. 2023). The proportion of fleshy fruited species with contrastively colored fruit associated with bird dispersal is high in colder biomes (71–98%) and relatively lower in tropical biomes (63–66%) (Sinnott-Armstrong et al. 2021). Synzoochory has been reported all over the world, except Antarctica, and is commonly observed in tropical habitats, temperate and Mediterranean forests, and arid and semiarid systems (Gómez et al. 2019). Myrmecochorous plant species are found around the world, except Antarctica, and are concentrated in open dry habitats of Mediterranean climates in Australia and the Cape Floristic Region of South Africa as well as in similar habitats and temperate forests in the Northern Hemisphere (Holarctic) (Lengyel et al. 2010). In Amazonia, the distribution of dispersal modes within plant communities reflects the availability of abiotic dispersal vectors; the proportion of wind-dispersed trees increases with mean annual wind speed, while the proportion of water-dispersed trees is higher in flooded forests compared with nonflooded forests (Correa et al. 2023). Ballistic dispersal tends to be less common than other dispersal modes (<10%) in the communities that have been studied (Muller-Landau & Hardesty 2005, Willson et al. 1990). Finally, diplochory occurred in 16.8% of recorded occurrences of plant–animal seed dispersal mutualisms in North America (Vander Wall et al. 2017).

Dispersal processes result in a spatial distribution of seeds around a parent plant, termed a seed shadow. The seed shadow depends on the mechanisms of seed limitation, in which seeds fail to arrive to all suitable sites due to limited seed availability (source limitation) or limited dispersal. Dispersal (or dissemination) limitation results from a limited number of seeds dispersed by vectors (quantitatively restricted seed dispersal), dispersal to short distances (distance-restricted seed dispersal), or spatially contagious seed dispersal (Schupp et al. 2002). These different mechanisms of dispersal limitation result in suitable sites remaining unoccupied, with implications for plant populations and communities. In general, dispersal distances tend to be greatest for plants with vertebrate dispersal vectors, followed by wind, ant, ballistic, and unassisted dispersal modes, and greatest for trees, followed by shrubs and herbs (Tamme et al. 2014, Thomson et al. 2011). Taller plant species tend to disperse their seeds farther than do shorter species, both across and within dispersal modes (Tamme et al. 2014, Thomson et al. 2011) despite larger plants having heavier seeds (Moles et al. 2004). In a tropical moist forest in Panama, community-wide spatially contagious seed dispersal was widespread among animal-dispersed plant species and for wind-dispersed species during the months of strong, consistent winds (Wright et al. 2016). The spatial distribution of seeds following dispersal can be described statistically by a dispersal kernel. Dispersal kernels of seed densities that best fit patterns of seed dispersal tend to be leptokurtic and fat-tailed (i.e., not exponentially bounded), with most seed movement concentrated around the source (Bullock et al. 2017). Dispersal kernels depend on the presence of other plants in the community and the presence of herbivores (Allbee et al. 2023), the vegetation structure that the seeds move through (Damschen et al. 2014), and the relative contribution of dispersal vectors to the total dispersal kernel (Rogers et al. 2019). While seed dispersal determines the initial spatial distribution of plants, a fundamental question emerges: Why do seeds disperse?

Dispersal kernel: probability density function that describes the distribution of seeds at different distances from a source plant

Total dispersal kernel: dispersal kernel resulting from the contributions of all dispersal vectors for all plants within a system of interest

Directed dispersal: nonrandom seed deposition into habitats within a spatially heterogeneous environment that results in a fitness advantage relative to random deposition

3. WHY DISPERSE? ADAPTIVE ADVANTAGES OF SEED DISPERSAL

In the last six decades, theory has advanced our understanding of why organisms disperse, but few empirical studies have examined this question (Duputié & Massol 2013). Dispersal of organisms is costly in energy, time, risk, and opportunity (Duputié & Massol 2013). For example, in fragmented landscapes with an inhospitable matrix, wind-dispersed diaspores of the annual herb *Crepis sancta* experienced high mortality, which resulted in rapid evolution toward a higher proportion of nondispersing diaspores (Cheptou et al. 2008). In the face of these potential costs, why do organisms disperse? The major selection pressures that increase dispersal, typically measured in theoretical studies as the proportion of dispersing offspring or the distribution of dispersal distances, are generally related to competition and spatiotemporal variation in local environmental conditions (Duputié & Massol 2013, Ronce 2007). With respect to plants, we discuss these selection pressures in terms of escape from conspecific competition, escape from specialized natural enemies, adaptation to ephemeral habitats, and directed dispersal to specific habitats (for a summary of the selection pressures hypothesized to increase seed dispersal, see **Figure 3**). These selection pressures may be acting in concert, but with varying degrees of importance.

3.1. Escape from Competition

Plants compete for light, water, approximately 20 mineral nutrients, and various trace metals to survive, grow, and reproduce. Models of the evolution of dispersal in theoretical organisms have investigated competition among conspecifics in general (i.e., overcrowding) and competition among relatives (i.e., kin competition; **Figure 3*a***). Distinguishing between overcrowding and kin competition is important, as these have different consequences for inclusive fitness (Ronce 2007). In theoretical models, individuals with higher dispersal have a selective advantage that allows them to escape overcrowding when conspecific densities vary in space and time (Levin et al. 2003, Ronce 2007). In theoretical models of sibling competition, dispersal evolves, even when dispersal is costly and there is no variation in crowding or environmental quality, and depends on a variety of factors, including patch size and outbreeding rates (Levin et al. 2003, Ronce 2007). Asymmetric competition between parent and offspring can also select for increased dispersal in species with overlapping generations (Levin et al. 2003, Ronce 2007).

Empirical evidence suggests that plant competition due to overcrowding or kin competition could be an important selective pressure for seed dispersal in some contexts. For example, seedling competition has been observed to be strong in grasslands (Germain et al. 2018) but weak in Neotropical forests (Paine et al. 2008). Some species experience strong kin competition (e.g.,

