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Cascading Impacts of Seed Disperser Loss on Plant Communities and Ecosystems

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Abstract

Seed dispersal is key to the persistence and spread of plant populations. Because the majority of plant species rely on animals to disperse their seeds, global change drivers that directly affect animals can cause cascading impacts on plant communities. In this review, we synthesize studies assessing how disperser loss alters plant populations, community patterns, multitrophic interactions, and ecosystem functioning. We argue that the magnitude of risk to plants from disperser loss is shaped by the combination of a plant species' inherent dependence on seed dispersal and the severity of the hazards faced by their dispersers. Because the factors determining a plant species' risk of decline due to disperser loss can be related to traits of the plants and dispersers, our framework enables a trait-based understanding of change in plant community composition and ecosystem functioning. We discuss how interactions among plants, among dispersers, and across other trophic levels also mediate plant community responses, and we identify areas for future research to understand and mitigate the consequences of disperser loss on plants globally.

1. INTRODUCTION

Seed dispersal is the primary opportunity for individual plants to move. Dispersal impacts plant populations by influencing recruitment and thus population persistence, as well as by affecting population spread and connectivity among populations (Levine & Murrell 2003, Levin et al. 2003) (**Figure 1**). The impacts of seed dispersal on plant recruitment arise from the combined effects of escape from high mortality near parent plants (Howe & Smallwood 1982), increased probability of reaching microsites suitable for germination (Howe & Smallwood 1982), and dispersal-related processes that improve the condition of the seed (e.g., inundation, gut passage, pathogen removal) (Fricke et al. 2013). Studies targeting each of these processes show substantial evidence for such benefits of dispersal on plant regeneration (e.g., Comita et al. 2014, Traveset & Verdú 2002).

Many animal seed dispersers face population declines, extinctions, and range reductions caused by habitat loss, land use change, overhunting, and invasive species (McConkey et al. 2012). Changes in animal populations in turn threaten the subset of plants that rely on animals for

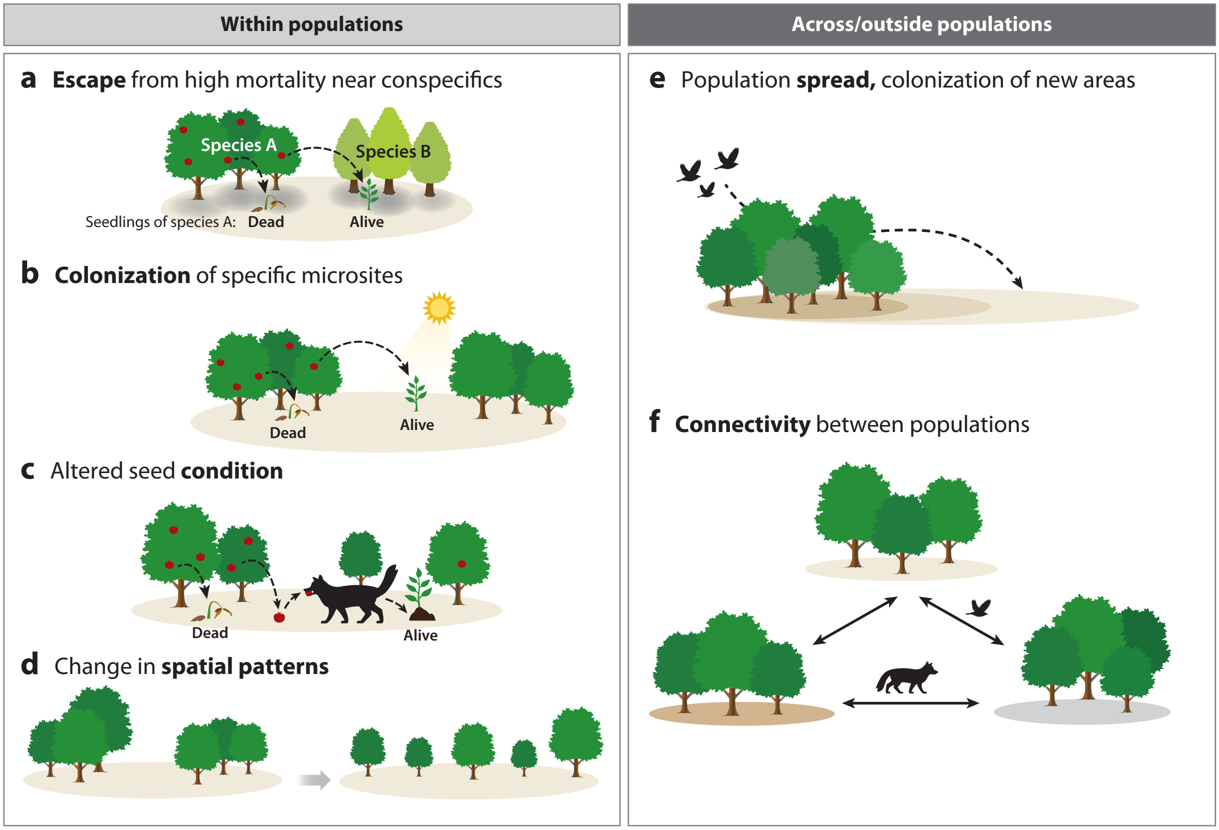


Figure 1

Impacts of seed dispersal on plant populations (*ovals*). (*Left*) Within populations, seed dispersal (*dashed arrows*) can affect population persistence by (*a*) allowing seeds to escape areas of high mortality near members of their same species, (*b*) allowing plants to reach specific microhabitats (e.g., high-light areas, favorable soil conditions) where they are more likely to survive, (*c*) altering the condition of seeds and thus increasing the probability of germination (e.g., flesh removal during gut passage), and (*d*) altering a population's spatial patterns. (*Right*) Across populations, seed dispersal also (*e*) enables populations to spread beyond existing range limits and colonize new areas and (*f*) facilitates connectivity between distinct populations, which can be important for preserving genetic diversity, rescuing declining populations, or maintaining metapopulations.

dispersal. Since prehistoric times, human arrival to new regions has caused widespread changes to animal assemblages (Galetti et al. 2018, Malhi et al. 2016) and likely to the seed dispersal process (Janzen & Martin 1982). For example, quaternary extinctions included the loss of nearly all megafauna in the Americas, including many species that likely dispersed seeds (e.g., gomphotheres, sloths, and horses). The role of extinct species as seed dispersers is inferred based on their traits, observation of seed dispersal by closely related extant species, and fossilized evidence of the seed dispersal process (Janzen & Martin 1982). Today, the seed dispersers most susceptible to defaunation are still primarily megafauna on continental land masses, including large-bodied frugivores in tropical forests (Young et al. 2016) and large-bodied herbivores globally (Atwood et al. 2020, Ripple et al. 2015), as well as the largest-bodied birds, bats, and lizards on islands (Pérez-Méndez et al. 2016, Traveset et al. 2012). Declines of common smaller-bodied birds and mammals (Davidson et al. 2009, Rosenberg et al. 2019) may also cause subtle but pervasive impacts on seed dispersal function globally.

