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REVIEW ARTICLE

Animal-mediated seed dispersal: A review of study methods

Noelle G. Beckman[1,2] | **Erin K. Kuprewicz**[3] | **Binod Borah**[4] | **James M. Bullock**[5] | **Amanda S. Gallinat**[6] | **Juan P. González-Varo**[7] | **Abir Jain**[8] | **Jun Ying Lim**[9] | **Carina I. Motta**[10] | **Omer Nevo**[11,12] | **Haldre S. Rogers**[8]

[1]Department of Biology and Ecology Center, Utah State University, 5305 Old Main Hill, Logan, Utah 84322, USA

[2]Smithsonian Tropical Research Institute, Apartado 0843-03092, Panama City, Republic of Panama

[3]Connecticut State Museum of Natural History and Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269, USA

[4]Department of Wildland Resources, Utah State University, 5200 Old Main Hill, Logan, Utah 84322, USA

[5]UK Centre for Ecology and Hydrology, Wallingford OX10 8BB, United Kingdom

[6]Department of Environmental Studies, Colby College, Waterville, Maine 04901, USA

[7]Departamento de Biología, Instituto Universitario de Investigación Marina (INMAR), Universidad de Cádiz, Puerto Real, Spain

[8]Department of Fish and Wildlife Conservation, Virginia Tech, 310 West Campus Drive, Blacksburg, Virginia 24061, USA

[9]Centre for Nature-based Climate Solutions and Department of Biological Sciences, National University of Singapore, Singapore

[10]Institute of Biosciences, São Paulo State University (UNESP), Campus Rio Claro, Av. 24A, 1515, Bela Vista, Rio Claro, São Paulo 13506-900, Brazil

[11]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, Leipzig 04103, Germany

[12]Institute of Biodiversity, Ecology and Evolution, Friedrich Schiller University Jena, Dornburgerstr. 159, Jena 07743, Germany

Correspondence

Noelle G. Beckman, Department of Biology and Ecology Center, Utah State University, 5305 Old Main Hill, Logan, Utah 84322, USA.
Email: noelle.beckman@usu.edu

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Abstract

By dispersing seeds, animals provide ecological functions critical for the ecology, evolution, and conservation of plants. We review quantitative and empirical approaches and emerging technologies to quantify processes and patterns of animal-mediated seed dispersal (zoochory) across its phases: from predispersal to post-dispersal. In addition, we consider approaches to studying seed disperser behaviors and plant traits, both of which influence all dispersal phases of animal-mediated dispersal. Finally, we discuss how we can use quantitative and empirical approaches to integrate across seed dispersal phases and address data gaps to improve our mechanistic understanding of zoochory and its consequences for ecology and conservation. To move towards generalization and predictability in seed dispersal ecology, we recommend the development of standardized protocols that can be widely implemented across systems with simultaneous and iterative development of theory and quantitative models. As approaches in studying animal-mediated seed dispersal continue to advance, exciting opportunities present themselves to increase our understanding of seed dispersal ecology.

KEYWORDS

frugivores, myrmecochory, plant movement, scatter hoarding, stomatochory, zoochory

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Dispersal of seeds is an essential part of reproduction for seed plants and an important ecosystem function that influences ecological and evolutionary dynamics with consequences across levels of biological organization (Beckman and Sullivan, 2023). Seed dispersal, the movement of a seed away from a parent plant, is the sole opportunity for many seed plants to escape distance- and density-dependent mortality, take advantage of ephemeral habitats across the landscape, get systematically deposited in habitats suitable for successful establishment, and expand their range (Howe and Smallwood, 1982; Beckman and Sullivan, 2023). The majority of seed plants globally rely on animals for the dispersal of their seeds (i.e., zoochory), and the proportion of animal-dispersed plants increases towards the equator with over 80% of animal-dispersed plants in tropical rainforests (Jordano, 2000; Rogers et al., 2021b). A variety of animals disperse seeds, including insects, mollusks, earthworms, mammals, birds, reptiles, fish, and crabs (Van der Pijl, 1982; Vittoz and Engler, 2007; Supplemental Table 1 in Beckman and Sullivan, 2023). However, the diversity of animal seed dispersers and their impacts on seed dispersal processes and patterns are often poorly described for most plant species (Rogers et al., 2019; González-Varo et al., 2024), hampering our ability to predict biodiversity and ecosystem responses in an era of global change. Seed disperser diversity, abundances, and movements are declining due to anthropogenic drivers with negative consequences for biodiversity and ecosystem function (Fricke et al., 2025). Quantifying processes underlying zoochory and the resulting patterns is important for a mechanistic and predictive understanding of its relative importance for plant fitness, population persistence and spread, metapopulation and metacommunity dynamics, biodiversity across multiple scales, ecosystem functions, and conservation (Beckman et al., 2020a; Rogers et al., 2021b; Beckman and Sullivan, 2023; Fricke et al., 2025).

Plants have a diversity of adaptations (i.e., dispersal syndromes; Van der Pijl, 1982; Valenta and Nevo, 2020; Beckman and Sullivan, 2023) that influence how, when, and where seeds are dispersed by animals. Dispersal syndromes reflect the mode of dispersal: ingestion and passage or regurgitation (endozoochory), carrying externally (stomatochory), external attachment (epizoochory), or movement by a seed-caching animal (synzoochory), ants (myrmechory), hornets (vespicochory), bees (melittochory), dung beetles, or by a carnivore that consumes prey that ingested seeds (diploendozoochory). Often, a seed can be dispersed multiple times sequentially or experience multiple modes of dispersal before landing in its final location (Rogers et al., 2019). Depending on the dispersal mode, plant adaptations may include traits that affect their detectability by and attraction of animals (e.g., color, scent, flavor), if and when diaspores are removed by animals during the departure phase of seed dispersal (e.g., nutritional or medicinal rewards, shape of seed-bearing organs and diaspores, appendage type and structure), diaspore movement paths during the relocation phase (e.g., specialized metabolites, diaspore size), or how and where seeds are deposited during the deposition phase (e.g., specialized metabolites, appendage type and structure; Van der Pijl, 1982; Vittoz and Engler, 2007; Siepielski and Benkman, 2008; Valenta et al., 2017; Nelson and Whitehead, 2021; Beckman and Sullivan, 2023). In actuality, a diversity of animals disperse seeds of many plants that are not predicted by their dispersal syndromes (Higgins et al., 2003; Howe, 2016; Green et al., 2022).

Plant traits interact with those of the animal seed disperser, including the animal's sensory capacities, physiology, dietary requirements, anatomy, foraging strategies, cognition and social structures, and the external environment to influence seed dispersal (Cortes and Uriarte, 2012). Together, plant traits, animal traits, and external factors influence whether, when, where, and how a diaspore is removed and, once removed by an animal, influence when, where, and how a diaspore is deposited, which ultimately affects the number of diaspores dispersed and subsequent plant survival, growth, and reproduction (Cortes and Uriarte, 2012). As zoochory is complex, highly context-dependent, and occurs over multiple spatial and temporal scales, it is challenging to study empirically, computationally, and mathematically (Beckman et al., 2020b). Researchers have developed many approaches for studying individual components of the seed dispersal process, but there is still a need to close the loop in our understanding of the process of animal-mediated seed dispersal and its consequences for ecology, evolution, and conservation (Wang and Smith, 2002), and to develop generalizable understandings of seed dispersal across systems.

Recent conceptual reviews on seed dispersal ecology provide open questions and future research directions but lack information on the range of methods available to conduct empirical research in seed dispersal ecology (e.g., Beckman et al., 2020a; Rogers et al., 2021b; Beckman and Sullivan, 2023). Herein, we review quantitative and empirical approaches and new technologies for studying seed dispersal. We first introduce three key frameworks to holistically study dispersal ecology and evolution (Figure 1) (Beckman and Sullivan, 2023). Drawing on these frameworks, we then review methodologies used to study processes at each phase of animal-mediated seed dispersal—source, relocation, and destination—as well as implications for the effectiveness of seed dispersal in terms of quantity and quality (Table 1). We then discuss methods to measure disperser behavior and plant traits, both of which influence seed dispersal across its phases. Finally, we discuss approaches that integrate across the phases of animal-mediated seed dispersal and approaches to address sparse data challenges common to the study of animal-mediated seed dispersal.

THE STUDY OF ANIMAL-MEDIATED SEED DISPERSAL

Several interdisciplinary, quantitative frameworks have been developed to study dispersal: the generalized gravity framework, the movement ecology paradigm, and the seed dispersal effectiveness (SDE) framework (Figure 1)

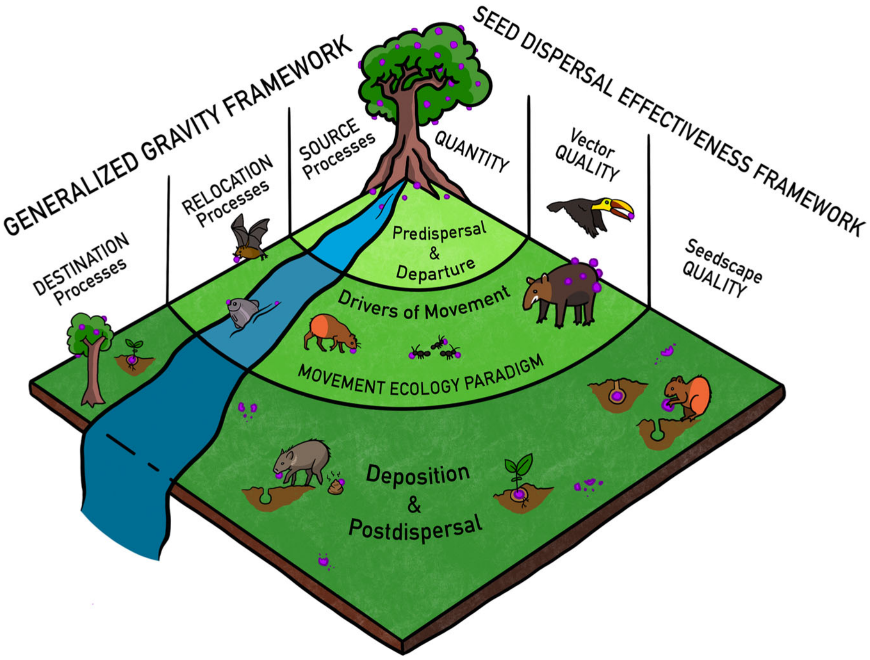

FIGURE 1 Interdisciplinary frameworks to study seed dispersal, integrating general spatial patterns and processes from the generalized gravity framework, movement ecology paradigm, and seed dispersal effectiveness framework. Seed plants, or spermatophytes, produce seeds—ripened, fertilized ovules comprising a testa, endosperm, and embryo—within seed-bearing organs during the predispersal phase. In angiosperms, seed-bearing organs are fleshy or dry fruit (i.e., mature ovaries), where fleshy fruit have higher water content in the mesocarp compared to dry fruit. In gymnosperms, these are cones or seeds on their own, and cones tend to be woody but can be fleshy. During the departure phase, animals remove diaspores—the units of dispersal. Diaspores contain the seed and surrounding structures removed during departure, which may be the entire seed-bearing organ or only a part of it. Following departure, diaspores are moved around the landscape by different animal vectors, carried internally or externally, and can result in successful dispersal, seed predation, or neither. After relocation, seeds are deposited by animals away from a source tree in varied microhabitats encompassing the seedscape—the environment surrounding a seed that influences later recruitment stages (Beckman and Rogers, 2013)—and are affected by postdispersal processes. Internal states, navigation capacity, motion capacity, and external factors of the diaspores and of the animals influence the movement path of diaspores. Diaspore traits and animal behavior influence the quantity and quality of dispersal throughout the phases of seed dispersal.