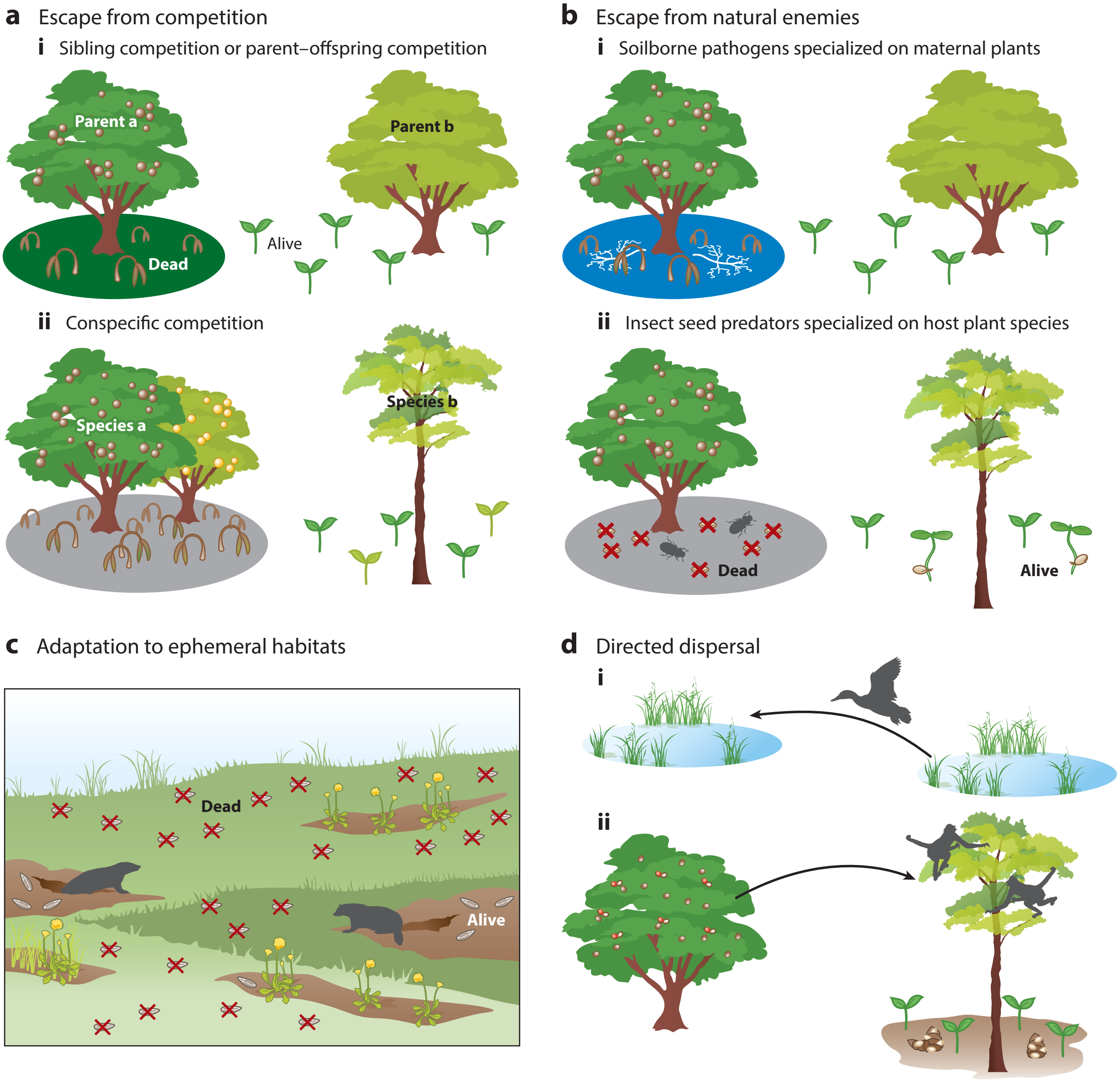


Figure 3

Selection pressures hypothesized to increase seed dispersal of plants are (*a*) conspecific competition, (*b*) escape from specialized natural enemies, (*c*) adaptation to ephemeral habitats, and (*d*) directed dispersal to specific habitats. (*a*) Escape from competition includes escape from (*i*) sibling competition or parent–offspring competition (*green oval*) and (*ii*) conspecific competition (*gray oval*). (*b*) Natural enemies can have differential effects at the (*i*) individual plant or (*ii*) species level. Blue and gray ovals represent zones of mortality by natural enemies. (*c*) An example of adaptation to ephemeral habitats is the association of prairie species with badger disturbances (Platt 1975). (*d*) Examples of passive directed dispersal include (*i*) seed dispersal of aquatic plants by waterfowl and (*ii*) seed dispersal by animals to latrines (Mason et al. 2022). Animal silhouettes adapted from **https://www.phylopic.org** (CC0 1.0).

the annual grass *Triplasis purpurea*; Cheplick & Kane 2004), while others experience kin selection, namely higher fitness with sibling neighbors (e.g., the annual mustard *Cakile edentula* var. *lacustris*; Donohue 2003). In contrast to kin competition, kin selection could reduce the selection pressure for dispersal or, if other factors as discussed below select for dispersal, increase selection for spatially contagious seed dispersal of siblings. In one of the few studies that investigated the influence of dispersal on the genetic neighborhood of seeds and its influence on plant performance, Kalisz et al. (1999) found that ants dispersing seeds of *Trillium grandiflorum* had varying effects on conspecific seed aggregation across years and, within aggregations, dispersal tended to reduce relatedness. While dispersal status, number of seeds in an aggregate, and relatedness were unrelated to seedling emergence, they have the potential to influence mating success of *T. grandiflorum* (Kalisz et al. 1999).

3.2. Escape from Natural Enemies

Natural enemies can inflict strong selection on plants that affect the traits, phenology, and dispersal of plants (Howe & Smallwood 1982, Kolb et al. 2007) (**Figure 3*b***). Natural enemies of plants include groups of organisms that differ in their life-history strategies, degree of host specialization, and movement; they include microbes, insects, mollusks, crabs, birds, and mammals. Seeds are susceptible to attack by natural enemies concentrated on or near the parent plant—those that respond to the parent plant itself (distance-responsive), the high densities of seeds concentrated on or near the parent plant (density-responsive), or both (Connell 1971, Janzen 1970).

Plants can experience substantial seed loss prior to dispersal (Kolb et al. 2007). The longer seeds remain attached to the plant, the more likely they are to be destroyed by natural enemies (Thompson & Willson 1978). Strategies of plants to minimize this predispersal seed mortality include investment in nutrient-rich fruit that facilitates rapid removal by animal dispersers to reduce exposure time, and increased defenses that deter natural enemies but can alter dispersal. For example, selection from a predispersal seed predator (the red squirrel *Tamiasciurus hudsonicus*) for increased seed physical defenses of limber pine (*Pinus flexilis*) shifted the mode of dispersal from Clark's nutcrackers (*Nucifraga columbiana*) to scatter-hoarding rodents (*Peromyscus*) (Siepielski & Benkman 2008). Increased physical defenses in the form of larger cones with thicker scales, fewer seeds, and thicker seed coats reduced removal of diaspores from the canopy by nutcrackers, subsequently increasing removal by ground-foraging scatter-hoarding rodents; in addition, thicker seed coats increased the likelihood of caching and dispersing seeds farther (Siepielski & Benkman 2008). Chemical defenses in ripe fruits can also deter natural enemies and alter dispersal. For example, amides in the ripe fruit of pepper plants (*Piper*) defend the fruit against predispersal fungal pathogens and seed predators but reduce the proportion and distances of seeds dispersed, by affecting the preferences, behavior, and physiology of its seed-dispersing bat (Nelson & Whitehead 2021).

At the postdispersal stage, mortality of seeds and seedlings due to natural enemies can be high (Forget et al. 2005). The survival of seeds and seedlings increases when escaping from distance- or density-responsive natural enemies specialized at the species level or soil microbial communities cultivated by conspecifics (Comita et al. 2014, Crawford et al. 2019), potentially conferring a fitness advantage for seed dispersal. Insect seed predators and pathogens are likely important selective agents for the evolution of seed dispersal because of their specialization on host plant populations (Benítez et al. 2013, Gripenberg et al. 2019).