Contemporary spatial or temporal gradients in the severity of disperser loss provide an opportunity to understand the role of animal-mediated seed dispersal in particular, and the seed dispersal process more broadly, in plant populations, communities, and ecosystems. In this review, we start by summarizing the patterns in dispersal modes across plant life history strategies and habitats. We then evaluate the cascading impacts resulting from the decline or loss of seed dispersers by addressing how disperser loss (*a*) impacts plant populations, (*b*) changes the composition and functional diversity of plant communities, (*c*) changes the dynamics of multitrophic systems, and (*d*) affects other ecosystem functions. We finish by highlighting both conservation strategies for restoring the ecological function of seed dispersal and future research priorities designed to fill critical gaps in our current knowledge. Although declines in dispersers are often coincident with declines in other ecological groups such as herbivores, here we primarily focus on studies that isolate the direct and cascading impacts of seed disperser loss.

2. PATTERNS OF ANIMAL-MEDIATED SEED DISPERSAL

Plants have evolved diverse strategies for dispersing seeds, many of which involve animals. Animal-dispersed plants include species that produce fruit flesh that primarily attracts vertebrate frugivores (endozoochory), fleshy lipid- and protein-rich structures attached to seeds that attract ants (myrmecochory), or physical structures that enable external attachment to vertebrates (ectozoochory). Many plants that exhibit traits associated with abiotic dispersal (e.g., ballistic, gravity, wind, or water dispersal) may still experience animal-mediated dispersal when they are consumed and defecated by vertebrate herbivores, in which case the "foliage is the fruit" (Janzen 1984). Other plant species benefit when some seeds are partially consumed and dropped, or are moved, cached, and later forgotten by seed predators (synzoochory) (Gómez et al. 2018). Besides seeds of angiosperms, animals can disperse diaspores of ferns (Boch et al. 2016) and bryophytes (Chmielewski & Eppley 2019) as well as the fruit-like structures of some gymnosperms (Givnish 1980). Thus, animal-mediated dispersal is found across the plant phylogeny.

The advantages of biotic dispersal over abiotic dispersal are that seed movement over longer distances is possible in areas with many physical barriers (e.g., forests) and that animals may move seeds to particular microsites suitable for germination (directed dispersal) due to habitat selectivity by the disperser (Wenny 2001). The nutrient-rich feces surrounding endozoochorously dispersed seeds may also increase germination (Traveset & Verdú 2002). However, the disadvantages of biotic dispersal are that population persistence and spread are dependent upon the reliability of animal partners, potentially making animal-mediated dispersal riskier than abiotic dispersal.

Defaunation: global, local, or functional extinction of animal populations or species from ecological communities; includes both the disappearance of species and declines in their abundance

Cascading impacts: comprehensive set of effects caused by a perturbation that triggers a chain of events

Ecosystem functions: processes that control the stocks, fluxes, stability, and interactions of energy, nutrients, and organic matter within an environment

Ectozoochory: dispersal of seeds or spores via transportation on the outside of animals (e.g., on their skin or feathers); also known as epizoochory

Myrmecochory: dispersal of seeds or spores by ants

Synzoochory: dispersal of seeds by seed-caching animals, which serve as both predators and dispersers

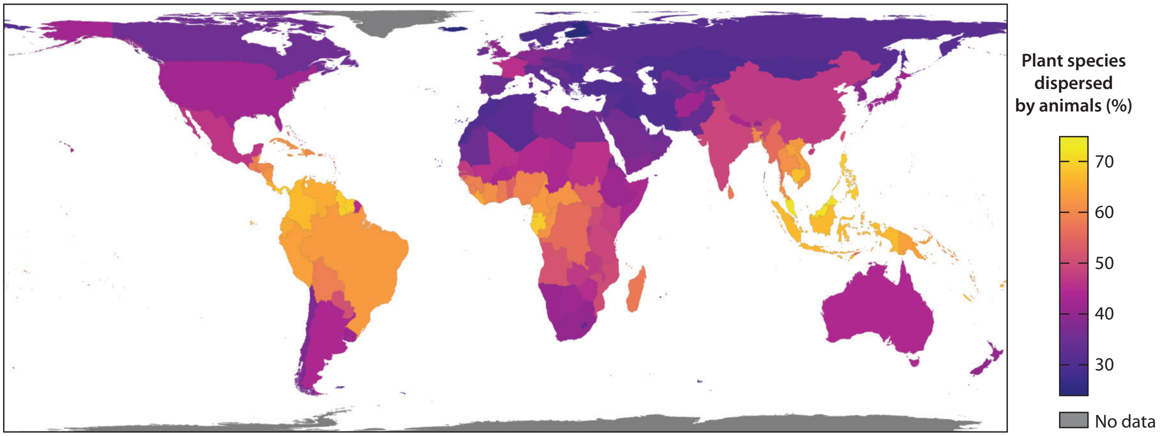


Figure 2

Global prevalence of animal-mediated seed dispersal. Country-level estimates for the percent of plant species dispersed by animals are shown by a color gradient, with gray indicating regions where estimates are unavailable. The status of plant species as either animal dispersed or not animal dispersed is derived from literature and trait databases or, for plants without these data, from a phylogenetic imputation method where status is based on phylogenetic relatedness to species with known status and species traits.

Additionally, fruit flesh may be costly to produce and may attract predators and pathogens in addition to dispersers (Fricke et al. 2013).

To estimate the prevalence of animal-mediated dispersal globally, we compiled data describing whether plant species are or are not primarily animal dispersed from literature and public trait databases (Fricke & Svenning 2020, Gómez et al. 2018, Hawes et al. 2020, Kattge et al. 2020, Maitner et al. 2018, Sinnott-Armstrong et al. 2018), covering 23,589 species from 4,666 genera and 352 families of seed plants (angiosperms and gymnosperms). We inferred the dispersal mode of species for which dispersal mode data are unavailable based on available data for related species (Goolsby et al. 2017). Using lists provided by the Botanical Information and Ecology Network (BIEN) database [~400,000 seed plant taxa in total (Maitner et al. 2018)], we estimated that 52% of seed plants are primarily dispersed by animals, a figure that agrees with a previous estimate obtained using a different approach (Aslan et al. 2013). **Figure 2** shows geographic variation in the percentage of species dispersed by animals based on country-level species lists. Although this analysis gives only coarse estimates based on diverse data sources, it shows that biotic dispersal is widespread globally and is more prevalent in the tropics, particularly in tropical forests (**Figure 2**).

Prior studies have shown that dispersal mode varies across latitudes, altitudes, habitats, and plant growth forms in largely predictable ways. Animal-mediated dispersal, especially by larger-bodied species, is more common in the tropics and at low elevation, whereas smaller-bodied animal and abiotic dispersal modes are prevalent at higher latitudes and elevations (Chapman et al. 2016, Chen et al. 2016, Vander Wall et al. 2017). Wind dispersal is more frequently found in open habitats, whereas animal-mediated dispersal is more common in closed habitats (Lorts et al. 2008). Dicots in general, and woody dicots in particular, are more likely to be biotically dispersed compared to monocots and herbaceous dicots (Tiffney & Mazer 1995). Tropical forest tree species are largely animal dispersed [75–90% (Jordano 2013)], along with up to 60% of the flora in temperate forest communities (Howe & Smallwood 1982, Willson et al. 1990). Plant species are predominantly abiotically dispersed in savannas, grasslands, and extreme environments such as deserts and alpine systems (Jordano 2013).