(Beckman and Sullivan, 2023). In its quantitative description of propagules moving between a source and destination, the generalized gravity framework explicitly considers the different phases of dispersal: source processes (including predispersal and departure processes), relocation processes, and destination processes (including seed deposition and postdispersal processes) (Jongejans et al., 2015). The movement ecology paradigm considers the proximate and ultimate mechanisms driving the movement of individuals during the relocation phase and characterizes the internal state (i.e., physiology or morphology of all organisms, neurology of animals), motion capacity (i.e., traits related to how organisms move), navigation capacity (i.e., traits related to when and where to move, such as sensory machineries or memories of animals or visual or olfactory cues of fruit), and external factors of an individual that influence the movement path (Nathan et al., 2008). The movement ecology paradigm is typically applied to animals but can be applied to plants (Damschen et al., 2008). The SDE framework connects these processes to predict the contribution of a disperser group to the reproduction of a dispersed plant group, quantified as the quantity component (i.e., number of seeds dispersed) multiplied by the quality per capita component (i.e., probability each dispersed seed produces a new adult; Schupp, 1993; Schupp et al., 2010). In developing a research question and designing a study, researchers can simultaneously apply these frameworks to explicitly consider processes across the phases of seed dispersal and identify generalities as well as knowledge and data gaps among systems (Jongejans et al., 2015; Burgess et al., 2016; Beckman and Sullivan, 2023). Ultimately, the frameworks utilized, methodological approaches employed, data collected, and the focal spatial and temporal scale(s) will depend on the research question (Table 1) (Bullock et al., 2006). The study system (e.g., plant species, disperser species, habitat, dispersal mode), available resources (e.g., equipment, materials, personnel, taxonomic knowledge), and potential constraints (e.g., budget, time) will further determine the methods used by the researcher.

SOURCE PROCESSES

Source processes can be separated into predispersal and departure processes. The predispersal phase begins with fertilization and ends with the maturation of seed-bearing

TABLE 1 Summary of animal-mediated seed dispersal processes, what component(s) to measure for each process, and methods currently available to measure each process.

Process	What to measure	How to measure
Source		
Predispersal	Maturation of seed-bearing organs, diaspores, or seeds (on the plant and abscission of seed-bearing organs)	• Observational approaches ◦ Visual census on plants (transects, plots, or marked plants) ◦ Traps or transects beneath crown ◦ High-resolution imagery from satellites and unmanned aerial vehicles • Data collection by volunteer science networks • Herbarium specimen assessment • Ex situ monitoring of living plant collections • Experimental approaches ◦ Abiotic factors (e.g., temperature, CO_2 concentrations, soil moisture, light availability, and nutrient additions) ◦ Biotic factors (e.g., exclosures, pesticides, simulated herbivory)
Departure	Diaspores departing from the plant itself or from underneath the crown (i.e., primary seed dispersal) or from temporary settlement locations away from the plant during later phases of dispersal (i.e., secondary or higher phases of seed dispersal)	• Observational approaches ◦ Direct monitoring (focal watches of seed dispersers visiting plants, line transect surveys to monitor diaspore removal by vectors, tracking and observing seed dispersers) ◦ Indirect monitoring via camera traps ◦ Seed traps or exclosures to quantify departure ◦ Interviews with local community members • Molecular tools to identify seeds associated with animals • Experimental approaches ◦ Animal foraging preference trials ◦ Seed adhesion experiments ◦ Artificial diaspores
Relocation		
	Seed movement from its point of departure to its destination	• Lagrangian methods: Tracking seed movement ◦ Direct observation ◦ Mark and follow individual seeds (thread, magnets, PIT tags, radio tags, fluorescence, isotopes) • Eulerian methods: Patterns of seed rain ◦ Seed traps ◦ DNA markers to identify the source plant of dispersed seeds • Quantitative models to predict seed movement (e.g., dispersal kernels, individual-based models, mathematical models) • Germination studies to assess quality
Destination		
Deposition	When, where, and how seeds are deposited in an environment	• Observational approaches ◦ Direct observations ◦ Censusing, mapping, or collecting deposited seeds along transects, seed traps, or from direct follows of animals • Experimental approaches ◦ Feeding animals in captivity ◦ Detachment experiments • Molecular tools to identify dispersers that deposit seeds (DNA barcodes), assess relatedness among deposited seeds, and determine species identities of deposited seeds
Postdispersal	Plant performance within the seedscape	• Censuses of seed and seedling performance and other relevant information (e.g., evidence of predation or fungal attack, environmental factors)

TABLE 1 (Continued)

Process	What to measure	How to measure
		• Seed and seedling addition experiments • Experimental approaches to isolate influence of abiotic and biotic factors
All	Behaviors of seed-dispersing animal vectors in space and time	• Behavioral coding • Traits rating • Experimental manipulation (in situ and ex situ) • Neurophysiological studies of brain activity in situ • Animal tracking (using GPS, geolocators, RFID technology) to quantify home ranges/territories and movement patterns • Sensors to measure kinematics, behavior, and physiology • Remote sensing of environmental factors • Statistical movement models
All	Diaspore traits	• Observational approaches • Experimental approaches ∘ Field ∘ Common garden ∘ Transplantation
All	Integration across phases	• Molecular tools • Network-based approaches • Process-based models
All	Addressing sparse data	• Statistical and machine learning models to simulate missing data • Synthesize available data • Standardized data collection protocols

Note: PIT = passive integrated transponder; RFID = radio frequency identification.

organs and seeds. During the predispersal phase, availability of limiting resources, such as light, water, and soil nutrients, and biotic interactions, including natural enemies and pollinators, affect the quantity, quality, and phenology of seed-bearing organs and seed production with consequences for SDE (Carvalheiro et al., 2021; Leal and Koski, 2024). Departure processes occur during the primary dispersal phase, when diaspores are initially removed from on or under the plant by animals, or during later (e.g., secondary, tertiary) phases as diaspores are removed by animals from temporary deposition sites. Studies of departure processes typically seek to measure the quantity component of SDE through the number of dispersal events and number of seeds removed per event and the quality component of SDE as influenced by the handling and treatment of the disperser.

Predispersal processes

Research questions commonly addressed at the predispersal phase relate to understanding phenological patterns in the production of seed-bearing organs and factors that determine their quantity and quality, for example, assessing phenological mismatches between seed and disperser availability (Sandor et al., 2021; Mendes et al., 2023). The predispersal phase is critically important to understanding the availability of diaspores, both in terms of timing and quantity, to animal seed dispersers. The most direct and systematic approaches to measuring the phenology and abundance of seed-bearing organs involve observational approaches to monitor the presence, development, and ripeness of seed-bearing organs on individual plants (Wheelwright, 1986; Chapman et al., 2005; Bush et al., 2018). These traditional approaches have provided valuable insights into maturation timing and abundance, particularly for common species and at single sites (Haggerty and Galloway, 2011; Datta and Rane, 2013; Gallinat et al., 2020; Núñez-Cruz et al., 2020). However, emerging approaches in field observation technology, volunteer science contributions, herbarium specimens, and botanical gardens can broaden the taxonomic scope, spatial extent, and temporal duration of seed maturation data. Manipulative experiments or comparative, observational studies are also useful approaches for studying the factors influencing production of seed-bearing organs and their traits (e.g., Cuartas-Domínguez and Medel, 2010; Le Roncé et al., 2020; Trunschke et al., 2020).

Observational approaches

Censusing seed-bearing organs developing on plants and those captured by seed traps are the two main observational approaches used to study predispersal processes (e.g., Benkman et al., 1984; González-Varo et al., 2021). Observations of seed-bearing organs on plants, such as within the canopy, are typically conducted along transects or in discrete plots, with data collected on the density and developmental stages of seed-bearing organs and the proportion of plants bearing mature seed-bearing organs (García et al., 2011; Denny et al., 2014). Phenological observations can be made at the community level by monitoring all reproductive seed-bearing plants either along a transect or in a plot without tracking individual plants, or at the individual level by monitoring marked plants; sampling at the community level will provide information on overall availability of seed-bearing organs (e.g., Muhanguzi et al., 2003; Camaratta et al., 2017; Bender et al., 2025), whereas following marked plants is better for understanding interindividual variation within a species and for studying rare species (e.g., Franklin and Bach, 2006; Takahashi et al., 2011; Boyle and Bronstein, 2012; Dunham et al., 2018; Datta et al., 2025). For small crop sizes, all seed-bearing organs on plants can be counted, but as crop size increases, researchers can subsample within the plant to scale up and estimate total number of seed-bearing organs for the individual plant (e.g., Jordano and Schupp, 2000; Foest et al., 2025). The phenology of seed-bearing organs can also be recorded using ordinal scales that describe the absence, onset, peak, and end of their availability (e.g., as four-point scales; Fournier, 1974; Denny et al., 2014; Elmendorf et al., 2016; Camaratta et al., 2017).