Results from theoretical models demonstrate the need for more detailed studies of the movement capabilities, specialization, and life histories of natural enemies to better understand the evolution of seed dispersal. In theoretical models, locally dispersing natural enemies specialized at the plant host species level can favor the evolution of long-distance dispersal (as defined in Jordano 2017) of seeds (Muller-Landau et al. 2003). If natural enemies specialize at the host genotype level rather than the species level, as has been found for pathogens (Laine et al. 2011), then natural enemies may select for local but not necessarily long-distance dispersal of seeds, and the evolution of seed dispersal distances would further depend on the spatial structuring of plant genotypes. In a theoretical study, spatially contagious seed dispersal increased the proportion of surviving seedlings that escaped natural enemies in a simulated landscape with a single tree (Beckman et al. 2012). This was due to a lower probability of encounters between natural enemies and seeds, as well as predator satiation (Beckman et al. 2012). Genotype-level specificity of natural enemies on hosts could select for seeds from a diversity of maternal plants dispersed together within spatially contagious seed dispersal. Finally, differences in life histories and movement of natural enemies may influence the evolution of seed dispersal, as simulations have shown that the type of natural enemy and their movement capabilities influence the absolute number and spatial patterns of surviving seedlings (Beckman et al. 2012). With limited information on the movement of soil pathogens and insect seed predators, we do not know which model assumptions or parameter ranges are most relevant for real systems.

Long-distance dispersal: dispersal that is outside the genetic neighborhood area, outside the geographic extent of the population, or both

Natural enemy: organism that reduces growth and survival of its host

Informed dispersal: dispersal decisions based on environmental or social cues

3.3. Adaptation to Ephemeral Habitats

Individuals with higher dispersal can have a selective advantage that allows them to take advantage of ephemeral habitats, such as treefall gaps in forests, landslides, or disturbance mounds created by animals (Howe & Smallwood 1982, Levin et al. 2003, Platt 1975, Ronce 2007) (**Figure 3*c***). There are two distinct reasons for dispersal as an adaptation to ephemeral habitats that are general to all dispersing organisms (Ronce 2007). The first is informed dispersal in response to ephemeral habitats that may arise through local disturbance. As habitat quality changes predictably over time, such as through ecological succession, individuals escape deteriorating habitat quality and disperse into more favorable habitats. For plants, such informed dispersal in response to habitat quality can arise via developmental plasticity of heteromorphic diaspores or diaspore morphing (Seale & Nakayama 2020). Deteriorating habitat quality, such as nutrient depletion or reduced soil moisture, can inform developmental plasticity in some heterocarpic plant species, which respond by producing a greater proportion of dispersing fruits (Seale & Nakayama 2020). Environmental changes can cause diaspores to transition between dispersing and nondispersing shapes (Seale & Nakayama 2020). For example, in response to high-humidity conditions unfavorable for dispersal, the dandelion pappus morphs into a closed conelike structure, reducing the probability of detachment compared with open disclike structures that occur under low humidity (Seale et al. 2022).

The second reason for dispersal as an adaptation to ephemeral habitats is when suitable habitats vary unpredictably in both space and time and dispersal acts as a bet-hedging strategy. With a bet-hedging strategy, traits reduce fitness variance of a genotype or life-history strategy, which trades off with lower expected fitness within a generation (i.e., the arithmetic mean) and maximizes long-term average fitness across generations (i.e., geometric mean) (Simons 2011). Because the benefits of a bet-hedging strategy are realized over several generations, identifying such strategies in nature is challenging (Simons 2011). Empirical evidence exists for bet-hedging strategies in plant species with simpler life histories (e.g., seed dormancy in annuals, delayed flowering in monocarps), but it is lacking for plant species with more complex life histories (Childs et al. 2010). The widespread dispersal of seeds across a landscape varying in habitat quality can be thought of as a diversified bet-hedging strategy where risk is spread among related individuals and the correlation in reproductive success among individuals is reduced (Childs et al. 2010).

In highly unpredictable environments, theoretical models predict the evolution of dispersal polymorphisms, in which some seeds remain locally to take advantage of the current favorable

EXTENDING THE CONCEPT OF DISPERSAL SYNDROMES FROM FRUIT TO PLANTS

Dispersal syndromes in plant ecology are typically thought of as a suite of covarying phenotypic fruit and seed traits (see the sidebar titled Fruit Dispersal Syndromes). However, plants exhibit dispersal syndromes in which dispersal ability covaries with other life-history traits, similar to what has been observed for some animal species (Beckman et al. 2018). Integrating information on dispersal—in this case, maximum dispersal distances—with life-history traits derived from demographic models has revealed plant dispersal syndromes described by three main axes of variation: the fast–slow life-history continuum, the dispersal strategy axis, and the reproductive strategy axis (Beckman et al. 2018). Species with fast life-history strategies, characterized by a high net reproductive rate, a long window of reproduction, a low likelihood of escaping senescence, and a low rate of shrinking of individual plants (retrogressive growth), disperse their seeds farther than do slow-living plants (Beckman et al. 2018). Longer dispersal distances may have evolved as a bet-hedging strategy for species with fast life histories. Future research should further explore how dispersal in space and dispersal in time covary with demographic life-history traits to form plant dispersal syndromes.

habitat and some seeds disperse farther in case local conditions become unfavorable the following year (Snyder 2011). Within a fruiting plant, variation in dispersal (e.g., in the fraction of diaspores dispersing, dispersal distances, disperser assemblage) can arise because of continuous variation in fruit traits or heterocarpy (Herrera 2017, Schupp et al. 2019). Within the common Mediterranean myrtle (*Myrtus communis*), the avian disperser assemblage differs among individuals, populations, and years due to intra- and interindividual variation in fruit size (González-Varo & Traveset 2016), with the potential to influence dispersal distances and variation in the quality of seedscapes in which seeds are deposited. An Australian species, *Corymbia torelliana* (Myrtaceae), has morphological adaptations for both gravity and bee dispersal (88% and 12% of seeds, respectively); bees dispersed seeds long distances, and bee-dispersed seeds had high likelihoods of germination (Wallace et al. 2008).

Long life spans, dispersal in space, and dispersal in time are all potential bet-hedging strategies that can correlate with one another, forming dispersal syndromes (see the sidebar titled Extending the Concept of Dispersal Syndromes from Fruit to Plants). Plant species with longer life spans can average risk across time; therefore, seed dispersal as an adaptation to ephemeral habitats may be more important for plant species with shorter life spans, such as annuals or short-lived perennials (Childs et al. 2010). In theoretical models, dispersal is predicted to trade off with dormancy in uncertain environments, but both can be favored when environmental conditions are highly variable in both space and time (Chen et al. 2020). A global-scale analysis revealed a negative correlation between dispersal distance and dormancy among plant species, and seeds of perennial species were more likely to disperse farther and less likely to be dormant than annuals (Chen et al. 2020).

3.4. Directed Dispersal

Directed dispersal has been predicted to arise from highly specialized fruit–frugivore mutualisms in cases where fruits exhibit specialized adaptations to lead dispersal vectors to specific habitats (Wenny 2001). Because mutualistic interactions between fruit and frugivores tend to be diffuse, directed dispersal has been thought to be rare (Mason et al. 2022, Wenny 2001). However, several authors argue that directed dispersal can evolve from diffuse seed dispersal mutualisms without requiring specialized adaptations to direct where seeds are deposited, and hence is more common than originally thought (Mason et al. 2022, Spiegel & Nathan 2010, Wenny 2001).