Many different animal species have been recorded dispersing seeds, and the importance of different taxa as dispersers varies across habitat types. Ants are particularly important for temperate forest understory herbs and in desert communities (Anjos et al. 2020, Willson et al. 1990). Scatter-hoarding small mammals are common in arid and semiarid systems, temperate and Mediterranean forests, and tropical forests (Gómez et al. 2018). Bats and primates play key roles as seed dispersers in tropical ecosystems, as do large herbivores (45–999 kg) (Fleming & Kress 2011). However, there is also ample evidence showing the contribution of large herbivores (e.g., deer, sheep) in temperate systems, especially for ectozoochorous seed dispersal (Albert et al. 2015). Megaherbivores [>1,000 kg (e.g., bison, extinct gomphotheres, elephants)] are thought to have been important in tropical and temperate systems, and in forests and savannas, but most megafauna were lost during the Pleistocene, so megaherbivores remain functionally important today primarily in Africa and Southeast Asia. Even plants in and around aquatic ecosystems benefit from endozoochory, as frugivory is present in all extant freshwater fish orders (Correa et al. 2015), and most waterbirds ingest and disperse seeds as they feed (Green et al. 2016). Note that these patterns emerge from synthesizing many studies conducted by different researchers across the world, but they are likely to be influenced by taxonomic or geographic biases. In addition, because many plant species have multiple dispersers, a given disperser species could be important for population persistence but not spread and connectivity, or vice versa.

3. EFFECT OF SEED DISPERSER LOSS ON PLANT POPULATIONS

To understand the risk of population decline for plants that rely on animals for dispersal, we adopt a framework commonly used in disaster planning, which posits that risk is the combination of vulnerability, hazards, and exposure (**Figure 3*a***). A plant species' intrinsic vulnerability, or potential for loss, is determined by the plant's demographic dependence on dispersal (**Figure 3*b***). Plants that require escape from high mortality near parent plants, specific microsites for germination, or changes to the condition of the seed during the dispersal process will have a higher intrinsic vulnerability to disperser loss (Aslan et al. 2019) (**Figure 1**). However, vegetative growth (clonal or resprouting) and the storage effect, wherein populations persist in a variable environment by waiting for favorable conditions, can confer resilience to disperser loss (Bond & Midgley 2001, Eriksson 1992, Kneitel & Chase 2004, Venable & Brown 1988). The threats to a species' dispersers represent the hazards (**Figure 3*c***). In this conceptual model, species that are highly vulnerable to disperser loss may not be at risk if the magnitude of hazards to their dispersers is low. Finally, the degree of risk depends on the exposure of processes to risk (**Figure 3*d***). For disperser loss, the processes exposed to risk include population persistence, spread, and connectivity. The species at highest risk are those most dependent on animal seed dispersers for population persistence, spread, and connectivity *and* whose partners are most likely to be negatively impacted by global change.

There is ample evidence that disperser loss affects plant populations (reviewed in Beckman & Rogers 2013, Farwig & Berens 2012, Howe & Miriti 2004, Kurten 2013, McConkey et al. 2012). Studies assessing impacts of disperser loss on plant regeneration have shown a decrease in seed germination (Cochrane 2003, Pérez-Méndez et al. 2018) and limitations in recruitment (Cordeiro & Howe 2003, Traveset et al. 2012, Wotton & Kelly 2011, Wright & Duber 2001). The spatial pattern of plants can be affected by changes in the disperser community, showing greater clustering with defaunation (Bagchi et al. 2018). However, clustering affects population growth or persistence only when associated with conspecific negative density-dependent mortality or inbreeding. The individual impacts of disperser loss have led to plant population collapse for some species. For instance, several tree species in the forests of West-Central Africa that depend upon elephant

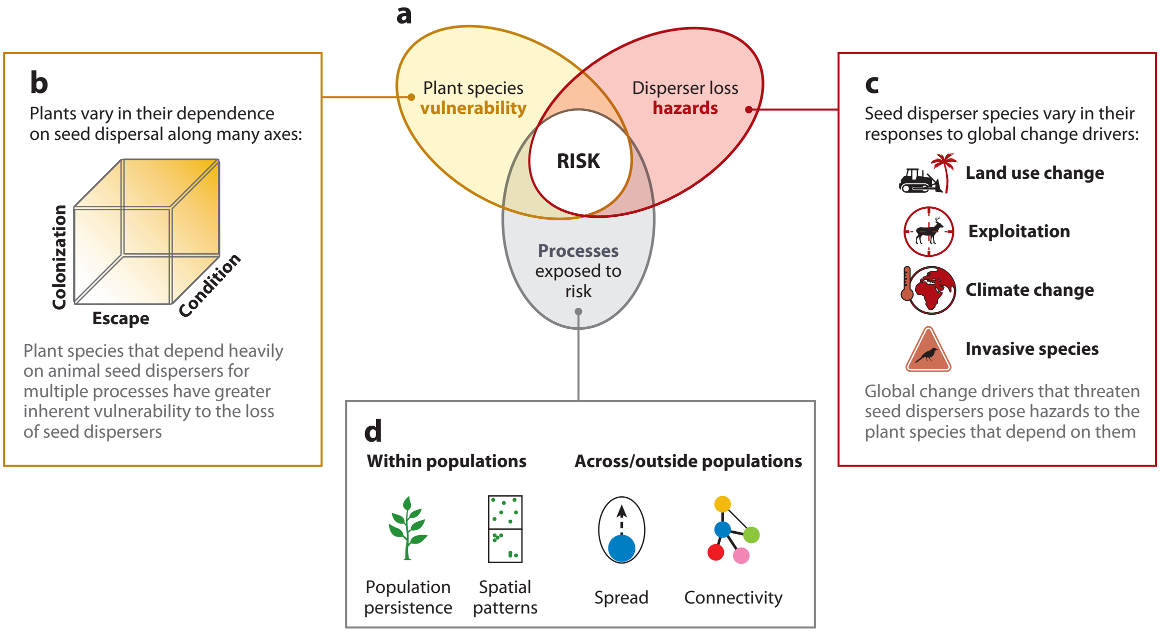


Figure 3

A conceptual framework for predicting the magnitude of risk to plant populations posed by seed disperser loss. (*a*) The degree of risk can be described as the product of three factors: a plant species' intrinsic vulnerability to disperser loss, the magnitude of hazards to seed dispersers, and the processes exposed to risk. (*b*) Species with greater dependence on seed dispersal for population persistence have greater vulnerability to disperser loss. (*c*) Several global change drivers pose hazards to seed dispersers. (*d*) The processes exposed to risk due to disperser loss include plants' population persistence, spatial pattern, spread, and connectivity. Risk is greatest for plant species that are highly dependent on dispersal for population persistence, spread, and connectivity and whose dispersers face severe hazards.

seed dispersal are facing dramatic declines due to ivory poaching (Beaune et al. 2013). In the southeastern Iberian Peninsula, the decline of mammalian seed dispersers (e.g., foxes) has led to poor regeneration, which forecasts local extinction of a keystone semiarid shrub, *Ziziphus lotus* (Rey et al. 2018).

Plants may experience reduced gene flow between populations and range contraction with disperser loss. Studies addressing changes in connectivity have found reductions in phenotypic and genetic plant diversity (Calviño-Cancela et al. 2012, Galetti et al. 2013) and in genetic connectivity among plant populations (Pérez-Méndez et al. 2017). Also, by simulating megafaunal defaunation, Doughty et al. (2016) found a 31% decrease in the range size of large-seeded tree species.