For taller plants, monitoring seed-bearing organs within the canopy is more challenging. A promising approach for directly monitoring abundance and phenology in the canopy is to use machine learning models (e.g., random forest, neural networks) to identify seed-bearing organs in high-resolution imagery from satellites or unmanned aerial vehicles (e.g., Broadbent et al., 2024), as has been developed to study flowers at the top of canopies (Dixon et al., 2021; Ma et al., 2022; Lee et al., 2023; Miura et al., 2023) and fruit production in orchards (Maheswari et al., 2021; Popescu et al., 2023). Alternatively, seed traps (see Kollmann and Goetze, 1998; Stevenson and Vargas, 2008 for seed trap designs) have been used to estimate phenology and abundances and to quantify the premature dropping and damage of reproductive parts (Beckman and Muller-Landau, 2007; Jackson et al., 2022). Researchers can use the number of reproductive parts captured in seed traps to estimate abundance for an individual, population, or community by, for example, using an estimate of crown size (e.g., Howe and Vande Kerckhove, 1981) or Bayesian approaches that incorporate information on plant status and spatial location (Clark et al., 2004). Seed traps, however, provide limited data on phenology for species that do not abscise mature seed-bearing organs (Tattoni et al., 2021; Wright et al., 2024a).

Monitoring the phenology of seed-bearing organs comes with challenges. For example, assessing the maturity and ripeness of seed-bearing organs is not straightforward, particularly when researchers work with many species at once. Frequently used traits such as fruit size, color, and texture (e.g., Wichura et al., 2024) can be subjective, and assessing quantitative metrics such as sugar content can be labor intensive, with accuracy varying among species (White and Stiles, 1985). In this issue, Nguyen et al. (2026) offer additional considerations for measuring the physiology of fleshy fruit maturation. In diverse ecosystems, such as tropical forests, animal behaviors such as feeding observations or scat contents have also been used to infer fruit and seed maturation patterns for seeds dispersed by animals, under the assumption that animals are selecting ripe fruit (e.g., Kurek et al., 2024). Monitoring phenology in tropical species is further complicated by the fact that many tropical plants fruit for extended periods—or even continuously—blurring the distinction between "fruiting" and "not fruiting." Consequently, often many individual plants must be monitored over multiple years to discern consistent fruiting patterns (Mendoza et al., 2017).

Volunteer science networks

In recent years, volunteer science networks focused on phenology, such as Nature's Notebook in the United States (https://www.usanpn.org/nn; Crimmins et al., 2022), PlantWatch in Canada (https://www.naturewatch.ca/; Beaubien and Hamann, 2011), SeasonWatch in India (https://www.seasonwatch.in/; Ramaswami et al., 2021), and Nature's Calendar in the United Kingdom (https://naturescalendar.woodlandtrust.org.uk/; Collinson and Sparks, 2008), have significantly expanded the geographic scope of maturation studies of seed-bearing organs, although these efforts remain heavily concentrated in temperate ecosystems of the Northern Hemisphere. These networks engage volunteers to record plant development stages across extensive regions, collectively generating millions of records (e.g., Crimmins et al., 2022). Global platforms that host volunteer-contributed photographs, such as the Macaulay Library at the Cornell Lab of Ornithology and iNaturalist, also provide opportunities to investigate patterns in plant phenology (Barve et al., 2020; Iwanycki Ahlstrand et al., 2022; Rzanny et al., 2024) and can be further used to leverage documented plant–animal interactions, such as frugivores (i.e., an animal that consumes fleshy fruit) feeding on diaspores, which can inform localized assessments of diaspore availability (Díaz et al., 2024).

While these data increasingly document variation in maturation times among individuals, species, and regions—variation that is critical for exploring the mechanisms underlying animal-mediated seed dispersal—they also introduce challenges associated with both non-expert identification of species and ripeness and opportunistic approaches to data collection. If an observer opportunistically identifies the presence of mature seed-bearing organs, it can be difficult to identify whether this is the onset, peak, or end of their availability for an individual. For those managing volunteer networks, as well as for scientists studying phenology, the development of species-specific protocols for identifying the ripeness of particular species (e.g., https://www.usanpn.org/nn/photoguide-list) will improve the quality of the data collected. For community science data users, utilizing observations of plants lacking seed-bearing organs before observations of plants with mature seed-bearing organs offers a path forward for addressing this challenge (see Crimmins et al., 2017).

Herbarium specimens

Current estimates suggest there are 396 million botanical specimens in herbaria worldwide (Thiers, 2025), and these records are increasingly being digitized (Soltis, 2017; Pearson et al., 2020; Heleno et al., 2024). By analyzing reproductive structures preserved on specimens, alongside their collection dates and locations, researchers can identify when plants produce seed (Gallinat et al., 2018; Lima et al., 2021; Park et al., 2023) and record phenology (Willis et al., 2017). The broad temporal coverage of herbarium-derived data also enables researchers to explore how seed maturation may be changing over time and in response to changes in the environment (Willis et al., 2017; Gallinat et al., 2018; Lima et al., 2021). Robust herbarium collections from the Global South provide a particularly valuable opportunity to fill major gaps in long-term fruiting phenology data (Davis et al., 2022).

Herbarium specimens have some limitations, however. Plants are not always collected with their seed-bearing organs, as flowers are often easier to press and store. Furthermore, pressed specimens magnify challenges associated with identifying ripeness and phenological stage. Developing criteria to assess ripeness becomes more difficult after plants have been pressed, dried, and stored long-term and seed-bearing organs have undergone changes (e.g., in color). It is often best to focus instead on other characteristics such as size and the apparent texture of seed-bearing organs when they were pressed (Gallinat et al., 2018). Similar to volunteer observations, temporally sporadic herbarium collections of seed-bearing plants can make it difficult to assess the different phenological stages of ripening, in such a way that can limit intraspecific analyses over time and with environmental cues (Gallinat et al., 2018; Park et al., 2023). However, specimens can provide useful comparisons of seasonality across plant species and within some species with short fruiting seasons and abundant specimens. Researchers using herbarium specimens should also be cognizant of geographic, temporal, and taxonomic biases in preserved collections (Daru et al., 2018).

Living collections

Botanical gardens offer opportunities to assess maturation phenology and seed abundance data for multiple plant species in shared settings (Krishnan and Novy, 2017; Primack et al., 2021). Observations from botanical gardens in North America, Asia, and Europe have been used to describe fruiting phenology and related functional traits for hundreds of plant species (Gallinat et al., 2018; Sporbert et al., 2022). While botanical gardens can be limited in the number of individuals of each species and the environmental gradients represented, they can leverage the value of other resources. Volunteer science networks like Nature's Notebook (Crimmins et al., 2022) mentioned above and PhenObs (https://www.idiv.de/research/projects/phenobs/; Nordt et al., 2021) specifically engage volunteers to monitor plant phenology in botanical gardens. Many botanical gardens also house herbaria that can be connected with present-day observations to combine temporal and taxonomic breadth (Primack et al., 2021).

Experimental approaches

Manipulative experiments increase our understanding of the ecological interactions and mechanisms affecting development, production, and quality of seed-bearing organs in zoochorous plants. Manipulations of temperature, CO_2 concentrations, soil moisture, light availability, and nutrient additions shed light on factors influencing seed-bearing organs and plant traits relevant for dispersal by animals (e.g., Bazzaz, 1990; Zhang et al., 2011). Long-term nutrient experiments, such as the one established by Wright et al. (2024b) in a Panamanian tropical forest, could be used to investigate effects of resource availability on the quantity and quality of seed-bearing organs produced, with implications for animal seed dispersers. Experimental approaches to quantify the effects of vertebrates, insects, and microbial organisms include the use of exclosures (e.g., Kurkjian et al., 2017), pesticides (e.g., Beckman and Muller-Landau, 2011), and simulated herbivory (e.g., Whitehead and Poveda, 2011). For plants with larger growth forms, these experiments can be conducted in the canopy (e.g., Nakagawa et al., 2005; Beckman and Muller-Landau, 2011; Tiansawat et al., 2017) using cranes, walkways, and towers (Stork et al., 1997; Lowman, 2009), which allow for long-term canopy access but require substantial resources to establish and maintain, typically have a limited spatial extent, and can result in non-independence of samples (Lowman et al., 2012). Experiments offer more controlled settings to isolate the effects of abiotic or biotic interactions at the predispersal phase but tend to be limited in spatial and temporal scales, especially for long-lived or large-stature plants. When designing an experiment, the potential for unintended effects (e.g., nutrient addition with the use of insecticides; Siemann et al., 2004) or additional challenges in replicating natural conditions (e.g., replicating real damage of insects with simulated herbivory; Waterman et al., 2019) should be considered as much as possible.

Departure processes

A variety of observational and experimental approaches are used to identify dispersers and their contributions to SDE at the departure phase. Oftentimes single approaches, with their own potential biases, are unable to holistically capture the diversity, frequency, and functional outcomes of plant–animal interactions, especially for uncommon interactions (González-Castro et al., 2022; Quintero et al., 2022). Synthesizing data collected from different methodologies can provide more complete characterizations (Quintero et al., 2022). Many of these approaches focused on the departure stage measure animal visitation and/or diaspore removal without assessing seed fate following handling of the diaspore; hence researchers should take care in interpreting the ecological function of the animal for the plant (e.g., dispersal vs. predation) if previous studies of the animal's function are unavailable. It should be noted that the ecological function of an animal for a plant can vary among individuals of an animal species (Zwolak, 2018; Zwolak and Sih, 2020; Bartel and Orrock, 2022) or among individuals of a plant species (Schupp et al., 2019).

Observational approaches

Observational approaches include directly observing animal foraging or interactions with plants, using cameras to indirectly observe visitors, indirectly measuring dispersal using seed traps, and drawing on local ecological knowledge of plant interactions with potential seed dispersers. Adequately describing the full community of dispersers, their contributions to SDE, and total seeds dispersed from individual plants based on direct observations requires substantial field effort (Quintero et al., 2022). Animal foraging can be directly observed through focal watches of seed-bearing plants (e.g., Snow and Snow, 1971; Albrecht et al., 2013; Sekar and Sukumar, 2015; Howe, 2024), transect walks (e.g., Moegenburg and Levey, 2003; Galetti and Pizo, 2013), and tracking and observing seed dispersers (e.g., Chapman, 1989; Fischer et al., 1996; Wehncke et al., 2004; Tonos et al., 2025; Wilcox and Tarwater, 2025). Direct observations have strengthened our knowledge of seed dispersal interactions (Forget and Wenny, 2005 and references cited therein) but require a high sampling effort and may provide an incomplete assessment of animal visitation and diaspore removal rates (Monteza-Moreno et al., 2022). In addition, directly observing foraging behaviors of some animals can be challenging depending on their size, motion capacity, typical behaviors, or environmental context (e.g., presence of hunting, ruggedness of the terrain, vegetational complexity of canopy and understory; Forget and Wenny, 2005; Fell et al., 2023).