To advance the conceptualization of directed dispersal, Mason et al. (2022) expanded the definition by differentiating active from passive directed dispersal. During active directed dispersal, plant adaptations direct dispersal vectors to favorable habitats, as originally proposed. A classic example is the dispersal of mistletoe by vertebrates. Mistletoe fruit have sticky pulp, and mammals and birds rub the pulp off on branches that are favorable for establishment (Amico & Aizen 2000, Reid 1989). Passive directed dispersal (**Figure 3*d***), in contrast, would result from the following conditions: (*a*) The dispersal vector is attracted to specific locations (e.g., via resource tracking), (*b*) seeds are deposited relatively more frequently in these locations, and (*c*) these locations are favorable to plants (Mason et al. 2022). While active directed dispersal may be rare, passive directed dispersal may be common. From a synthesis of the literature, Mason et al. (2022) identified 13 examples of plant–animal interactions where passive directed dispersal likely occurs because all three conditions can be met. These included potentially new examples of directed dispersal, such as dispersal to licks and watering holes and deposition in soil disturbed by the vector (see table 1 of Mason et al. 2022). We propose that this conceptualization of directed dispersal can be applied to abiotic dispersal vectors. Wind can disperse seeds along habitat corridors, as has been observed for artificial seeds dispersed along savanna corridors surrounded by pine plantation forest (Damschen et al. 2014). Water can disperse seeds of aquatic plants along a hydrological gradient, depositing seeds in specific microhabitats most favorable for their establishment (Soons et al. 2017).

Directed dispersal of seeds can result in spatially contagious seed dispersal, presenting a paradox where higher deposition of seeds in favorable habitats could lead to an increase in density-dependent mortality (Spiegel & Nathan 2010). Using analytical and simulation models, Spiegel & Nathan (2010) found intermediate levels of directed dispersal to be optimal (an evolutionary stable strategy), but they also showed that higher levels can lead to faster establishment and higher persistence of the mutant strategy within the population. To maintain intermediate levels of directed dispersal, plants can have high intraspecific variation in traits related to directed dispersal or a combination of contrasting traits (i.e., positively and negatively associated with directed dispersal) (Spiegel & Nathan 2010). Dispersal of seeds by multiple vectors of the same plant might result in this optimal intermediate level of directed dispersal, whereas reliance on a single disperser to consistently disperse seeds to suitable seedscapes may be risky over large spatiotemporal scales or may lead to high densities of seeds, resulting in density-dependent mortality (Spiegel & Nathan 2010).

3.5. Relative Importance of Adaptive Advantages

Escape from competition or natural enemies, adaptation to ephemeral habitats, and directed dispersal to specific habitats may act simultaneously to select for increased dispersal (e.g., proportion of dispersing individuals, longer dispersal distances) within a plant population. For example, increased dispersal in response to specialized natural enemies or ephemeral light environments has been suggested for the adaptive advantages of dispersal of the wind-dispersed, tropical canopy tree *Platypodium elegans* (Augspurger 1983). Plants may need to rely on multiple dispersal vectors to provide more than one of these adaptive advantages. For example, multiple dispersal vectors may disperse diaspores during the primary stage of dispersal (Wenny 2001) or through diplochory (Vander Wall & Longland 2004) (**Figure 2**). Vander Wall & Longland (2004) describe five diplochorous dispersal syndromes: wind dispersal followed by synzoochory, ballistic dispersal followed by ant dispersal, and endozoochory followed by dispersal by dung beetles, scatter-hoarding rodents, or ants. They propose that the first phase of diplochory tends to result in long-distance dispersal or escape from density-dependent mortality near the parent plant, whereas the second phase results in escape from mortality due to natural enemies or directed dispersal to suitable microsites. For example, for diplochorous species within Euphorbiaceae that are dispersed primarily through ballistic dispersal and secondarily by ants, the two phases of dispersal represent a coordinated dispersal strategy (Chen et al. 2019). Diplochorous species disperse seeds farther than species with seeds dispersed solely through ballistic means or ants, and ballistic dispersal further contributes to escape from predation and ant dispersal to directed dispersal (Chen et al. 2019).

Distinguishing the relative importance of different advantages of seed dispersal for plant fitness provides insights into current selective pressures on plants that enable generalization across plant functional groups and ecosystems (Aslan et al. 2019, Wenny 2001). Quantifying the relative importance of each of these selective advantages requires information on the spatial distribution of seeds deposited across the landscape, the suitability and distribution of microsites in which seeds are deposited (i.e., seedscapes), how this suitability shifts with plant ontogeny, and spatiotemporal variation in suitable microsites relative to dispersal. Under the hypotheses of escape from competition and natural enemies, seed and seedling survival are expected to increase with distance from the parent plant or decrease with increasing densities of conspecific or related seeds and seedlings irrespective of the location of suitable microsites. In the last several decades, studies have shown an advantage to escaping from the nearest adult tree or high conspecific densities, but they typically have not isolated the mechanism underlying observed patterns of distance- and density-dependent survival (Comita et al. 2014). While there is growing support for the role of soil pathogens in driving these patterns (Comita et al. 2014), it will be important for future studies to examine the mechanisms contributing to patterns of plant survival. As the spatial and temporal scales of natural enemy attack and competition differ, these disparate mechanisms differentially influence the evolution of dispersal as well as the consequences of dispersal. Few studies have adequately distinguished directed dispersal to suitable microsites from dispersal that is adapted to take advantage of ephemeral habitats (Wenny 2001). Seed dispersal adapted to ephemeral habitats requires quantifying an advantage in the geometric-mean fitness across multiple generations and appears detrimental for fitness within a generation (Simons 2011). Under this hypothesis, the expected number of seeds arriving in microhabitats should be proportional to the abundance of available sources, size of microhabitats, and distance of microhabitats from source plants (Mason et al. 2022, Wenny 2001). Directed dispersal predicts disproportionately higher deposition into microhabitats with a higher probability of each seed surviving to reproduction compared with dispersal adapted to ephemeral habitats (Mason et al. 2022, Wenny 2001).

4. SEED DISPERSAL FRAMEWORKS TO LINK PROCESSES TO CONSEQUENCES

Obtaining a more synthetic understanding of dispersal processes across the wide variety of dispersal vectors that ultimately lead to plant spatial patterns and fitness necessitates the integration of relevant knowledge and approaches from a variety of disciplines (see the sidebar titled Understanding Seed Dispersal: An Interdisciplinary Endeavor). Since Howe & Smallwood's (1982) review, several frameworks have been proposed that unify the conceptual understanding of dispersal relevant for seed dispersal ecology (for a graphical synthesis of these frameworks, see **Figure 4**). The generalized gravity framework (GGF) explicitly considers all phases of the dispersal process, the movement ecology paradigm (MEP) specifies the mechanistic components of the dispersal process, and the seed dispersal effectiveness (SDE) framework quantifies the outcomes of dispersal processes to estimate the contributions of dispersal vectors to plant fitness. We describe these frameworks generally and discuss how their integration can deepen our understanding of seed dispersal processes and consequences.