4. IMPACT OF SEED DISPERSER LOSS ON PLANT COMMUNITIES

Community-level consequences of seed disperser loss derive from the population-level changes to regeneration described above, along with resulting changes to interactions among plant species and interaction cascades among plant and disperser assemblages. These consequences may involve changes to a plant community's spatial pattern, species abundance distribution, and species, functional, and phylogenetic diversity (Levine & Murrell 2003). In recent years, studies of a host of accidental experiments in which dispersers have declined or disappeared (HilleRisLambers et al. 2013, Markl et al. 2012), in combination with extinction simulation models, have contributed to a better understanding of the role of biotic dispersal in plant communities.

To assess the community-level impacts of disperser loss, we first consider processes that mediate the impact of disperser loss on plant community composition. We draw on bipartite species interaction networks in **Figure 4** to illustrate the patterns of interactions within communities. We distinguish between direct impacts on plants that result from the loss of seed dispersal function and indirect impacts caused by altered species interactions after disperser loss. We adopt the response traits and effect traits framework following Suding et al. (2008) to distinguish between traits that predict a species' response to global change and those that predict the effect of species on ecosystem processes under global change. We also consider how seed disperser loss may affect the future assembly of communities under climate change by affecting the dynamics of range-shifting species.

4.1. Direct Impacts: Plant Response Traits Reflecting Vulnerability to Disperser Loss

The patterns in plant species' dependence on animal dispersal across a community will determine the magnitude of change in species, functional, and phylogenetic diversity after disperser loss (**Figure 4*b***). Theory and empirical evidence suggest that life history trade-offs reflected in plant traits control plant species' dependence on seed dispersal and thus their response to disperser loss (Levine & Murrell 2003).

Seed size is a key trait that can reflect an intrinsic vulnerability to disperser loss. Seed size mediates the competition-colonization (Tilman 1994) and tolerance-fecundity trade-offs (Muller-Landau 2010). These trade-offs describe how small-seeded species have limited ability to compete or tolerate unfavorable abiotic conditions but a greater ability to disperse to sites that have favorable conditions or few competitors, thus making small-seeded species more dependent on dispersal. Empirical data support this strong dependence on dispersal by small-seeded plants. Small-seeded species are typically less shade tolerant than large-seeded species (Hewitt 1998) and are more negatively affected by the natural enemies that cause density-dependent mortality (Lebrija-Trejos et al. 2016). Further, small-seeded, fleshy-fruited species have been shown to exhibit larger benefits of gut passage for germination (Fricke et al. 2019), which suggests that they depend more on dispersers to change the condition of the seed. Plant species with strong dependence on animal dispersal for regeneration are intrinsically more vulnerable to the loss of their seed dispersers. In the unusual scenario in which all animal-dispersed plant species were to lose all dispersers, we predict that those with small seeds would be the first to decline.

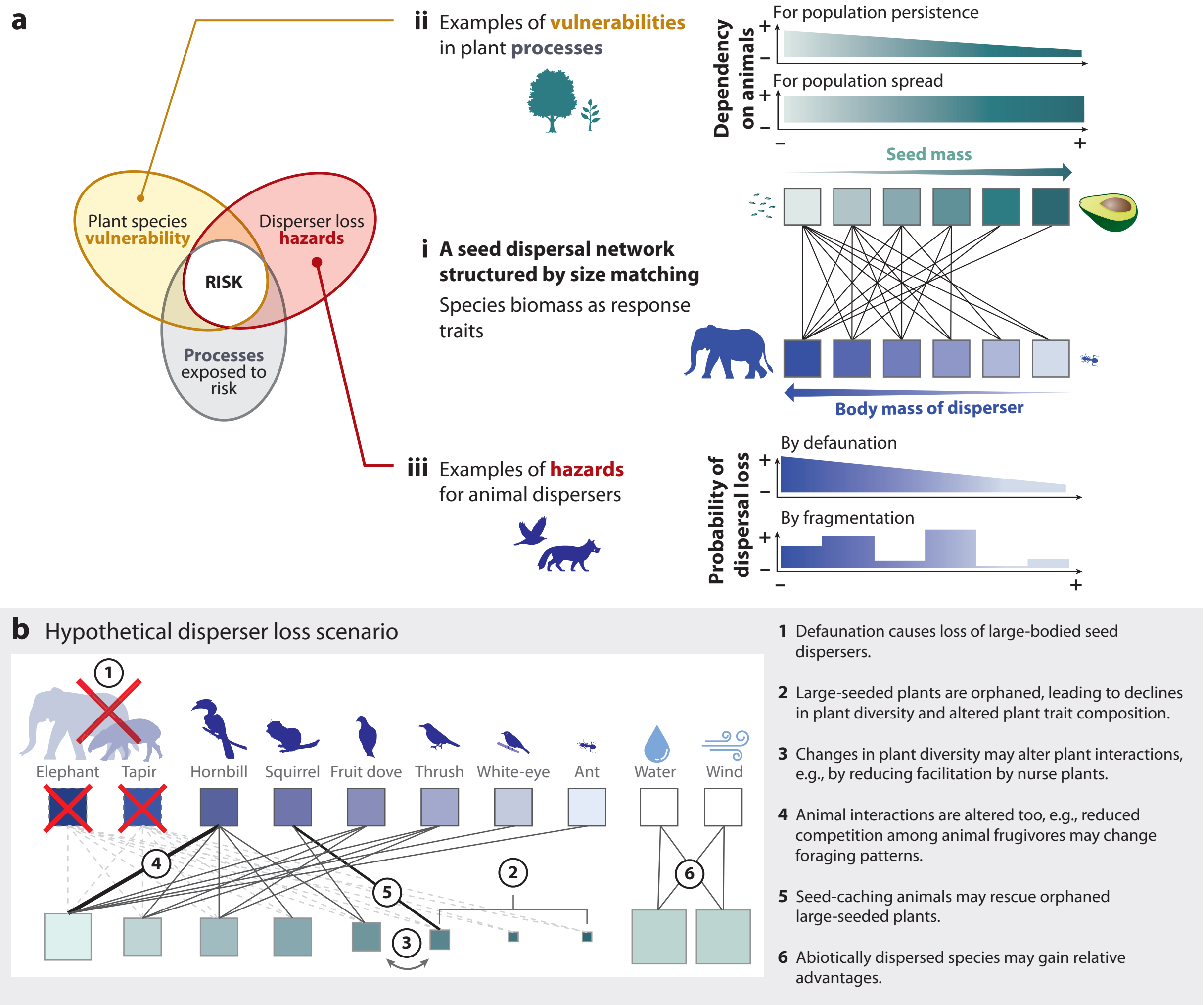
Population spread and connectivity in biotically dispersed plants almost entirely depend upon animals, unlike recruitment, which may be possible for some biotically dispersed plant species in the absence of seed dispersers. At local scales, dispersal loss is expected to reduce species diversity by limiting the colonization of species from the regional species pool into a local community (Levin et al. 2003). Similarly, disperser loss can reduce diversity by limiting immigration from nearby growing populations that could rescue a shrinking population (Shmida & Ellner 1984). The effects of disperser loss can increase beta diversity among patches through an increase in species turnover when these processes are conceptualized within a metacommunity. While such complete community-wide disperser loss is rare, empirical tests are possible in the forest on Guam where the accidental introduction of the brown tree snake caused the functional extirpation of all vertebrate dispersers (Savidge 1987, Wiles et al. 2003). Consistent with the predictions that disperser loss reduces local (alpha) diversity and increases among patch (beta) diversity, Wandrag et al. (2017) showed that bird loss from Guam halved the richness of plant species recruiting in canopy gaps, while increasing seedling beta diversity across canopy gaps when compared to neighboring islands where seed dispersers are present.