Imaging systems, including still, video, time-lapse, and motion-triggered cameras, enable remote data collection of animals visiting seed-bearing organs and removing diaspores (e.g., Seufert et al., 2010; Monteza-Moreno et al., 2022; Séguigne et al., 2022; Villalva et al., 2024). The earliest use of cameras for seed dispersal–related research was in the 1990s and early 2000s, where researchers documented frugivory and diaspore removal from the ground (e.g., Miura et al., 1997; Beck and Terborgh, 2002; Jansen and den Ouden, 2004; Kitamura et al., 2004) and canopy (e.g., Otani, 2001; Jayasekara et al., 2003). Since then, advances in sensor sensitivity, image resolution, battery life, and compact design have made cameras a reliable tool for evaluating animal visitation ranging from ants (Bologna et al., 2017) to elephants (Sekar and Sukumar, 2015).

Cameras can be used to document when departure of the diaspore occurs, which animal removes the diaspore, and how each individual interacts with the diaspore (e.g., Villalva et al., 2024). While the majority of studies adopt a phytocentric approach by positioning cameras toward diaspores, a few have employed a zoo-centric setup by attaching cameras to animals to observe their foraging choices (Rutz et al., 2007; Tezuka et al., 2022; Holcombe, 2024). Cameras can be used across all growth forms (herbs, shrubs, climbers, trees), strata (ground to canopy), and diaspore types (e.g., Moore et al., 2020; Coutant et al., 2022; Campagnoli et al., 2025). Diaspores may be monitored while still attached to the parent plant, after they have fallen to the ground, or in an experimental setting (e.g., Jayasekara et al., 2007; Selwyn et al., 2020; Silva et al., 2020; Landim et al., 2025).

Cameras provide many benefits over alternative observational approaches such as focal watches. They offer continuous monitoring (Séguigne et al., 2022), significantly increasing the sample size and the likelihood of capturing rare events (Brockelman et al., 2022; Villalva et al., 2024). Cameras provide a record of interactions that can be confirmed later and can be deployed in otherwise inaccessible locations such as treetops or cliff edges (e.g., Moore et al., 2021; Zhu et al., 2022). Arboreal camera traps are expanding our understanding of canopy-level departure processes of diaspores, helping to reduce the ground-level bias in many studies (Rivas-Romero and Soto-Shoender, 2015). Cameras utilizing infrared technology can record diaspore handling behavior by nocturnal visitors without the disturbance of a light or flash. Lastly, while reviewing images manually can be extremely time consuming, artificial intelligence and standardized workflows have improved the process (e.g., Villalva and Jordano, 2025).

Monitoring interactions using camera traps also has limitations. Each new study requires effort to select the right camera, settings, and placement method, based on the specific requirements of the study system, habitat, or focal plants (Randler and Kalb, 2018; Palencia et al., 2022). While canopy access is possible, it typically requires tree climbing skills and equipment, leading to a common bias towards capturing only the lower portion of trees or selecting lower-stature plants as focal species (Moore et al., 2021; Landim et al., 2025). As at least one camera is needed for each plant to monitor interactions and diaspore removal, sampling effort for plants with one or a few seed-bearing organs may be even more limited than for plants with larger crop sizes. After successfully setting up the cameras, images may still be plagued by poor visibility due to sun glare or rain and by false positives because of wind moving the vegetation (Apps and McNutt, 2018; Silva-Rodríguez et al., 2025). Cameras may also attract or repel animals, affecting estimates of removal rates (Meek et al., 2014). They are also prone to theft or vandalism by people, increasing the overall cost of the project (Meek et al., 2019). Furthermore, diaspore removal can be difficult to count when animals obscure the view, are far away, move quickly, or destroy the plant (Campos et al., 2018). Even with these limitations, the use of imaging systems over the past three decades has dramatically increased observational data on animal movement of diaspores (Trolliet et al., 2014; Meek et al., 2020).

Finally, seed traps, exclosures, and local knowledge provide additional approaches for estimating diaspore removal. For plants that produce seed-bearing organs with parts that are not dispersed, seed traps positioned under focal trees can be used to estimate seed removal by comparing total seeds collected to total production of seed-bearing organs (e.g., Beckman and Muller-Landau, 2007). Another approach is to census seed-bearing organs on branches with and without exclosures (e.g., wire mesh: Iwanycki Ahlstrand et al., 2022; bags: Willson and Whelan, 1993); however, this introduces challenges by altering the microenvironment around enclosed organs and thereby potentially influencing abortion and abscission rates. Interviews with local communities (including indigenous people) can offer complementary information on seed dispersers drawing on local knowledge and provide a rich source of information, especially in hyperdiverse tropical ecosystems where repeated direct observations are challenging (Ong et al., 2021; Durand-Bessart et al., 2024). For example, Ong et al. (2021) identified 2063 frugivory interactions using a combination of methods (i.e., interviews, field surveys, published records) in a hyperdiverse rainforest of Peninsular Malaysia. Interviews with indigenous people alone identified the majority of these interactions (97% based on one or more interviews, 85% based on two or more interviews), while field surveys (i.e., feeding signs observed on fruit, camera traps, fecal inspection) alone identified 13% of the total frugivory interactions (Ong et al., 2021). While information from local ecological knowledge on frugivory interactions is fairly comprehensive, there are several limitations to consider with this approach, including the taxonomic resolution (i.e., questionnaires may deal with closely related animal or plant species), lack of information on the frequency of frugivory interactions, and the introduction of biases depending on the culture and personality of the interviewee and based on more complete knowledge for certain animal groups (Ong et al., 2021).

Molecular tools

Departure processes are often studied during the relocation or deposition phase by identifying seeds found in animal gut or fecal contents (e.g., mist-netted birds; Rumeu et al., 2023) or that have been dropped after handling or regurgitation. To overcome challenges of seed identification based on morphology, molecular tools are increasingly used to aid in the identification of seeds associated with frugivores (Galimberti et al., 2016; Viana et al., 2016; Timóteo et al., 2018; González-Varo et al., 2021; Motta et al., 2026). DNA barcoding involves amplifying short sections of DNA from specific genes and matching information to reference libraries to identify single seed species. DNA barcoding faces challenges in achieving species-level identifications and often requires combining multiple barcode regions (e.g., *rbcL*, *matK*, ITS) due to the limited resolution of small gene regions, as well as incomplete reference libraries (Ando et al., 2020; Espinosa Prieto et al., 2024). In fact, DNA barcoding has been used to help morphological identification of seeds by short-listing plant species at the genus or family level through sequence matching with reference libraries and then checking seed reference collections (Viana et al., 2016; Timóteo et al., 2018; González-Varo et al., 2021).

DNA metabarcoding allows for the identification of multiple plant taxa from fecal content rather than analyzing the seeds individually, which offers a more cost-effective approach to seed identification (Ando et al., 2020; Tang et al., 2022). Metabarcoding mainly targets DNA of the fruit pericarp from multiple plant species that have been consumed and digested by frugivorous seed dispersers (García et al., 2024). However, DNA metabarcoding of fecal matter could identify frugivory (or even folivory or other forms of herbivory) without guarantee of animal-mediated seed dispersal (e.g., pulp pecking). Consequently, natural history information is key to discerning between frugivores and seed dispersers (García et al., 2024), between direct and indirect (e.g., accidental or secondary) plant consumption (Tercel et al., 2021), and between consumption of the seed-bearing organ and that of other parts of the plant such as pollen, nectar, or leaves (Motta et al., 2026). DNA metabarcoding faces the same challenges in achieving species-level identifications as those described above for DNA barcoding. Herbarium and living collections can expand DNA reference libraries, but these methods still require the integration of morphological data, seed reference collections, and species distribution records. We acknowledge that molecular research capacity remains unevenly distributed globally, with particularly strong financial and infrastructural barriers in the Global South (here used to refer to low- and middle-income countries historically marginalized in global research systems;

Zhang et al., 2023; Holcombe, 2024). More specifically, reference genomes remain scarce relative to species richness in low-latitude regions (Global South), while whole-genome sequencing efforts continue to focus disproportionately on taxa from the Global North, thereby constraining the development of studies that rely on available genetic data (Linck and Cadena, 2024).

Experimental approaches

Experimental approaches to study departure processes vary by the mode of seed dispersal. Departure will partly depend on the composition, abundance, and food preferences of animals visiting the plants or on factors that influence seed adhesion to dispersers. Approaches can vary from release of real or artificial diaspores in controlled environments to manipulative, natural, or accidental experiments in natural settings.

Under the assumption of optimal foraging theory, seed dispersers make complex foraging decisions based on their judgements of food item values (e.g., Vander Wall, 2010; Wang et al., 2016). From the animal perspective, accessible diaspores with high nutritive value are the most prized and should be chosen and subsequently removed from the source plant faster and in higher numbers than diaspores perceived to have lower value (e.g., Cousens et al., 2010). Large diaspores are nutritively valuable but may also be bulky and difficult to transport (Muñoz and Bonal, 2008; Correa et al., 2015). Preference trials or choice experiments in feeding ecology fall into two categories: binary choice trials and cafeteria-style trials (i.e., more than two food choices). Ideally, to measure animal preference, researchers would employ a fully factorial design of paired offerings (i.e., all possible pairs of offerings are presented and monitored within the environment) that are replicated in space and time. Binary choice experiments allow investigators to discern true choices made by animals and to detect nuances in selection for plant traits by dispersers that may be obscured in multi-offering trials (Raffa et al., 2002; Kuprewicz and García-Robledo, 2019). However, deploying many binary choice offerings in a full factorial design may be logistically impractical; such studies require large amounts of seeds and time, which may not be available. Cafeteria-style experiments allow for many seeds with varying traits to be offered to animals simultaneously in a realistic multi-choice environment, greatly reducing replication efforts in the field or lab. The main drawback of offering more than two choices in preference trials is that true foraging choices made by animals may be obscured (Raffa et al., 2002).