UNDERSTANDING SEED DISPERSAL: AN INTERDISCIPLINARY ENDEAVOR

Interdisciplinary advances in theory, quantitative methods, standardized data collection, and trait-based approaches aid our ability to scale from processes that determine the movement of an individual seed to population and community dynamics (Aslan et al. 2019, Beckman et al. 2020a). For example, an understanding of the mechanisms of dispersal for abiotically dispersed plants can be studied at the intersection of ecology and fluid dynamics (e.g., Nathan et al. 2011, Seale et al. 2022) and, for animal-dispersed plants, at the intersection of plant demography and animal movement (e.g., Borah & Beckman 2022, Cortes & Uriarte 2012). Various approaches exist to scale from the movement of individual seeds to higher-level consequences, ranging from complex mechanistic simulations to mathematical approximations (Beckman et al. 2020b). Each approach has its own advantages and disadvantages in terms of generalizability, realism, precision, tractability, data requirements, and computational resources (Beckman et al. 2020b). In addition, the quantity and accessibility of data relevant for seed dispersal continue to increase, including data on animal movement, environmental factors, interaction networks, plant demography, and plant and animal traits (see summary in the supporting information of Beckman et al. 2020b).

4.1. Generalized Gravity Framework

The GGF, presented by Jongejans et al. (2015) as a unifying quantitative framework for dispersal, enables common representations of dispersal processes across taxa using mathematical functions, with the goal of generalizing understanding of dispersal across all organisms and contexts. Within the GGF, dispersal is broken into three phases: (*a*) source processes, which include predispersal and departure processes, (*b*) relocation processes, which result in diaspore movement, and (*c*) destination processes, which include seed deposition and postdispersal processes (Jongejans et al. 2015) (**Figures 2** and **4*a***). Describing dispersal according to the GGF allows one to determine whether dispersal patterns are more strongly mediated by source, relocation, or destination processes. Some generalities that have emerged from this framework are the contributions of air, water, and humans to long-distance dispersal for many organisms; the role of landscape structure in resulting dispersal patterns across organisms; and the application of similar mathematical formulations across organisms (e.g., vectored dispersal of pathogens and pollen) or to represent different dispersal mechanisms (e.g., wind versus water) (Jongejans et al. 2015). Explicitly describing mathematical functions for each phase of dispersal helps identify information of the dispersal process that is missing or understudied.

4.2. Movement Ecology Paradigm

The MEP, proposed by Nathan et al. (2008), seeks to find generalization in movement across taxa, and answer questions about "why, how, where, and when organisms move" (p. 19053). The MEP focuses specifically on understanding the mechanisms underlying the observed movement path, from individual steps to movement phases to a lifetime movement track. It characterizes three components of a focal individual—internal state, motion capacity, and navigation capacity—and a fourth component, external factors, which together influence movement of the focal individual (Nathan et al. 2008) (for the relationships among the mechanistic components of the MEP, see **Figure 4*b***). The movement path of an organism can be modeled with mathematical functions describing each mechanistic component and their interactions (Nathan et al. 2008). When applying the MEP specifically to seed dispersal, the four components must be considered from the plant perspective and, if relevant, the vector perspective. For plants, internal states (why an individual moves) arise over evolutionary time in the form of plant traits associated with dispersal syndromes

Movement phase: sequence of steps associated with a particular goal (or goals) of an organism

Internal state: state of the focal individual that influences its motivation and readiness to move

Motion capacity: refers to traits of the focal individual that enable movement

Navigation capacity: refers to traits of the focal individual that enable spatial and temporal orientation during movement

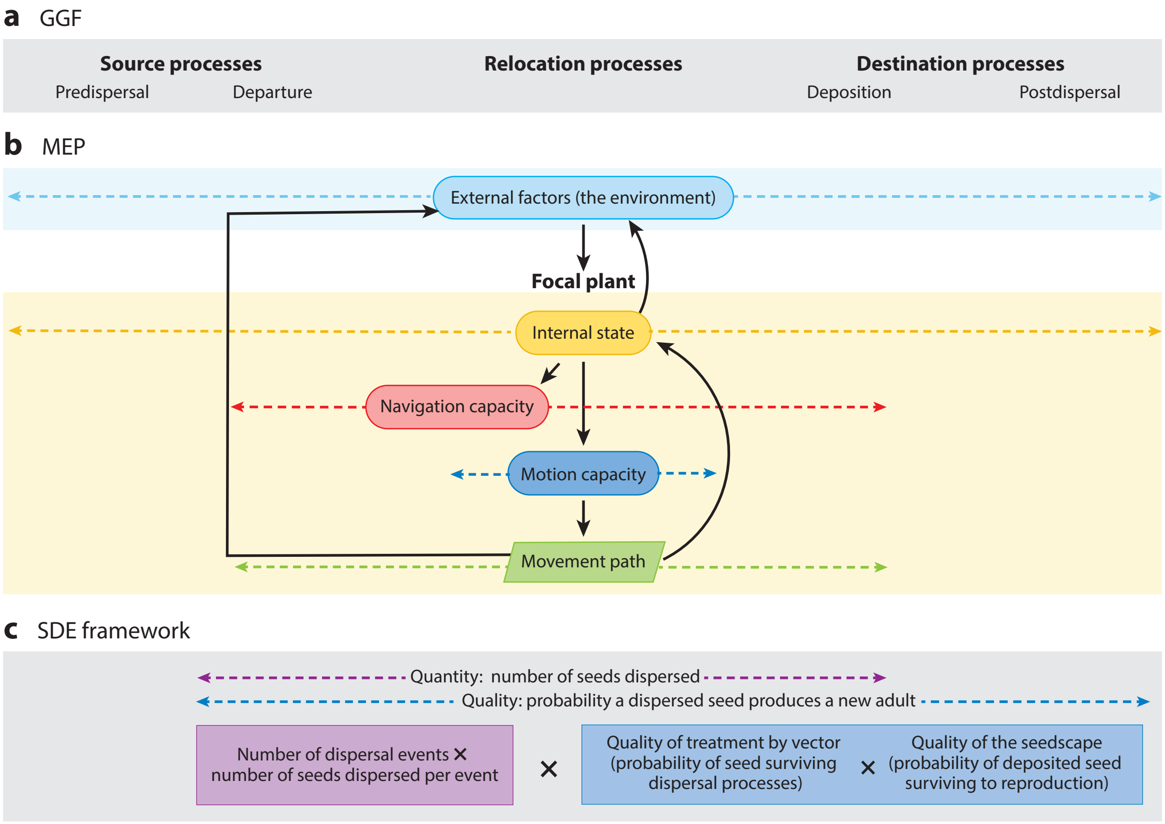


Figure 4

Synthesis of frameworks to study dispersal. (*a*) Dispersal processes as characterized by the generalized gravity framework (GGF) include source, relocation, and destination processes (Jongejans et al. 2015). (*b*) The movement ecology paradigm (MEP) describes proximate and ultimate drivers of movement that fit within the processes described by the GGF (Nathan et al. 2008). Movement of a diaspore begins at the departure phase and ends at the deposition phase of the GGF. The four mechanistic components of the movement ecology paradigm include the internal state (why move?), motion capacity (how to move?), navigation capacity (when and where to move?), and external factors. Solid arrows represent the relationships among these components and the resulting movement path. (*c*) The seed dispersal effectiveness (SDE) framework (Schupp 1993) quantifies the outcomes of source, relocation, and destination processes. The SDE framework is quantified as the quantity component of SDE (*purple box*) multiplied by the quality component of SDE (*blue box*). Dashed arrows indicate how each component of the MEP and SDE relates to the GGF.