Species interaction network: representation of the biotic interactions within a community in which species (nodes) are connected by trophic or nontrophic interactions (links or edges)

Response trait: morphological, biochemical, physiological, phenological, or behavioral characteristic of a species that influences its susceptibility to environmental change

Effect trait: morphological, biochemical, physiological, phenological, or behavioral characteristic of a species that underlies its impacts on ecosystem properties, and thus, its functional contribution

Metacommunity: set of interacting communities linked by the dispersal of multiple potentially interacting species



1 Defaunation causes loss of large-bodied seed dispersers.

2 Large-seeded plants are orphaned, leading to declines in plant diversity and altered plant trait composition.

3 Changes in plant diversity may alter plant interactions, e.g., by reducing facilitation by nurse plants.

4 Animal interactions are altered too, e.g., reduced competition among animal frugivores may change foraging patterns.

5 Seed-caching animals may rescue orphaned large-seeded plants.

6 Abiotically dispersed species may gain relative advantages.

Figure 4

(*a*) Hypothetical outcomes of disperser loss in a size-structured seed dispersal network. (*i*) Seed dispersal interactions in an intact fruit-frugivore network depend on size-based trait matching. Plant and animal species in this network are shown with squares, interactions among them are shown with black lines, and darker shading indicates larger seed mass or animal body mass. Large-seeded plants tend to have the fewest partners, whereas large-bodied animals have the most partners. (*ii*) Plant response traits such as seed size/mass may predict a plant species' dependence on animals for population persistence and population spread, and thus the plant's vulnerability to animal declines. The height of the green bars represents the hypothetical magnitude of vulnerability for plants given their traits, with small seeded plants having higher dependence on dispersers for persistence than large-seeded plants and all species having high dependence on dispersers for spread. (*iii*) Animal response traits such as body mass can predict the likelihood of disperser decline due to global change drivers. The height of the blue bars represents the magnitude of the hazard to each animal in the network. In this hypothetical example, the probability of disperser loss via defaunation is greater for large animals, whereas consequences of fragmentation are species specific and independent of body mass. (*b*) A hypothetical scenario of community changes following loss of large-bodied seed dispersers, showing potential direct and indirect consequences of disperser loss. Note that this network includes biotically and abiotically dispersed plants. As in panel *a*, darker shading indicates larger seed mass or animal body mass. The size of the plant squares indicates relative abundance following defaunation, the width of the black lines indicates seed dispersal interaction frequency, and the grey dashed lines indicate lost interactions.

4.2. Direct Impacts: Plant Response Traits Reflecting Hazards Facing Their Dispersers

While the maximum potential consequences of disperser loss may be shaped by plant species' intrinsic dependence on dispersal (**Figure 4*b***), the realized impacts of disperser loss for plants also depend on which seed dispersers are susceptible to the hazards that cause declines or restriction of movement (**Figure 4*c***). Body mass and range size are strong predictors of mammal and bird vulnerability to extinction, with larger-bodied species (particularly in mammals) and species with small range sizes facing highest risks (Dirzo et al. 2014, Osuri et al. 2020, Ripple et al. 2017). The greatest threat to mammals and arguably to birds is harvesting, and larger-bodied animals have the greatest chance of being harvested (Osuri et al. 2020, Ripple et al. 2017). Studies focused on the consequences of the loss of large vertebrates and seedling recruitment have typically found lower seedling recruitment of large-seeded species in response to defaunation of the focal large disperser taxa (Kurten 2013). Large vertebrates also disperse many small-seeded fruits, but their relative importance to small-seeded plants is uncertain.

The size-biased loss of seed dispersers may reduce species diversity and cause directional shifts in functional composition at regional scales. It has been hypothesized that the loss of Pleistocene megafauna may have led to the loss or range reduction of plant species with a megafaunal fruit syndrome (large fruits often protected by a tough endocarp) (Guimarães et al. 2008, Janzen & Martin 1982). However, a recent meta-analysis failed to find a genetic signal of disperser loss in plants with megafaunal fruit syndrome when compared to plants without that syndrome (Collevatti et al. 2019). The link between large-bodied seed dispersers and large-seeded plant communities has also been studied by examining macroevolutionary patterns in plants and dispersers. Brodie (2017) took advantage of a natural experiment produced by the fact that the biogeographic barriers (including Wallace's Line) in the Indo-Malay Archipelago are stronger for animals than for plants, leading to regions with phylogenetically similar plant communities and naturally depauperate frugivore assemblages dominated by small-bodied birds. By analyzing the fruit traits of vertebrate-dispersed plant species within 42 genera across the archipelago and controlling for phylogeny, Brodie (2017) found that average maximum fruit length was 40.2% and 46.5% smaller in the depauperate regions. This result suggests that trait-matching among vertebrate and plant assemblages might control trait distributions at large spatial scales over deep temporal scales.

Although size-differential harvesting of animals is a dominant pattern, other processes can change the local abundance or movement of seed disperser species. Habitat fragmentation selectively reduces seed disperser diversity based on animal response traits such as body mass, flight abilities, and habitat specialization (Osuri et al. 2020). Fragmentation results in the reduction of particular seed dispersers, including birds and large-bodied mammals, which can lead to the loss of plant species and functional diversity via a reduction in seed dispersal and recruitment (Cordeiro & Howe 2003, Stevenson & Aldana 2008; but see Markl et al. 2012). The very smallest vertebrate species tend to have small ranges and are particularly susceptible to habitat loss (Ripple et al. 2017). Small vertebrates also tend to be poorly studied relative to large-bodied species and receive little conservation funding (Ripple et al. 2017); therefore, less is known about the impacts of their loss on seed dispersal.

One might hypothesize that plant species with few disperser species, which we will call specialized, would be at higher risk of experiencing the effects of disperser loss than generalized plant species that attract many dispersers. Counterintuitively, however, Fricke et al. (2017b) found that generalized species were more intrinsically dependent on mutualistic interactions and thus had higher vulnerability than specialized species. Through use of the framework developed by Chomicki et al. (2020), these vulnerable species with many partners could be categorized as obligate generalists, or at least closer to obligate on the facultative-obligate spectrum. Obligate generalist species depend strongly on dispersal for escape from areas of high mortality, colonization of suitable microsites, and gut passage to increase germination, and thus are vulnerable to disperser loss. Their wide array of partners (Fricke et al. 2017b), however, makes the loss of all dispersers an unlikely hazard, reducing the overall risk.

Rewiring: ability of species to switch partners in response to a perturbation, such as the disappearance of their primary disperser; interaction rewiring could mitigate coextinctions

Simulations have been used to assess the impacts of hazards such as climate change or overexploitation on plant communities. A simulated loss of dispersal function predicted a decline in the total number of seeds and plant species dispersed (Rumeu et al. 2017), impoverishment of seedling communities in terms of abundance, species diversity and seed size (Donoso et al. 2017b), negative impact on plant population viability due to an increase in spatial aggregation across the entire life cycle (Caughlin et al. 2015), and substantial reductions in community-wide long-distance seed dispersal (Donoso et al. 2020, Pires 2017). Overall, these studies have predicted that the magnitude of seed dispersal function lost due to altered disperser communities is not linear, reinforcing the idea that the order and identity of the disperser lost could have profound implications for plant communities.