The presentation of diaspores to seed dispersers within an experiment will depend on the organism and appropriate habitat scale, for example, small plastic containers that allow for removal on or in the litter by ants (Gorb and Gorb, 2003; García-Robledo and Kuprewicz, 2009) and consideration of appropriate height for arboreal animals (e.g., Whitehead et al., 2016). Disperser enclosures can be used for more controlled environments (e.g., Trabelcy et al., 2022; Gelambi and Whitehead, 2023). However, experiments with captive vertebrates require building an appropriate environment and specialized training in capturing and keeping wild animals in captivity. In addition, captive animals (both captive-born or wild-caught) often have different diets, physiological systems, and behaviors than wild animals (e.g., Mason, 2010; Fischer and Romero, 2019; Turko et al., 2023), which can affect results and inferences regarding seed dispersal processes.

To measure attachment of diaspores dispersed by adhesion to animals, including humans (Wichmann et al., 2009), researchers have used laboratory and field experiments. In the lab, fruits or diaspores are manually brushed along different animal coats (Couvreur et al., 2004; Will et al., 2007). In the field, mobile dummies (e.g., bicycles, mammal dummies) or humans bearing materials with different adhesion properties (e.g., fur or feather characteristics, clothing types) move through vegetation (Castillo-Flores and Calvo-Irabién, 2003; Mouissie et al., 2005; Sato et al., 2023; Lukács et al., 2024). Studies of diaspore adhesion should consider the interaction of disperser and plant characteristics (Cousens et al., 2010; Sato et al., 2023), including the height at which diaspores are presented relative to that of the animal; diaspore ripeness, which influences the amount of force required to detach; and how diaspore size (e.g., mass, length), appendage type (i.e., none, awns, bristles, hooks, viscid outgrowth), and structure within appendage type are influenced by the adhesion properties of the animal (Sorensen, 1986; Will et al., 2007). As diaspores dispersed by adhesion may be available for relatively longer time periods compared to diaspores consumed by dispersers, researchers should also consider censusing how the disperser assemblage and resulting departure rates shift during the period of diaspore availability (Sato et al., 2023). Obviously, such artificial, experimental approaches may not capture the range or complexity of attachment processes, but they are useful for understanding the potential roles of dispersal agents and processes that might be difficult to capture in purely observational studies.

Experimental approaches can consider the use of artificial diaspores to measure diaspore removal rates or test the influence of fruit and diaspore traits on departure processes. Artificial fruit or diaspores can be used to compare dispersal rates between regions under a natural or accidental experiment (Diamond, 1983; Galetti et al., 2003; HilleRisLambers et al., 2013); to determine foraging preferences in response to nutrients, specialized metabolites, or morphology (e.g., Kuprewicz and García-Robledo, 2019; Gelambi and Whitehead, 2023); or to record visitors through the marks they leave on the artificial diaspore (e.g., Alves-Costa and Lopes, 2001). A high degree of replication and manipulation of specific seed traits are possible through the use of artificial seeds. For example, Kuprewicz and García-Robledo (2019) used artificial diaspores made from polymer clay and peanuts to tease apart the role of diaspore morphology and chemistry in the decisions of scatter-hoarding rodents. Drawbacks of using artificial seeds in experimental methods include the large amount of time required to construct many artificial seeds and the time-consuming necessity of running pilot studies to ensure that animals treat artificial seeds like natural seeds.

RELOCATION PROCESSES

Relocation processes encompass the movement of a seed from its initial location until its final destination. Relocation processes affect the quality component of SDE depending on the treatment of the seed by the disperser and by influencing a seed's movement path and dispersal distances. Relocation processes can result in both local and long-distance dispersal. Long-distance dispersal is quantified as dispersal outside of the geographic population, the genetic neighborhood, or both, and has implications for meta-population dynamics, range expansion, or gene flow (Jordano, 2017). Quantifying the relocation of seeds by animals is challenging. Ideally, the source plant from which an animal removed a specific seed must be identified, the movement of the seed must be tracked, and the deposition site of the same seed must be located; moreover, when the seed is dispersed sequentially by more than one disperser, these measures must be repeated for each disperser until the final destination is reached. We can measure relocation processes by tracking the movement of individual seeds ("Lagrangian" methods) or quantifying spatial patterns of seed rain at specific locations ("Eulerian" methods) (Bullock et al., 2006). The Lagrangian approach has advantages for studying relocation processes because it can provide the true set of dispersal distances and paths, compared to the Eulerian approach, which offers a comprehensive look at the seeds or seedlings landing within deposition sites and hence tends to provide information on the combined result of both relocation and destination processes.

Several challenges exist in measuring the outcome of relocation processes. Different seeds in a population may be dispersed by different dispersers, and an individual seed may go through multiple dispersal steps by the same disperser species (e.g., seeds stolen from caches by scatter-hoarding rodents; Jansen et al., 2012) or by different disperser species (e.g., when diaspores are dispersed by frugivores and then secondarily dispersed by dung beetles, scatter-hoarding rodents, or ants; Vander Wall and Longland, 2004). Another critical challenge for measuring relocation is that seeds are difficult to track when they move outside the search area defined by the researcher (e.g., long-distance dispersal of seeds by migratory birds; Viana et al., 2016) or become undetectable in some other way (e.g., buried by scatter-hoarders, taken very high into tree canopies). More fundamentally, seeds may die during relocation, for example, due to predation by animal dispersal agents (Vander Wall et al., 2005) or through other mortality factors. Because seeds may be lost or die during the relocation processes, it is important not to treat the destination of (successful) dispersers as an unbiased measure of relocation processes. Finally, many of these methods often combine relocation and destination processes, and estimates of seed dispersal distances can vary depending on the method used (e.g., direct observations, molecular methods, phenomenological modeling, and mechanistic modeling), as they integrate different processes of seed dispersal (Gelmi-Candusso et al., 2019).

During the study design phase, investigators should consider these caveats of studying relocation processes and potential limitations in inference for their focal system. Bullock et al. (2006) discuss an iterative approach to optimize study designs for tracking or trapping seeds and minimize bias or errors using a combination of data collection and simulation studies, although to our knowledge this has never been implemented. Optimization and integration of diverse methods can provide a deeper understanding of the complicated, multi-faceted aspects of relocation processes.

Tracking seed movement

For animals with short dispersal distances or that predictably reuse transport routes, it may be possible to directly track the distances that individual seeds are moved. This approach is used often when tracking primates, where researchers follow animals for the entire day, observing frugivory and collecting fecal samples (e.g., Fuzessy et al., 2022). However, as this is not possible for most species, creative approaches to mark and relocate seeds are often required (Forget and Wenny, 2005). These methods vary according to diaspore size, dispersal mode, and the relocation metrics of interest, for example, total displacement, the movement path, or the proportion of seeds moving in and out of a location. Following the movement of individual seeds can be labor intensive, leading to low sample size (Nathan et al., 2003; Bullock et al., 2006); typically provides information on relocation provided by one disperser species rather than the assemblage; and is more feasible for seeds dispersed by large-bodied and diurnal dispersers (Rogers et al., 2019).

Marking methods include using thread tags (Forget, 1996; Xiao et al., 2006; Kuprewicz, 2013), radio transmitters (Hirsch et al., 2012a), magnets (Alverson and Díaz, 1989), fluorescent materials (Levey and Sargent, 2000), isotopes (Carlo et al., 2009), and seed mimics (González-Varo et al., 2013). Drilling into the seed to attach threads or insert tags can be used to relocate larger seeds, which are typically dispersed by scatter-hoarding animals. Radio transmitters mounted on or in seeds allow for quantifying long-distance dispersal distances over short time spans (Pons and Pausas, 2007), whereas thread tags are typically fastened to a seed for visual searching (Forget and Wenny, 2005). Telemetric thread tags that turn on/off with a magnet provide an intermediate solution that combines the benefits of thread tags (minimal cache disturbance) with those of radio transmitters allowing for longer-term monitoring (Hirsch et al., 2012a). Another method includes passive integrated transponder (PIT) tags, which have the benefit of being recoverable indefinitely without influencing animal behavior and have minimal effects on seed and seedling fates for the tested plant species (Suselbeek et al., 2013). Fluorescent microspheres or powder applied to diaspores have a short half-life and therefore are useful for diaspores with rapid removal rates (Levey and Sargent, 2000). If applied to pulp, the fluorescent microspheres are detectable in defecations that contain pulp. Stable isotope enrichment relies on the fact that plants sprayed with ^{15}N-urea reliably produce isotopically enriched seeds and seedlings; the drawback is that only a few plant sources can be enriched within a landscape (Carlo et al., 2009). Color-coded artificial seed mimics embedded in pulp and experimentally offered to animals in the field can be used to measure seed dispersal distances, either mediated by a group of frugivore species or by individual species (González-Varo et al., 2013).

Issues around the use of several of these marking methods include the introduction of visual cues that can influence disperser decisions, the necessity of disturbing the cache to recover the seed (e.g., radio isotopes, internal tags), the ability of animals to sever threads, and the addition of increased weight to the diaspore. Marking methods that require visually searching for diaspores are most profitable if diaspores are deposited in specific habitats or over short dispersal distances, such as dispersal directed to specific deposition sites (Levey and Sargent, 2000; Gorb and Gorb, 2003). Not all methods allow for identification of individual seeds, and not all allow for the tracking of seeds until germination or seedling establishment.

Spatial patterns of seed rain at specific locations

To quantify spatial patterns of seed rain, researchers can count, map, and collect seeds at specific locations following deposition, typically using seed traps. If seed sources are isolated from each other such that seed shadows are nonoverlapping, dispersal distances from the initial location to deposition can be calculated for focal seed sources. However, with overlapping seed shadows, all potential seed sources can be mapped and dispersal kernels (i.e., statistical distributions of dispersal distances; Nathan et al., 2012) can be fit using inverse modeling (e.g., Ribbens et al., 1994; Nathan et al., 2012; Bullock et al., 2017; Nuñez et al., 2018; Marchand et al., 2020). Eulerian approaches can be used to describe spatial patterns of seed rain at various phases of relocation (e.g., primary, secondary, etc.) or across phases of relocation, from initial departure to final location (i.e., total dispersal kernel; Nathan, 2007; Rogers et al., 2019). For example, seed traps elevated above the ground capture dispersal by arboreal animals that typically act as primary dispersers but not dispersal by terrestrial animals. Some approaches can lead to ambiguities as to whether the final destination has truly been recorded, leading to potential biases. In such cases, data represent the number of seeds that reach that minimum distance or location, rather than total displacement, and the analysis needs to reflect that (e.g., Bullock et al., 2011; Hirsch et al., 2012b).