(Damschen et al. 2008). These internal states determine a diaspore's motion capacity (how an individual moves), such as the pappus (or plume), a morphological trait of dandelion diaspores that influences terminal velocity, and navigation capacity (when and where an individual moves), such as seed release traits that affect when seeds are released from the plant. A diaspore's internal state, motion capacity, and navigation capacity are all influenced by external factors. For abiotically dispersed plants, the physical properties of air and water must be considered (Damschen et al. 2008); for animal-dispersed plants, the four components of movement must also be considered from the dispersal vector perspective (Borah & Beckman 2022).

4.3. Seed Dispersal Effectiveness Framework

The SDE framework, proposed by Schupp (1993), quantifies the contribution of a dispersal vector or assemblage of vectors to the production of new adult plants. SDE is typically quantified as a quantity component (i.e., the number of seeds dispersed) multiplied by a quality component (i.e., probability a dispersed seed produces a new adult) of seed dispersal (Schupp et al. 2010) (for more details, see **Figure 4*c***). An effective dispersal vector for one focal plant (e.g., individual, species, or community) could be less effective or even antagonistic for another, while another dispersal vector could be equally effective for the same focal plant, but with different contributions to the quantity and quality components. Information on the components of SDE from experiments and observational studies can be incorporated into process-based models to evaluate the consequences of dispersal for higher levels of ecological organization (Beckman et al. 2020b). The SDE framework has been applied primarily to seed dispersal by animals. However, it can be applied to other dispersal modes and has been generalized to quantify the effectiveness of mutualisms beyond seed dispersal (Schupp et al. 2017).

4.4. Integration of Frameworks

We suggest that an integration of these complementary frameworks can provide a more holistic understanding of dispersal and its consequences (**Figure 4**). The GGF ensures an explicit consideration of different phases of dispersal, specifically, source, relocation, and destination, that facilitates generalization across organisms. The MEP conceptualizes the fundamental mechanisms that produce the movement path and influence departure, relocation, and deposition processes. **Table 1** provides examples of mechanistic components of the MEP integrated into the phases of dispersal, from departure to deposition, of the GGF. Some mechanistic components are general across all dispersal modes, while others are unique to specific dispersal modes (**Table 1**). In addition, external factors influence the predispersal and postdispersal phases of all dispersal modes. The SDE framework operationalizes the effectiveness of a dispersal vector (or assemblage) in terms of the immediate and delayed outcomes of dispersal processes described by the GGF and MEP (Schupp et al. 2017). Adequately describing the mechanisms, processes, and outcomes of seed dispersal as depicted by each of these frameworks requires complex mechanistic models and intensively collected data. We can reduce complexity by generalizing across species and systems using interdisciplinary approaches (see the sidebar titled Understanding Seed Dispersal: An Interdisciplinary Endeavor) and by making appropriate simplifying assumptions. While all of these frameworks provide a quantitative representation of dispersal, we are not advocating that all dispersal biologists need to develop a mathematical description of their study system to address their research questions, and one framework may be more appropriate for certain research questions. However, simultaneously considering each of these frameworks when designing studies allows us to intentionally reflect upon different perspectives of dispersal ecology and make our assumptions explicit for dispersal processes (GGF), mechanistic components resulting in movement (MEP), and quantity and quality components of SDE, facilitating generalization. **Figure 5** illustrates the integration of seed dispersal frameworks with a hypothetical example.

4.5. Stochasticity and Determinism

The relative contributions of stochastic versus deterministic processes affects our understanding, predictive ability, and future research efforts toward understanding dispersal processes. The assumption that dispersal is a purely stochastic process was popularized by the neutral theory of biodiversity (Hubbell 2001) and has had a profound influence on ecological studies, especially at the community level (Lowe & McPeek 2014). However, this is a simplistic view, as dispersal varies across species and continues to be shaped by natural selection (Lowe & McPeek 2014). While it is difficult to predict the outcome of an individual dispersal event, higher-order patterns (e.g., at the population or community level) can be predicted by variously parameterized probability distributions (Shoemaker et al. 2020). Therefore, our understanding of stochastic

Table 1 Examples of mechanistic components from the MEP that influence departure, relocation, and deposition processes of the GGF and affect the quantity and quality components of SDE[a]

Dispersal mode	Mechanistic components of plant movement	Departure processes	Relocation processes	Deposition processes
All	External factors	Microsite to landscape heterogeneity in abiotic and biotic conditions. For example, vegetation composition and structure influence departure, relocation, and deposition processes.		
	Internal states	Fruit morphology, chemistry, developmental plasticity, diaspore morphing		
		Fruiting phenology (i.e., timing both within and between years of fruit production)	Not applicable	Not applicable
Animal	External factors	Frugivore community and movement ecology. Dispersal processes depend on the movement paths of frugivores, which result from their internal states (e.g., physiological or psychological characteristics), motion capacities (e.g., biomechanical or morphological characteristics), and navigation capacities (e.g., cognitive and sensory characteristics) that interact with the external environment.		
	Navigation capacity	Visual and olfactory cues of fruit	Not applicable	Fruit chemistry and morphology influencing defecation patterns
	Motion capacity	Not applicable	Fruit chemistry and morphology influencing gut retention time	Not applicable
Nonanimal	External factors	Physical properties of air and water (e.g., speed, direction, anisotropy, temporal and spatial dynamics)		
	Navigation capacity	Buoyancy (water), seed release (wind, ballistic), release height (wind, ballistic)	Not applicable	Buoyancy (water), falling velocity (water), release height (wind, ballistic)
	Motion capacity	Not applicable	Buoyancy (water), falling velocity (water), release height (wind, ballistic), terminal velocity (wind)	Not applicable