4.3. Indirect Impacts: Altered Interactions Among Plant Species

In addition to the direct impacts on a plant community, seed disperser loss may indirectly alter plant communities through changes in positive or negative interactions among plant species. If nurse plants (i.e., plant species that facilitate seedling establishment of other species below their canopy) decline following loss of their dispersers, the facilitated plant species will also decline. Valiente-Banuet & Verdú (2013) describe such an indirect impact of disperser loss in degraded semiarid habitats in Mexico: Bat-dispersed columnar cacti failed to recruit due to disperser limitation, affecting other species that use the cacti as a nurse plant. Altered competition among plant species is also likely to result from direct changes to the plant community following disperser loss. In Nigeria, hunting of primates has led to reduced dispersal of large-seeded species, which has released wind-dispersed seedlings from competition (Olsson et al. 2019). The loss of large-seeded plant species, which are often stronger competitors and more tolerant of environmental hazards (Moles & Westoby 2006), is likely to shift the community toward small-seeded wind- or animal-dispersed species.

4.4. Indirect Impacts: Impacts on Plants of Altered Interactions Among Dispersers

The decline or loss of particular dispersers may alter interactions among remaining seed dispersers, in turn affecting the plant community. The remaining seed disperser species could either compensate for or aggravate disruptions to seed dispersal processes. However, we still know very little about the mechanisms and magnitude of interaction compensation and rewiring, when a species that has lost its partner forms new links to extant species, within seed dispersal communities. There is evidence for compensation for the loss of seed-dispersing megafauna by mammals such as primates, rodents, tapirs, agoutis, and introduced pigs and livestock (Kurten 2013, Pedrosa et al. 2019), enabling plant species that exhibit megafaunal dispersal syndromes to persist. While some of these animals are smaller than the extinct megafauna and are unlikely to swallow and defecate megafaunal seeds, they have been observed carrying seeds long distances, providing effective dispersal away from the parent plant (Blanco et al. 2019).

Most seed dispersal networks appear to be modular, with plants and dispersers forming distinct subgroups that interact more with each other than with members of other subgroups. Thus, the potential number of animal species able to compensate for the loss of a disperser by increasing their consumption of the affected plant species is limited to those within the subgroup rather than the entire community (Donatti et al. 2011). Furthermore, seed dispersers are not always functionally redundant, as some dispersers are more effective than others for a given plant species, which can limit the ability of remaining species to compensate for lost species. Even if a species has a wide dietary overlap with an extinct or declining disperser, it may not be an effective seed disperser if it deposits seeds in a poor location for germination or acts more as a seed predator than a disperser (e.g., Campos-Arceiz et al. 2012). It is thus important to include information on the quality of dispersal when predicting whether coextinction will result, rather than assuming all partners are equally effective, as many coextinction models do.

Plant recruitment data so far indicate that terrestrial seed dispersers do not fully compensate for the loss of arboreal dispersers, and small frugivores cannot always be replaced by dispersers that partly overlap in body size (Kurten 2013). Bat species, in particular, are unlikely to be replaced by other dispersers, not only because of the specific traits of the fruits they consume but also due to the distance to which they transport the seeds; this is worrisome, as bats, among mammals less than 1 kg, are the most threatened by hunting (Ripple et al. 2016). Scatter-hoarding rodents in Asian and African tropical forests are generally less than 1 kg and thus likely incapable of handling large seeds in a way that might allow them to compensate for the loss of large frugivores (Kurten 2013). Recent evidence shows that rather than compensation, the loss of dispersers may lead to interaction deficits wherein remaining dispersers are freed from competition and can specialize on their preferred fruits at the expense of less desirable fruit species, thus exacerbating the negative effects on biodiversity (Fricke et al. 2017a). Finally, communities experiencing widespread disperser loss may not even have the potential for compensation, as is the case on the island of Guam, which has lost all native vertebrate frugivores (Rogers et al. 2017).

Coextinction: the local or global extinction of a species resulting from the local or global extinction of a species on which it depends

Interaction deficit: reduction in ecological function that arises when changes in behavior or abundance of species remaining after a primary extinction are insufficient to compensate for the interactions lost due to extinction

Nested community: community in which the interactions of specialized species are subsets of the interactions of generalized species

4.5. Indirect Impacts: Feedbacks and Coextinction

Feedbacks may occur among plants and seed disperser assemblages over long temporal scales following seed disperser loss (**Figure 4*d***). While the long timescale of these feedbacks precludes most empirical studies, models can be used to predict extinction cascades or coextinctions. One of the primary modeling approaches used to predict coextinctions in mutualistic interactions is the topological coextinction model (Dunne et al. 2002, Memmott et al. 2004). Starting with empirical observations from an interaction network, the model simulates an initial extinction and then records the resulting losses that occur when a species no longer has an extant partner. The basic coextinction models overlook variation in species' dependence on dispersal by assuming that all plant species require partners to persist; they focus instead on which species are most likely to lose their partners. Key predictions from these topological coextinction models are that species with more partners are less likely to experience extinction, and that more connected and nested communities are more robust to extinction. This leads to the prediction that specialized plant species or those with few potential partners, as is often the case for large-seeded species, are more vulnerable to coextinction. These implications of the topological coextinction model, which does not explicitly consider traits, were addressed by Donoso et al. (2017b) to show the pervasive consequences of frugivore downsizing within seed dispersal networks.

One extension to the topological coextinction model accounts for variation between species in their relative dependence on mutualistic interactions for reproduction or survival (Vieira & Almeida-Neto 2015). This model can be used to determine the probability of coextinction in response to simulated animal extinctions while considering plant species' intrinsic dependence on the mutualism. Applications of this model suggest that the mutualist species that are most likely to lose their partners are those least dependent on mutualistic interactions for reproduction and survival (Fricke et al. 2017b), a finding that, intriguingly, contrasts with that found for plant-pollinator mutualisms (Traveset et al. 2017). The inverse relationship between plant dependence on the mutualism and susceptibility to disperser loss can buffer species from disperser loss and may explain the persistence of animal-dispersed plants long after the disrupted mutualism.

4.6. Dispersal and Plant Range Expansion

Plant species distributions have undergone large shifts in response to environmental changes over deep timescales (Huntley & Webb 1989). Plant ranges, and changes in ranges, are constrained in part by seed dispersal. Vertebrate declines (Andermann et al. 2020) may have influenced macro-ecological patterns since the Last Glacial Maximum. Across all plant species (including both biotically and abiotically dispersed species), there is evidence for widespread dispersal limitation that has impeded tree species at high latitudes from filling their range of suitable habitats (Svenning et al. 2008). We do not know of studies that have specifically considered how individual plant species' range filling (or lack thereof) during this period of climate change relates to coincident losses of their seed dispersers. However, the findings that plant species with Pleistocene megafaunal dispersal syndromes have smaller ranges than other animal-dispersed plant species (Doughty et al. 2016) suggest that past disperser loss may have limited climate-induced range shifts in the past.

Recent disperser loss is likely to shape how plant communities respond to twenty-first-century climate change (Corlett & Westcott 2013). Terrestrial mammal extinctions and declines since the late Pleistocene have substantially reduced biotic connectivity, with negative implications for seed dispersal (Berti & Svenning 2020). Climate-induced range shifts in seed dispersers may reduce seed dispersal (Mokany et al. 2014), and dispersal vectors are likely to affect plant species' ability to respond to a changing climate (Schleuning et al. 2020). There is surprisingly little research that specifically examines how seed disperser decline influences the ability of plant communities to shift their ranges, despite a recognition that this is likely to be important.