To estimate seed dispersal distances, we can also use DNA markers to identify the source plant of animal-dispersed seeds sampled in seed traps or collected opportunistically from the ground along transects, beneath parent plant crowns, or while following animals (Godoy and Jordano, 2001; Pérez-Méndez et al., 2016; González-Varo et al., 2017). The target DNA markers rely on the fact that the seed endocarp is maternal tissue and, thus, has the same genotype as the mother (source) plant (Godoy and Jordano, 2001). Hence, if an endocarp is present, one can obtain genotype matchings with uncertainty statistics by genotyping the endocarp and the leaves of potential source plants (e.g., Galpern et al., 2012). This scenario makes it possible to determine where the diaspores came from and, thus, to uncover seed dispersal distances between maternal plants and seed deposition sites (Jordano et al., 2007; Pérez-Méndez et al., 2016; González-Varo et al., 2017). As discussed above, this approach is limited by the high financial and infrastructural requirements of molecular research. Moreover, it requires careful selection of the study system, as large plant populations demand genotyping many potential maternal plants to achieve successful genotype matches with the analyzed endocarps.

Predicting seed movement from models

Seed dispersal distances can be predicted using phenomenological or mechanistic models. One quasi-mechanistic approach is to predict dispersal distances using equations that describe the distance an animal moves (e.g., movement speeds calculated from relocation data of the animal's daily travel paths) and the time between diaspore departure and deposition (e.g., gut retention times, detachment processes). These are considered quasi-mechanistic as equations describe the outcomes rather than the underlying mechanisms of these processes (Cousens et al., 2010). Dispersal distances can also be predicted from dispersal kernels, which are typically phenomenological but can be mechanistically derived. Details on widely used dispersal kernels and fitting methods can be found in Nathan et al. (2012) and Bullock et al. (2017). Process-based models, such as individual-based models (e.g., Tonos et al., 2025) or mathematical models (e.g., Neubert and Parker, 2004; Neupane and Powell, 2015), can predict the movement path and dispersal distances of seeds by incorporating mechanisms driving animal movement (e.g., navigation processes, motion processes, internal state dynamics), processes of gut transit or seed detachment, interactions between animal and diaspore characteristics, and external factors (Cousens et al., 2010; Cortes and Uriarte, 2012; Borah and Beckman 2022;

Morales and Morán López, 2022). If there is detailed knowledge of the dispersal system, process-based models can capture the probability of long-distance dispersal events that are often missed in empirical approaches. Phenomenological models are useful for describing patterns (e.g., Bullock et al., 2017) and approximating more detailed mechanistic models (Beckman et al., 2020b). On the other hand, process-based models include mechanistic representations of processes rather than static relationships, which is useful for predicting responses under environmental change or in novel environments; however, process-based models tend to require more empirical information and computational resources (Beckman et al., 2020b).

Quality of dispersal during relocation

Germination studies can provide information on the effect of treatment during relocation processes on seed viability. The most robust studies use per-seed germination rates from the entire seed-bearing organ (simulating lack of dispersal), typically whole fleshy fruit, as the baseline for comparison to seeds that have been handled by animals (i.e., carried, regurgitated, ingested and passed), as well as a manually depulped treatment to separate the effects of flesh removal from that of animal handling (Samuels and Levey, 2005; Rogers et al., 2021a). The use of feeding trials ensures that all seeds for treatments of whole seed-bearing organs, those handled by animals, and those manually depulped (for fleshy seed-bearing organs) come from a similar pool at the start, which is impossible in trials using seeds obtained via opportunistic collection in the wild. Studies that characterize the whole process—from an animal's initial interaction with each plant species, to the immediate result of the interaction (ingested, handled, or destroyed), and the subsequent impacts on germination—can help generalize knowledge of plant species' dependence on animals, as well as the importance of diverse animal vectors, for seed dispersal (Gawel et al., 2023). While it can be challenging to estimate the number of seeds consumed by an animal, studies that quantify both the number of seeds consumed and the number of seeds that pass intact and then germinate make it possible to estimate the proportion survival and determine whether an animal falls closer to the seed predator or seed disperser side of the spectrum (Schupp et al., 2010).

Germination trials have limitations. First, while using captive animals can overcome obstacles associated with studying animals in the wild, working with captive animals has its own challenges as discussed above. Germination results can depend on the experimental setting of the animal as demonstrated by DeSisto et al. (2025), who compared the germination of seeds ingested by captive and wild animals. In addition, for some plant species, particularly those that are large-seeded or less abundant, collecting adequate sample sizes for germination treatments of seeds can be logistically challenging. Finally, seeds of many tropical tree species are recalcitrant, meaning they are sensitive to desiccation and low temperatures, conditions that are typically used for long-term seed storage (Tweddle et al., 2003), and lose viability in storage (Sautu et al., 2006; Waiboonya et al., 2019). Sensitivity to desiccation is an important consideration, especially for large-seeded species, as desiccation tolerance decreases with increasing seed size (Pritchard et al., 2004; Daws et al., 2005; Daws et al., 2006). As recalcitrant seeds typically cannot be stored long-term and require germination soon after collection, this introduces further constraints when working with diverse species, especially in tropical forests without distinct fruiting seasons. Seed storage is an active area of research in conservation (De Vitis et al., 2020; Walters and Pence, 2020; Walters et al., 2025).

DESTINATION PROCESSES

Destination processes include both deposition and postdispersal processes. Deposition processes are determined by animal behavior, physiology, and morphology of the disperser; external factors, such as the surrounding vegetation; and diaspore traits that influence where, when, and how seeds are deposited. Deposition processes affect the quantity of seeds dispersed to a seedscape and the quality of seed dispersal due to treatment by the disperser during this phase of dispersal (González-Varo et al., 2019; Beckman and Sullivan, 2023). Via deposition in the seedscape, dispersal influences a variety of postdispersal processes, including competition, mortality due to natural enemies, and suitability of abiotic conditions for plant performance (Howe and Smallwood, 1982; Beckman and Rogers, 2013; Beckman and Sullivan, 2023).

Deposition processes

As noted earlier, approaches discussed under "Relocation processes" often include deposition processes. Here, we focus on approaches that aim to isolate and describe the deposition processes. Determining which methods to use for measuring when, where, and how seeds are deposited is based on whether seeds are cached, defecated, regurgitated, dropped, detached from an animal (in the case of epizoochory), or other means.

Observational approaches

Direct observations of animals can detect the method of seed deposition, which may vary within animal species and depend on external factors. Some species may deposit seeds in multiple ways—for example, duikers (Cephalophinae) deposit seeds via defecation or regurgitation after ingestion or via detachment following external adhesion (Dehaudt et al., 2024). As the composition and spatial arrangement of deposited seeds affect postdispersal processes via abiotic and biotic interactions (e.g., Janzen, 1970; Connell, 1971; Loiselle, 1990), spatial patterns of seeds within and among deposition sites can be quantified by mapping deposited seeds along transects, seed traps, latrines, or from directly tracking animals (e.g., Fragoso, 1997; Wehncke et al., 2004). Furthermore, external factors can influence deposition patterns as demonstrated in the study by Aukema and Martínez del Rio (2002), where taller host tree heights with mistletoes (*Phoradendron californicum*) had greater seed deposition from the avian frugivore *Phainopepla nitens*. While censusing or collecting deposited samples, additional information can also be collected on disperser identity and the microhabitat quality of deposition sites, important for postdispersal processes (Quintero et al., 2022). As discussed earlier (under "Departure processes"), directly observing animals can be challenging. Finding and mapping seeds can also present logistical challenges, for example, smaller seeds are more difficult to find, or the disperser may deposit seeds in inaccessible locations (e.g., tree canopies).

Experimental approaches

Experimental methods for understanding where, when, and how seeds are deposited include captive feeding trials and experimental adhesion studies. Experimentally feeding animals in captivity can help determine how diaspore traits, disperser diets, and disperser traits and physiology influence the method of deposition (e.g., Abraham et al., 2021; Bracho-Estévanez et al., 2024). For seeds dispersed by adhesion to animals, researchers have attached diaspores varying in traits to animals, mobile dummies, animal coats, or human attire to measure seed detachment probability and how different adhesion properties (e.g., surface characteristics, height of attachment, location on animal) influence the rate of and force required for detachment in laboratory and natural settings (e.g., Sorensen, 1986; Fischer et al., 1996; Castillo-Flores and Calvo-Irabién, 2003; Mouissie et al., 2005; Tackenberg et al., 2006; Wichmann et al., 2009; Cousens et al., 2010). These approaches have the added advantage that the data obtained can be used to fit phenomenological models of the deposition process. For example, Bullock et al. (2011) fitted exponential functions for seed/fruit retention on or in animals, showing that dropping rates decreased with time or distance, which incidentally suggests that using mean retention times could underestimate seed dispersal distances. Similarly, Bracho-Estévanez et al. (2024) used gamma functions to describe distributions of seed retention time in five passerine species, showing that seed size was negatively related to retention time. While using live animals better reflects natural conditions, manipulations are not possible (e.g., of the substrate) and, as discussed earlier, using captive animals introduces distinct challenges. In addition, it is difficult to manipulate conditions such as habitat structure that will affect deposition processes as well as animal movement (Nield et al., 2020).

Postdispersal processes

There are a variety of empirical and quantitative approaches to elucidate postdispersal processes that influence the quality of seed dispersal and consequences for higher levels of ecological organization that will depend on a researcher's goals, research questions, and logistics. Relevant methods for postdispersal processes include censusing of seed and seedling performance across different microhabitats, seed and seedling addition experiments in microhabitats in which dispersers deposit seeds and microhabitats that are avoided by dispersers, and more targeted experimental approaches that identify the mechanisms influencing seed and seedling performance, such as manipulating abiotic factors (e.g., light and soil moisture) and biotic factors (e.g., excluding natural enemies or mycorrhizae) (Moore and Chapman, 1986; Gibson, 2015). We refer readers to recent special issues (Beckman et al., 2020a) and reviews (Rogers et al., 2021b; Beckman and Sullivan, 2023) for additional recommendations about research questions focused on studying postdispersal processes.