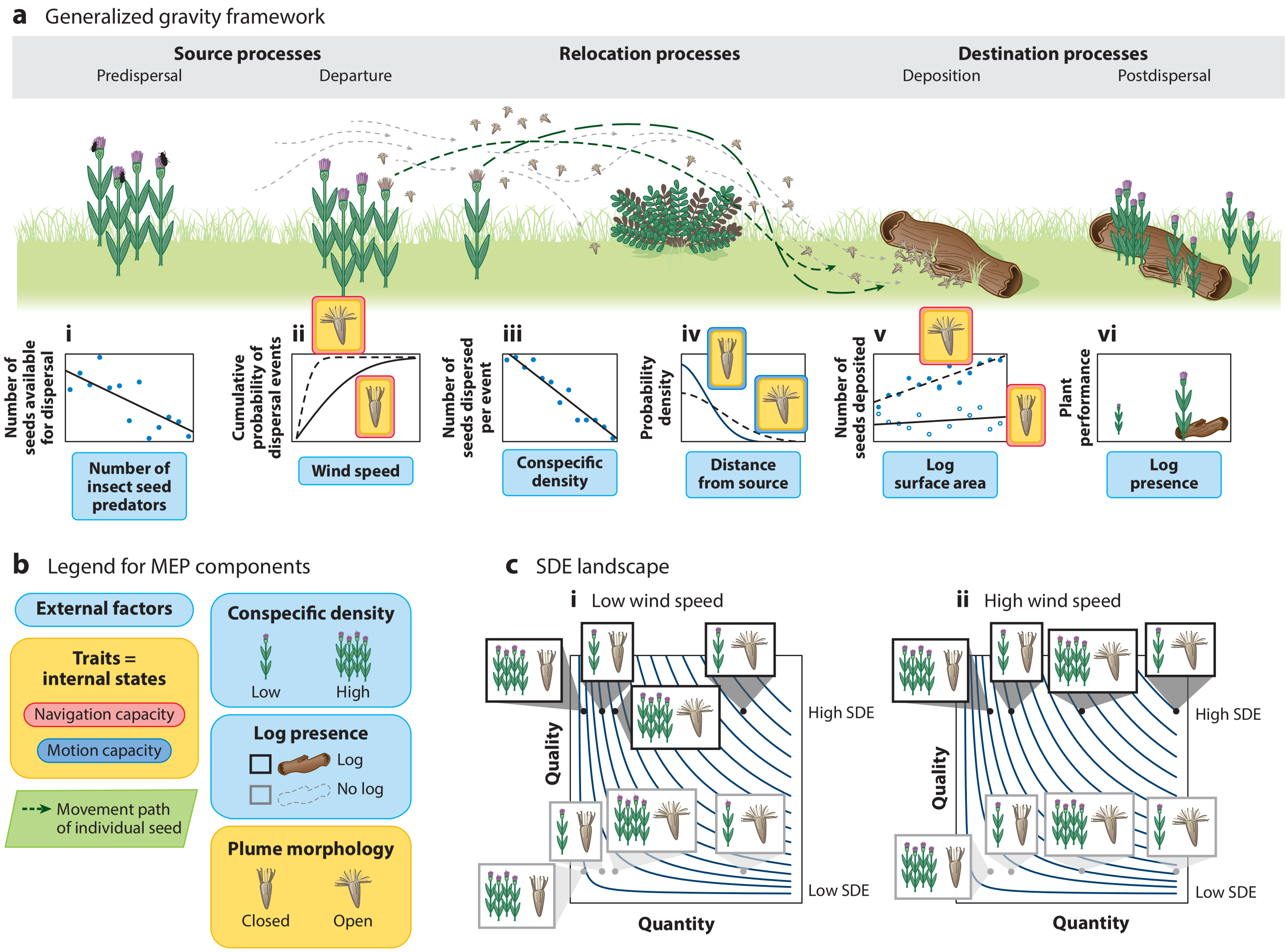
[a] External factors, such as abiotic conditions, availability of resources, competition for resources, natural enemies, and mutualistic partners (e.g., pollinators, mycorrhizae), influence fruit production at the predispersal phase and survival, growth, and recruitment at the postdispersal phase. Operationalizing these processes mathematically will help unify our understanding of dispersal.

Abbreviations: GGF, generalized gravity framework; MEP, movement ecology paradigm; SDE, seed dispersal effectiveness.

versus deterministic processes with respect to dispersal depends on the scale of the research study (Lowe & McPeek 2014, Shoemaker et al. 2020). For example, it is impossible to predict exactly where and when an individual seed will land after it is released from a parent plant; however, the distances over which a population of seeds disperse can be described and predicted with dispersal kernels (Bullock et al. 2017, Nathan et al. 2012). Despite the variability observed in underlying stochastic processes, the structure that arises in the form of probability distributions allows us to make predictions about seed dispersal (Shoemaker et al. 2020).

5. HIGHER-LEVEL CONSEQUENCES OF SEED DISPERSAL

Dispersal is a key driver of plant population and community dynamics (Levine & Murrell 2003, Schupp & Fuentes 1995). Long-standing theory lays out the importance of dispersal for



(Caption appears on following page)

Figure 5 (*Figure appears on preceding page*)

Using a hypothetical wind-dispersed species as an example, we illustrate a synthesis of the GGF, MEP, and SDE framework. We extend the GGF to (*a*) incorporate pre- and postdispersal processes and (*b*) highlight the MEP components within each. During the predispersal phase, insect seed predators reduce the number of seeds available for dispersal. During the departure phase, the number of dispersal events depends on wind speed and its interaction with plume morphology, and the number of diaspores released by wind during each dispersal event reduces with plant density. During the relocation phase, diaspores travel on wind currents above the vegetation canopy and along the ground once seeds land. The distance traveled depends on plume morphology and wind speed. During the deposition phase, the number of diaspores that are trapped by logs depends on the interaction of plume morphology and log surface area. During the postdispersal phase, diaspores deposited on logs have higher plant performance. (*c*) We estimate SDE of diaspores dispersed under distinct wind conditions from parent plants growing in a range of conspecific densities and deposited in seedscapes varying in quality. Isoclines illustrate varying quantity and quality components that result in the same SDE. For more details on the literature that supports relationships described in this figure, see the extended caption in the **Supplemental Material**. The process of integrating these different frameworks clarifies our assumptions and illuminates future directions. For instance, in this hypothetical example we make assumptions such as: (*i*) Limiting resources do not influence plant traits and their effect on dispersal, and (*ii*) plume morphology, which influences navigation capacity, interacts with wind dynamics to influence the likelihood of deposition on logs. Both of these are interesting avenues for future research. Abbreviations: GGF, generalized gravity framework; MEP, movement ecology paradigm; SDE, seed dispersal effectiveness.

Supplemental Material >

population persistence, range expansion and shifts, and community assembly and coexistence (Beckman et al. 2020b, Levin et al. 2003, Levine & Murrell 2003). While empirical support can be found for some of these theories, more often, empirical tests of theory either are lacking (Bolker et al. 2003, Logue et al. 2011) or do not support the theory (Levine & Murrell 2003). This is probably because many events occur between seed dispersal and adulthood that make it difficult to isolate the effects of dispersal on plant fitness and population and community patterns (Beckman et al. 2020b, Levine & Murrell 2003). Despite this discordance between theory and empiricism, many trends have arisen that indicate the importance of dispersal for plant populations and communities.