5. CROSS-TROPHIC IMPACTS OF DISPERSER LOSS

The decline or extinction of a seed disperser may trigger declines or extinctions in plants, which in turn cascade to affect species not involved in seed dispersal, particularly if these species are highly specialized and dependent on the affected plant. However, information regarding partner specificity and dependence is scarce, making it difficult to accurately predict such cascading impacts. As a plant species' abundance declines, its interactions become progressively less frequent (Valiente-Banuet et al. 2015). This interaction loss may lead to local or global species extinction if there is inadequate compensation or rewiring. Further, the extinction of a keystone plant species, or one with an effect disproportionate to its abundance, can have cascading effects on other species interactions, either by causing a redistribution of interactions (i.e., rewiring interactions) or by modifying interaction strength (Poisot et al. 2015, Tylianakis & Morris 2017). Such cascading effects across interaction types become particularly problematic when there are correlations between interaction types (e.g., if animals move seeds and mycorrhizae simultaneously) (Correia et al. 2019a). Here we provide some documented or potential examples of cascading impacts affecting other species interactions.

5.1. Plant-Pollinator Interactions

The decline or extinction of plant species due to disperser loss may negatively affect pollinators of those plants. In a study of all angiosperms in Wisconsin, 11.9% were biotically pollinated and produced fleshy fruits, whereas only 0.1% were abiotically pollinated and produced fleshy fruits (Givnish et al. 2020). If this pattern of linked biotic pollination and dispersal is widespread, then disperser loss could cascade to affect pollinators via negative effects on the shared plant species. We do not know whether plants that are highly dependent upon animal dispersers are likely to have specialized pollinators that would be susceptible to coextinction. *Crescentia alata* is a tree with a megafaunal fruit syndrome that is now widespread in the dry forests and savannas of Costa Rica likely due to dispersal by introduced horses. *C. alata* is also an important resource for nectivorous bats during the rainy season. Janzen & Martin (1982) hypothesized that loss of Pleistocene megafauna may have led to dramatic reductions in *C. alata* distribution and abundance, with cascading impacts on bats, until horses were introduced 400 years ago. Pollination in palms (family Arecaceae), predominantly animal dispersed, is rather generalized, with flowers being visited by various insects. For this family, disperser loss would affect pollinator species only if some of the pollinators are highly specialized on the palms (Barfod et al. 2011, Muñoz et al. 2019). In the case of fig trees, the loss of their highly generalized dispersers might involve the loss of the plant and in turn of the highly specialized fig wasp that pollinates it (Cook & Rasplus 2003). In general, the effects of plant decline on pollinators will depend upon the pollinator's capacity to shift to other available plant species in the neighborhood.

When seed dispersers (e.g., fruit bats, birds) also pollinate plants, disperser loss may also have direct impacts on pollination. In the Galapagos, 80% of bird species are both pollinators and dispersers (Hervías-Parejo et al. 2020). Some animal species serve as both a pollinator and a seed disperser for the same plant species (Fuster et al. 2019), making those species particularly susceptible to the effects of defaunation. More than 200 double-mutualist species have been identified to date, mostly found in tropical islands, arid systems, or mainland mountain tops (Fuster et al. 2019). In addition, if plant populations become more fragmented and isolated after disperser loss, the pollination assemblage of the plant species might also change, in turn influencing inbreeding rates, pollen limitation, and overall reproductive success (Bennett et al. 2020).

Because pollination and seed dispersal are sequential events in the reproductive process, plant recruitment depends on effective pollination and dispersal. Pollination and dispersal are influenced by a shared biotic and abiotic environment, so factors affecting success or failure in one interaction may affect the other as well. Yet, pollination and dispersal are often considered independent life history strategies. Further research is needed to fully understand whether certain combinations of pollination and seed dispersal strategies are particularly susceptible to the effects of defaunation.

5.2. Plant-Mycorrhizal/Rhizobial Interactions

Seed dispersers can transport fungal spores as well as seeds and, in so doing, promote arbuscular mycorrhizal diversity (Correia et al. 2019a, Gehring et al. 2002, Stephens & Rowe 2020). The loss of these dispersal agents could affect microbiota composition and function, although this has not yet been explored. One community-level study found no correlation between seed dispersal mode and mycorrhizal fungi colonization (Correia et al. 2019b). The disappearance of a plant species could translate into changes in mutualistic and antagonistic interactions with the soil biota, altering plant-soil feedbacks (Van der Putten et al. 2001).

5.3. Plant-Herbivore or Seed Predator Interactions

Evidence for disperser loss cascading to affect herbivores and seed predators, either vertebrates or invertebrates, is mixed. Vertebrate herbivores, mostly mammals, are rarely specialized (Oksanen & Olofsson 2018), so the decline or extinction of a plant population might trigger only a diet shift with no effect on the herbivore population. However, if vertebrate herbivores perform differently on some foods than on others (Choat & Clements 1998), or if they must adopt a different foraging method or move into a new habitat, the loss of a plant resource could have fitness consequences for the herbivore. By contrast, insect herbivores are often specialized (Crawley 1989, Forister et al. 2015) and are thus likely to be more vulnerable to plant decline or disappearance. Invertebrate predispersal seed predators may benefit from a loss of frugivores, as fruit stays longer on the tree, providing more opportunity for seed predation (Anderson et al. 2021). Alternatively, defaunation may shift the relationship between predispersal seed predators, as was seen in Panama, where one seed predator of the palm *Attalea butyracea* dominated in an intact forest and another dominated in a defaunated forest (Peguero et al. 2017).

Functional role: contribution of a species to ecosystem processes, expressed through its morphological, physiological, and life history traits

The loss of vertebrate seed dispersers is often coincident with changes in vertebrate seed predator and herbivore assemblages because seed dispersers are often also seed predators or herbivores, or both groups are hunted simultaneously. Using vertebrate exclosure experiments in hunted and protected areas, Kurten et al. (2015) showed that defaunation reduced both dispersal and predation of large seeds. The combined effect of seed disperser and seed predator loss will vary depending upon the plant species, its traits (specifically seed size), and the magnitude of frugivore loss, as well as the seed predator identity (Dirzo et al. 2007). Further studies are needed to test how widespread these patterns are.

6. IMPACTS OF DISPERSER LOSS ON ECOSYSTEM FUNCTIONS RESULTING FROM SEED DISPERSAL

Over the past two decades, there has been a growing interest in understanding the relationship between biodiversity and ecosystem functioning (BEF) (Hooper et al. 2005, Reiss et al. 2009). Seed dispersal is itself an ecosystem function, as described in Section 4, but it has only recently received attention in the BEF literature (Winfree 2020). Observational studies of seed disperser assemblages have revealed a positive relationship between the diversity of seed dispersers and dispersal function (e.g., number of dispersed seeds or seed deposition in areas with a high probability of seedling recruitment) (Garcia et al. 2018, Gaston et al. 2018), emphasizing the need for conservation of diverse disperser communities to maintain diverse, functioning, and resilient ecosystems (Fricke et al. 2017b). Disperser diversity is also related to what we call derived ecosystem functions, or functions provided by plant communities that emerge from the seed dispersal process. The main derived functions affected by defaunation so far are (*a*) succession and ecosystem structure, (*b*) biomass and carbon storage, and (*c*) nutrient cycling and nitrogen availability.