QUANTIFYING DISPERSER BEHAVIOR

The departure, relocation, and deposition processes of animal-mediated seed dispersal are inherently dependent on the internal states, motion capacity, and navigation capacity of animal seed dispersers; their capacity for dispersing seeds; and their response to external factors, such as the structure of the habitat(s) through which they are moving and the spatial distribution of resources and risks (Cortes and Uriarte, 2012; Borah and Beckman, 2022). How to measure the internal states (e.g., physiology, neurological) and traits (e.g., morphology, physiology, behavior, sensory) associated with animal foraging and movement and animal-mediated diaspore transport and deposition will vary based on the animal, the mode of seed dispersal, and the research question. Here, we focus on recent advances in assessing animal behavior. Acknowledging the complex roles animal behaviors play in seed dispersal is integral to understanding the mechanisms behind diaspore removal; how far seeds are dispersed; and when, where, and how seeds are deposited within and throughout landscapes. Depending on the questions investigated, researchers may be interested in studying the probability an animal encounters and removes diaspores, seed dispersal distances, or the quality and spatial distributions of seedscapes.

Traditionally, methods to quantify disperser behavior have relied on collecting species-level behavioral averages (Gosling, 2001; Hunter et al., 2022 and references therein). However, social status and personalities, that is, systematic variation in behavioral tendencies, of individual seed dispersers are increasingly found to affect seed dispersal processes across its phases and outcomes for SDE, especially regarding high-quality long-distance dispersal events, which are rare but important (Zwolak, 2018; Zwolak and Sih, 2020; Bartel and Orrock, 2022). For example, seed handling behaviors related to boldness have been found to greatly influence the shapes of seed dispersal kernels, seed fates, and potential for germination and establishment (Brehm et al., 2019; Zwolak and Sih, 2020; Boone et al., 2022; Brehm and Mortelliti, 2022). Relevant approaches to measure boldness, aggression, sociability, activity, and exploratory tendency via behavioral coding techniques, experimentation (in the field and lab), and traits rating (i.e., rating personality traits of individuals based on a numerical scale; Cheng et al., 2023) should be considered at the study design phase (Bell, 2007; Sih et al., 2015; Cheng et al., 2023). Recent technological and analytical advances to assess brain activity in the field allow researchers to conduct neurophysiological studies on the effects of animal behavior on dispersed seeds in situ (Sanguinetti-Scheck and Gálvez, 2024). We can apply the concept of "keystone individuals" (Modlmeier et al., 2014)—analogous to "keystone species," where the behavior of certain individual animals exerts a relatively large effect on the overall performance of a group (sensu Sih and Watters, 2005)—to understand the nuanced mechanisms behind where, how, and why seeds are moved by keystone individual animals within landscapes. Studies considering the effects of individual variation in behavior among seed dispersers are still nascent in our field, with much to be explored, including in bird and mammal systems, where most research connecting animal personalities to seed dispersal has been conducted to date (Howe, 1986; Modlmeier et al., 2014; Brehm et al., 2019; Zwolak and Sih, 2020; Boone et al., 2022; Brehm and Mortelliti, 2022), as well as in other animal systems.

Movement behaviors that occur concomitantly with physiological processes have long been understood to shape seed dispersal distances (e.g., using radio-tagging and mark–recapture techniques to track animal movements among sites while fruits and seeds pass through digestive systems) (Fell et al., 2023 and references therein). Recent advancements in technology, including GPS, geolocators, and radio frequency identification (RFID), enable high-resolution tracking for a greater number of animal species encompassing even very small body sizes, while complementary sensors provide additional information on kinematics, behavior, and physiology (Kays et al., 2015). Data processing tools of animal relocation data and movement models to identify patterns and infer potential drivers have advanced rapidly alongside technological advances and increasing access to big data (Getz, 2022; Nathan et al., 2022; Kays et al., 2023; Getz et al., 2024). In addition, remote sensing can complement on-the-ground environmental measurements for more fine-scaled study of the effects of environmental factors on animal behavior and the resulting patterns of seed dispersal (Davies and Asner, 2014; Russo et al., 2023; Russo et al., 2024). Applying emerging methods in movement ecology allows researchers to understand the mechanisms driving animal movement, including personality-dependent movements and implications for individual space-use (e.g., home range, site fidelity, and habitat selection) (Spiegel et al., 2017; Rumeu et al., 2025), and connect emergent patterns of animal movement to processes across the phases of seed dispersal and SDE (Borah and Beckman, 2022).

DIASPORE TRAITS RELEVANT TO DISPERSAL BY ANIMALS

Diaspore traits, such as the mode of presentation on (e.g., upward-pointing vs. hanging, individual vs. clustered) or off the plant, morphology (size, shape, hardness), chemistry (scent, palatability, nutrients), and visual presentation (color), are considered internal states that influence the navigation and movement capacities of diaspores (Damschen et al., 2008; Beckman and Sullivan, 2023). Diaspore traits are influenced by predispersal processes, such as pollination (Leal and Koski, 2024) and nutrient availability during development, and influence each phase of the dispersal process: predispersal (e.g., Beckman and Muller-Landau, 2011), departure (e.g., Muñoz et al., 2017), relocation (e.g., Bracho-Estévanez et al., 2024), deposition (e.g., Dehaudt et al., 2024), and postdispersal (Beckman and Rogers, 2013). Diaspore traits affect selection by animals (Valenta and Nevo, 2020) and play a major role in structuring seed dispersal networks (Crestani et al., 2019; Wang et al., 2024). Relating diaspore traits to the dispersal process and its outcomes aids in generalization across systems, facilitates understanding of plant populations and communities, and highlights natural variation found in either plants or animals (Aslan et al., 2019; Saatkamp et al., 2019).

Given the importance of functional traits in the seed dispersal process, standardized methods are key to synthesize studies. For example, simple traits, such as size, can be measured in a variety of ways, such as units of mass, volume, or surface area, that may differ based on the question and objective of the research study. Therefore, in developing a research project, a researcher should provide an operationalized definition of the functional trait relevant for the research objectives (Valenta and Nevo, 2022) and choose an appropriate method to measure the defined functional trait. While more work needs to be done to operationalize functional traits, several resources provide protocols for standardized measurement of key traits relevant for dispersal, including a published handbook for plant functional traits (Pérez-Harguindeguy et al., 2013) and a comprehensive review focused on fleshy fruit dispersed by animals (Nguyen et al., 2026).

While most studies measure variation among species, it is increasingly acknowledged that there is a noteworthy degree of intraspecific variation in diaspore traits, both within and among individuals, that influences dispersal processes (Herrera, 2017; Schupp et al., 2019; Nevo et al., 2022; Gelambi and Whitehead, 2023) with consequences across levels of biological organization (Snell et al., 2019). As such, studies must consider the level of variation to focus on and the implications of ignoring intraspecific variation (e.g., potential for systematic bias) (Schupp et al., 2019; Snell et al., 2019).

When comparing among plant species, there is value in both a phylogenetically confined approach that focuses on a single well-resolved lineage (e.g., Hodgkison et al., 2013) or on a community of more far-related species that inhabit a common habitat (e.g., Nevo et al., 2018).

When exploring diaspore-related trait variation, both experimental and observational approaches can be used to describe patterns at various levels of biological organization and isolate drivers of observed variation. Field, common garden, and reciprocal transplant experiments offer controlled environments that help isolate factors driving variance in the trait of interest, for example, whether variability arises from genetic variability or phenotypic plasticity (Johnson et al., 2019). The collection of seed-bearing organs from the wild allows for the quantification of trait variation in natural conditions and is also more practical when studying plant species with life histories that render common garden experiments impractical.

After more than a century of research, the study of diaspore traits is entering the age of big data: large datasets of plant traits are becoming available and enabling large synthesis projects (e.g., D^3: The Dispersal and Diaspore Database, Hintze et al., 2013; TRY plant trait database, Kattge et al., 2020; The LEDA Traitbase, Kleyer et al., 2008; Seed Information Database, Society for Ecological Restoration et al., 2023; GIFT, Weigelt et al., 2020). These databases have already been used for broad-scale analyses of the evolution of fruit color (Onstein et al., 2020; Sinnott-Armstrong et al., 2021), the prediction of seed dispersal distances from traits (Tamme et al., 2014), and plant investment in dispersal structures (Thomson et al., 2018). As a caveat, these databases tend to rely on easy-to-measure traits (e.g., size) or easy-to-deploy methods (e.g., qualitative descriptions rather than empirical measurements of color), tend to ignore intraspecific variation, and do not include more complex traits like nutrient content or chemical profiles. As such, there is vast potential for fully unlocking the patterns driving or driven by fruit trait variation (Nguyen et al., 2026).

APPROACHES INTEGRATING ACROSS SEED DISPERSAL PHASES

A variety of approaches can be used to integrate information across phases of animal-mediated seed dispersal to advance our understanding of seed dispersal processes, seed dispersal effectiveness, and consequences across levels of biological organization depending on the availability of data (Beckman et al., 2020b). Here, we discuss molecular tools, network-based approaches, and process-based models.