5.1. Populations

Dispersal is a key demographic process that can influence population dynamics (Levin et al. 2003). Quantifying the contribution of seed dispersal or specific dispersal vectors to population persistence and growth requires comprehensive data on the effects of seed dispersal across a plant's life cycle, from fruit removal to the reproduction of a new plant, and population models that can integrate these effects (Beckman et al. 2020b). Few studies have quantified the effects of seed dispersal on the growth rate of plant populations, and these studies provide insight into the importance of dispersal for plant populations. For the canopy tree *Miliusa horsfieldii* in Thai tropical forests, for example, the loss of seed dispersal by animals increased the probability of local population extinction tenfold, as predicted by model simulations of dispersal loss (Caughlin et al. 2015). *M. horsfieldii* seeds dispersed by animals escaped distance- and density-dependent mortality, and the simulated loss of dispersers increased spatial aggregation around parent trees fourfold, contributing to increased negative density dependence and a reduced likelihood in population persistence (Caughlin et al. 2015). For the tree *Frangula alnus* in a temperate forest in eastern Poland, increasing the proportion of seeds dispersed by animals resulted in higher population growth rates (up to $\lambda = 1$, which indicates constant population sizes) compared with a scenario in which all seeds were dispersed by gravity ($\lambda < 1$, which indicates declining population sizes); this relationship was even stronger under the assumption that *F. alnus* seeds rely exclusively on animals for dispersal to forest gaps (Rehling et al. 2023). Rehling et al. (2023) measured SDE as the reduction in population growth rates following the loss of each of the 20 animal dispersers and found that it was related to the quantity but not the quality component of SDE. Similarly, population sizes remained constant when considering all seed dispersers of the cactus *Neobuxbaumia tetetzo* in deserts of south central Mexico and declined in the absence of seed dispersers (Godínez-Alvarez et al. 2002). Successful establishment of columnar cacti depends on arrival under nurse plants, and population persistence of *N. tetetzo* depended on higher probabilities of seed removal and deposition in high-quality seedscapes by the long-nosed bat *Leptonycteris curasoae*, in contrast to that resulting from dispersal by three bird species (Godínez-Alvarez et al. 2002).

How populations spread in space is central to predicting and managing species responses to global change (Jongejans et al. 2008). Spatial spread occurs when populations grow and disperse to new locations, often characterized by a spreading speed predicted from mathematical models (e.g., Harsch et al. 2017) or estimated from empirical data. Paleobotany and mathematical results reveal that low-probability long-distance dispersal events likely drove plant range spread after glaciation (Clark 1998). Dispersal vectors that differ from a plant's observed or predicted dispersal mode (i.e., nonstandard mechanisms of dispersal) can disperse seeds long distances, with disproportionate effects on range shift and expansion (Higgins et al. 2003). In addition, intraspecific variation in dispersal can increase spatial spread (Snell et al. 2019). Species interactions, such as herbivory, can also alter spatial spreading of populations (Sullivan & Shaw 2023). Dispersal can rapidly evolve during population spread, and this evolutionary change can influence range expansion; on average, theoretical and empirical evidence suggests that eco-evolutionary feedbacks accelerate range expansion (Miller et al. 2020). These results suggest that an understanding of dispersal distance, especially long-distance dispersal, is critical to forecasting the ability of plant populations to track shifting climate optima or spread following introduction (Neubert & Caswell 2000).

Recruitment limitation: reduction in a species' abundance from its maximum due to a limited number of recruits at any previous stage of recruitment

Establishment limitation: limitation of a plant population by the number and availability of suitable sites for establishment to subsequent recruitment stages

5.2. Communities

Dispersal plays a key role in community assembly and coexistence. During community assembly, dispersal from a regional species pool determines the identity of species that arrive and the timing and order of their arrival, which influence both species' relative abundances across spatial scales and local community dynamics (Fukami 2015, HilleRisLambers et al. 2012). Within a local community, dispersal affects competitive dynamics among species (e.g., dispersal trade-offs with other traits or through spatial interactions; Bolker et al. 2003) and shapes interactions with natural enemies (e.g., Janzen–Connell mechanisms; Connell 1971, Janzen 1970). Dispersal limitation aggregates conspecifics, and, in theoretical studies, these spatial dynamics can slow down competitive dynamics or promote coexistence, depending on the competitive interactions within the community (Bolker et al. 2003, Levine & Murrell 2003). Dispersal can also promote plant diversity, for example, when animals preferentially disperse seeds of rare species, thus disproportionately increasing their relative abundance in the seed rain relative to that of fruiting adults (i.e., rare-biased seed dispersal; Carlo & Morales 2016). Finally, while there is a dearth of studies on the effects of intraspecific variation in dispersal on community dynamics, Snell et al. (2019) hypothesize that intraspecific variation in the timing of species arrival alters community assembly and that intraspecific variation in dispersal quantity and distance alters species richness.

Empirical studies demonstrate that the role of dispersal in plant community assembly and coexistence depends on the extent to which population sizes of plants are limited by dispersal versus other forms of recruitment limitation, such as source limitation or establishment limitation. The relative contribution of seed versus establishment limitation can be investigated with seed addition experiments, in which seedling recruitment in plots to which seeds have been added is compared with that of control plots to which no seeds are added. A meta-analysis of seed addition experiments demonstrated that most plant species are seed limited, with greater seed limitation for species in early successional and disturbed sites, large seeded species, and species with relatively short-lived seed banks (Clark et al. 2007). However, the effect of seed limitation was small and plant recruitment was more strongly limited by seedling establishment than by seed limitation

(Clark et al. 2007). These small effect sizes of seed limitation were likely due to both high establishment limitation and shortcomings with the experimental design of seed addition experiments (Clark et al. 2007). In terms of dispersal limitation, several empirical studies suggest that plants are generally dispersal limited and that the degree to which dispersal is distance restricted or spatially contagious depends on the dispersal mode (Tamme et al. 2014, Wright et al. 2016). In an Iowa grassland, the presence of herbivores had variable effects on distance-restricted dispersal at the species level (Allbee et al. 2023), potentially based on the life-history stage at which the herbivores consume plants (Sullivan & Shaw 2023). In a California grassland, dispersal limitation constrained local diversity in a scale-dependent manner, with the largest gains in species richness following species additions occurring at or above 100 m (Germain et al. 2017). In addition, plant communities in which dispersal has been reduced due to declines or extirpations of seed dispersers have lower local diversity and shifts in community composition compared with plant communities with intact disperser assemblages (Beckman & Rogers 2013, Rogers et al. 2021b). Importantly, dispersal–diversity relationships found at the seedling stage are not always maintained into adulthood (Levine & Murrell 2003). Thus, a focus on stage- and trait-specific understandings of how these relationships form and shift through recruitment is imperative.

6. CONCLUSIONS

Howe & Smallwood (1982) posited ecological and evolutionary hypotheses for the advantages of seed dispersal and outlined the environmental forces that influence the timing and mode of dispersal. Here, we have situated the study of seed dispersal into the broader theoretical literature of dispersal. Focusing on the explosion of seed dispersal research over the last four decades (**Figure 1**), we have provided an overview of the theoretical and empirical evidence for the ultimate causes and consequences of seed dispersal. We have integrated studies across a variety of different perspectives (e.g., evolution, plant ecology, zoology, demography), each of which tends to have its own research priorities.

Seed dispersal is an important but complicated process that requires knowledge of multiple life-history stages, vector behaviors, and interactions with the environment. This necessitates an interdisciplinary approach to fully understand dispersal from evolutionary and ecological perspectives (see the sidebar titled Understanding Seed Dispersal: An Interdisciplinary Endeavor). The three dispersal frameworks we have discussed can guide future research to gain a more mechanistic and predictive understanding of dispersal processes. This integration can help advance our understanding of the different sources of recruitment limitation that influence plant spatial patterns, population growth, and diversity. The use of large-scale, publicly available data relevant for dispersal will help advance our understanding of dispersal ecology, especially when combined with distributed experiments that span geographic and ecosystem scales. Tighter integration of theory with this widely available and replicated empirical research will move the field beyond the scale dependence of most current studies to further both general and context-dependent understanding of seed dispersal.

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