Molecular tools

By applying molecular tools, researchers can gain insight into seed dispersal processes from departure to deposition phases. Molecular tools can help identify which animal species removed diaspores and deposited seeds at distinct micro- and macrohabitats (González-Varo et al., 2019, 2023; Quintero et al., 2024). Targeting residual animal DNA on the surface of seeds dispersed through endozoochory (González-Varo et al., 2014), DNA barcoding analyses have proven ideal for identifying bird and mammal species that dispersed seeds sampled in seed traps, along transects, and through direct searches (e.g., Schlautmann et al., 2021; García-Rodríguez et al., 2022; González-Varo et al., 2022, 2023; Quintero et al., 2024). These studies were conducted across diverse ecosystems, including temperate lowland forests (e.g., Schlautmann et al., 2021; García-Rodríguez et al., 2022; González-Varo et al., 2022, 2023; Quintero et al., 2024), alpine (montane) forests (García-Rodríguez et al., 2022) and Mediterranean woodlands (González-Varo et al., 2023; Quintero et al., 2024) in Europe, and high-mountain xeric woodlands in the Canary Islands (González-Varo et al., 2022). Under dry conditions, DNA barcoding enabled successful identification of dispersers even several weeks—and in some cases, months—after seed deposition (González-Varo et al., 2014, 2022). Such wide temporal windows offer the possibility of rapid, single-day sampling of frugivore-dispersed seeds, which can be valuable in locations where periodical fieldwork is not feasible owing to accessibility or logistic constraints (González-Varo et al., 2022). Conversely, very wet conditions seem to foster DNA contamination and degradation (González-Varo et al., 2014), which means that this approach could be challenging in certain ecosystems. Importantly, seeds can remain intact after DNA barcoding analysis, as DNA extraction to identify animal seed dispersers targets only the animal DNA present on seed surfaces. This allows DNA barcoding analysis to be used in tandem with DNA microsatellite genotyping of endocarps in individual seeds to jointly identify disperser species, locate the source plant (González-Varo et al., 2017), and determine maternal contributions to seed rain (Isla et al., 2024). The rationale for the latter is that DNA microsatellite genotyping can determine how many individual plants contributed to the seed rain at a particular location, as well as the degree of relatedness among dispersed seeds (Garcia and Grivet, 2011).

Network-based approaches

Network-based approaches offer a powerful and standardized method to simplify complex patterns, quantify observations, and gain insight into how seed dispersal interactions structure ecological communities (Carlo and Yang, 2011). Seed dispersal interactions can be represented and analyzed as a network graph, with species representing nodes and interactions among species as the edges that link them (Jordano, 1987; Bascompte and Jordano, 2007; Delmas et al., 2019). By analyzing seed dispersal networks, researchers can compare seed dispersal interactions across space and time (Schleuning et al., 2016), characterize the structure of and factors that shape the network (Eklöf et al., 2013; Ong et al., 2021; Durand-Bessart et al., 2023), or analyze the relative role and contribution of individual species in a given network (Pigot et al., 2016). The module membership of species can provide insights as to which other seed dispersers are likely to share the same fruit resources and therefore the vulnerability of seed dispersal networks to the loss of any given seed-dispersing species (Rogers et al., 2021b). Network-based approaches are increasingly combined with other analytical tools to study the impacts of human activities on seed dispersal functionality more broadly. For example, Donoso et al. (2020) used counterfactual extinction simulations to evaluate the relative impact of size-dependent frugivore interactions on long-distance seed dispersal distance capacity of the remaining seed disperser assemblage and the structural integrity of networks. Interpretation of networks and network-based metrics must be met with caution as they are influenced by sampling and inherent biases in interpretation (Dormann et al., 2007; Blüthgen and Staab, 2024). For example, the interactions of a less abundant species may be poorly sampled relative to those of a more abundant one, and so abundant species may appear disproportionately more generalized relative to a less abundant one. Most networks to date are in actuality frugivory rather than seed dispersal networks; they rely on interaction data based on the quantity of seeds removed by frugivores at the departure phase without assessing quality components of seed dispersal throughout dispersal phases. Future studies should incorporate the functional outcomes of interactions to more accurately describe seed dispersal networks (Simmons et al., 2018; González-Castro et al., 2022; Dáttilo, 2025) and examine shifts in dispersal outcomes as networks change in response to global change (e.g., Borah and Beckman, 2025).

Process-based models

Finally, process-based models can help us integrate diverse empirical information from technological advances, observations, and experiments to evaluate the importance of processes operating at different spatiotemporal scales and at different phases of seed dispersal (Jongejans et al., 2015; Beckman et al., 2020b). These range from computational (e.g., Cousens et al., 2010; Cortes and Uriarte, 2012; Morales and Morán López, 2022) to analytical models (e.g., Levin et al., 2003; Jongejans et al., 2008). Developing and analyzing process-based models present challenges as incorporating realistic dispersal processes occurring at multiple spatiotemporal scales in heterogeneous environments and evaluating their influence across levels of biological organization can be computationally and mathematically intractable (Beckman et al., 2020b). Individual-based models are one such tool that can be used. In recent years, there have been advances in standardizing the development, implementation, and analysis of individual-based models to examine the emergent properties that arise from the nonlinear dynamics of interacting individuals (Grimm and Railsback, 2005, 2011; Grimm et al., 2006, 2020). Analytical models can approximate the movement of individual seeds by animals and be included as submodels in individual-based models to allow simulation at higher levels of biological organization or larger spatiotemporal scales (Beckman et al., 2020b). Exciting future directions remain in integrating empirical, mathematical, and statistical approaches to incorporate departure, relocation, and deposition processes and estimate dispersal kernels from all contributing dispersers (i.e., total dispersal kernel), as well as incorporating post-dispersal processes (total effective dispersal kernel; Rogers et al., 2019). Researchers can analyze these kernels to explore the contributions of dispersers to plant spatial patterns or to simulate the effects of dispersal disruption for conservation and management (Rogers et al., 2019).

APPROACHES TO ADDRESS SPARSE DATA

Despite decades of ecological studies, seed dispersal interactions for many species, much less their outcomes for SDE, are either incompletely known or remain unobserved; however, increased availability of and access to ecological data and quantitative advances offer opportunities to generalize across systems and subsequently predict for management and conservation purposes (Farley et al., 2018; Nathan et al., 2022; Beckman and Sullivan, 2023). The global development and consolidation of large biodiversity trait (e.g., Kissling et al., 2019; Kattge et al., 2020; Tobias et al., 2022) and interaction databases (e.g., Fricke and Svenning, 2020; Lim et al., 2021; Liang et al., 2024) have fueled the development of statistical and machine learning models to simulate missing data, for example, to predict interaction likelihoods between plants and dispersers, dispersal distances, or germination success using available data on plant traits or trait associations between diaspores and the frugivores that consume them (Tamme et al., 2014; Fricke et al., 2022; Nunes Martinez and Mistretta Pires, 2024). Such approaches can aid in predicting plant responses to global change for many species when data tend to be sparse (e.g., Fricke et al., 2022; Bogen, 2024).

There is potential to fill data gaps across the phases of seed dispersal by synthesizing the growing availability and accessibility of ecological data relevant for animal-mediated seed dispersal (available data summarized in Beckman et al., 2020b) and by developing standardized data collection protocols that can be implemented globally across a network of researchers. The development of standardized data collection protocols will depend on the research question and objectives, including which phases of dispersal are relevant; available resources of the network of researchers; and the benefits, limitations, and feasibility of collecting data from observations or a coordinated distributed experiment (Fraser et al., 2013; Borer et al., 2014). To ensure comparability across systems, metrics of dispersal can be standardized based on the interdisciplinary frameworks to study dispersal—generalized gravity framework, movement ecology paradigm, and SDE framework—while methods to measure these metrics may be standardized at a lower level as methods may necessarily vary by system details (e.g., dispersal mode, habitat, plant stature). In addition, protocols can be developed for use by volunteer science networks, more commonly used to study plant phenology, to collect data across the phases of the animal-mediated dispersal process. For example, several recent studies have involved volunteers monitoring the quantity of seed dispersal by frugivores (Bath-Rosenfeld, 2019) or seed arrival and germination (Vega et al., 2021), engaged elementary school children in experiments of seed removal (Miczajka et al., 2015), or used existing volunteer science platforms (i.e., Macauley Library and iNaturalist) to characterize bird–plant interaction networks (Díaz et al., 2024).

DISCUSSION

With advances in theory; empirical, quantitative, and computational methods; and increased availability and access to data, future research can continue to unravel the complex, multi-faceted nature of animal-mediated seed dispersal and provide novel insights regarding the mechanisms underlying seed dispersal and its consequences. As seed dispersal is the main opportunity for seed plants to move locations, this is especially urgent under global change (McConkey et al., 2012; Neuschulz et al., 2016; Rogers et al., 2021b). Interdisciplinary frameworks to study seed dispersal (generalized gravity framework, movement ecology paradigm, SDE framework) will guide investigators to design studies with the appropriate combination of pilot studies, careful observation, thoughtful experimental design, and quantitative models to discern the important processes and consequences of seed dispersal. Of paramount importance in the study of zoochory is deeply understanding the study system, the natural history of all study species (plants and animals), and the appropriate temporal, spatial, and taxonomic scale to address the research question. By combining empirical information on the processes of seed dispersal with quantitative models, we can integrate information from disparate sources and from across the phases of animal-mediated seed dispersal, leading to improved predictions of seed movement in novel, changing environments. Developing standardized protocols that can be implemented across the globe via coordinated studies or for use in volunteer science networks while simultaneously and iteratively advancing theory and quantitative models is a necessary next step for generalizing across systems.

AUTHOR CONTRIBUTIONS

All authors contributed to writing the original draft and revisions. Authors are listed alphabetically following N.G.B. and E.K.K. N.G.B. conceived and led the paper and led sections not mentioned in the following: predispersal processes led by A.S.G., departure processes and animal personalities by E.K.K., camera traps by A.J. and H.S.R., quality during relocation by H.S.R., network approaches and statistical and machine learning models by J.Y.L., molecular approaches by C.I.M. and J.P.G.V., animal movement by B.B., traits by O.N., and relocation processes by J.M.B. and N.G.B. E.K.K. led development of Figure 1 and Table 1.

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CONFLICT OF INTEREST STATEMENT

Noelle G. Beckman is a guest editor of this special issue of *Applications in Plant Sciences* but took no part in the peer-review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

No original datasets were used in the preparation of this review.

ORCID

Noelle G. Beckman https://orcid.org/0000-0001-5822-0610
James M. Bullock https://orcid.org/0000-0003-0529-4020
Amanda S. Gallinat https://orcid.org/0000-0003-0397-6562
Juan P. González-Varo https://orcid.org/0000-0003-1439-6475
Abir Jain https://orcid.org/0000-0002-6409-3352
Jun Ying Lim https://orcid.org/0000-0001-7493-2159
Carina I. Motta https://orcid.org/0000-0001-7127-7638
Omer Nevo https://orcid.org/0000-0003-3549-4509
Haldre S. Rogers https://orcid.org/0000-0003-4763-5006

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