Assessing how the decline of seed dispersers could impact ecosystem functions requires a comprehensive framework based not only on the number of species but also on species identities and their functional roles (Brodie et al. 2018, Schleuning et al. 2015). Unraveling the shape of the relationship (**Figure 5**) between biodiversity and a given ecosystem function is crucial to understanding whether the most vulnerable disperser species are also those contributing most to the function, as well as to determining the redundancy and complementarity among species with respect to an ecosystem function (McConkey & Brockelman 2011). Trait-based approaches aim to describe how structure and function of ecological communities emerge from properties of the individual organisms. In particular, BEF relationships will depend on the correlation between (*a*) a disperser species' vulnerability to extinction (determined by disperser response traits) and (*b*) the effectiveness of seed dispersers for plants that provide a particular ecosystem function (determined by the plant effect traits) (**Figure 5**). Here we summarize current knowledge on how seed disperser loss impacts derived ecosystem functions and highlight some relevant disperser response and plant effect traits.

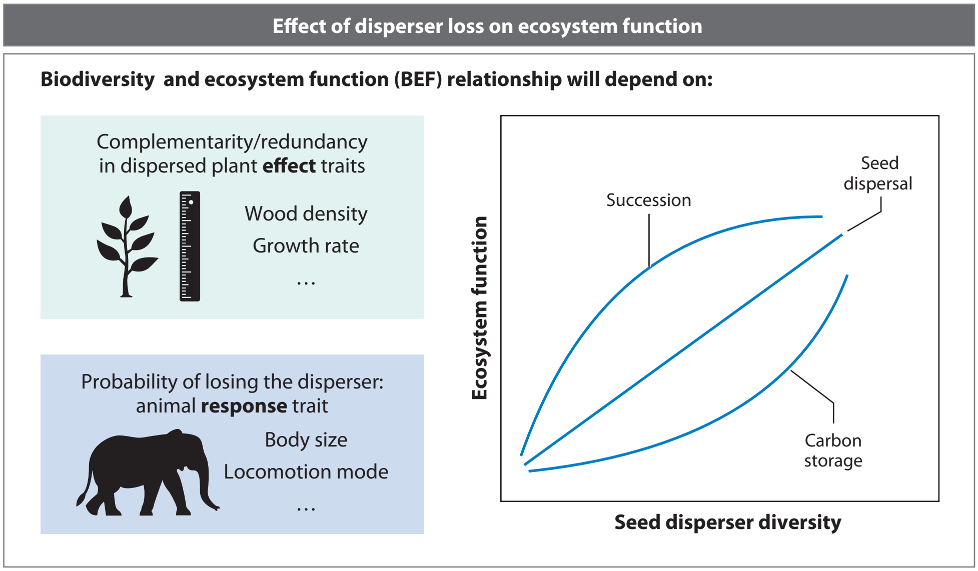


Figure 5

The effect of disperser loss on ecosystem functions such as seed dispersal, succession, and carbon storage depends on the likelihood of losing the particular dispersers for the plant species that provide those functions. The combination of plant effect traits (e.g., wood density) and disperser response traits (e.g., body size) can inform predictions on the shape of these functions.

6.1. Successional Processes

Seed dispersers can influence successional processes and the physical structure of ecosystems through their impact on the local species pool competing for space after a disturbance. Typically, pioneer species germinate in response to cues such as light and temperature and then grow quickly before the larger-seeded, slower-growing, more dispersal-limited species catch up (Tabarelli & Peres 2002). Pioneer species tend to produce plentiful seeds that are wind dispersed, ectozoochorous, or endozoochorous but with small seeds that make them accessible and desirable to many frugivore species. Therefore, in systems with moderate to high productivity, seeds from pioneer species are often present in the seed bank prior to disturbance or arrive in the seed rain shortly after disturbance. Systematic shifts in the local species pool as a result of changes in the disperser community will shift the composition of the community over time.

The impact of frugivore loss on forest structure depends on which groups of frugivores have been lost. In areas that have experienced the loss of large-bodied frugivores, regenerating plant communities tend to be dominated by small-seeded plants that are good colonizers, often spread by small-bodied frugivores, leading to a community with traits characteristic of an early successional state (Gardner et al. 2019). In areas where all dispersers have been lost, the plants that are good colonizers may be unable to reach newly available space, tilting the scales in favor of later successional, slow-growing species that are able to germinate and grow without dispersers, and disrupting the normal gap colonization dynamics, as has happened on the island of Guam (Wandrag et al. 2017). Typically, pioneer species are short-lived in comparison to the large-seeded, slower-growing, dispersal-limited plants, and highly dependent upon reaching high-light environments, so pioneer species could become locally extinct after a short period of disperser loss and subsequent lack of recruitment.

Given that much of the world's forests have been degraded, and forest restoration is a key component of climate change mitigation efforts, the role of dispersers in forest regeneration is of great conservation importance. A meta-analysis quantifying the impacts of defaunation on natural forest regeneration showed an overall significant negative impact in real-world systems linked to the loss or exclusion of dispersers (Gardner et al. 2019).

6.2. Carbon Storage

Defaunation differentially affects large-bodied dispersers, and thus large-seeded plant species, which tend to have higher wood density than small-seeded species, leading to a reduction in overall biomass and carbon storage in defaunated forests. The late Pleistocene and early Holocene extinctions of seed-dispersing megafauna were estimated to reduce carbon content in the Amazon by ~1.5% (Doughty et al. 2016). Likewise, several simulation studies in the Neotropics and Africa suggest that forests experiencing reductions in large-bodied seed dispersers may contain 2–6% less aboveground biomass compared to faunally intact forests due to changes in plant communities (Bello et al. 2015, de Paula Mateus et al. 2018, Peres et al. 2016, Razafindratsima et al. 2018). A study using a pan-tropical data set indicated that generalizations about aboveground carbon storage may not hold across the global tropics (e.g., see Southeast Asian and Australian forests in Osuri et al. 2016), but that finding has been called into question in Chanthorn et al. (2019). The latter study concluded that the impact of disperser defaunation on the carbon deficit is not necessarily lower in Asian forests compared to other tropical forests, reinforcing the idea of a general loss of carbon storage as a consequence of disperser loss. The time frame over which a loss of carbon storage as a result of defaunation may occur is still largely unknown. Spatially explicit, individual-based models of the Brazilian Atlantic Forest predict a lag of about a century between disperser defaunation and biomass loss (de Paula Mateus et al. 2018). Obtaining a better understanding of this time lag between the occurrence of seed disperser loss and the spike of carbon emissions is a critical step to guide risk assessments, as is conservation monitoring and planning to avoid ecosystem function debts.

6.3. Nutrient Cycling

Large mammals, including seed dispersers, often play a role in nutrient cycling within and across ecosystems (Dirzo et al. 2014, Young et al. 2016), yet there are few detailed studies on how losing seed dispersers can impact soil functions and biogeochemical cycles. Villar et al. (2020) performed a long-term ground-dwelling frugivore exclusion experiment in the Atlantic Forest of Brazil to test the potential impacts of defaunation on soil nitrogen cycling. The primary frugivores in this system are peccaries and tapirs, who depend upon the fruit of a hyperdominant palm in the dry season. The presence of these mammalian seed dispersers was linked to increased ammonium concentration, particularly with increasing abundance of the palm species, likely due to excretion. In addition, the ground-dwelling frugivores redistributed nutrients across the landscape from areas with high fruit abundance to areas with few fruiting palms. Finally, the authors hypothesized that foraging and mechanical impacts on the understory by the frugivores stimulated the performance of soil-nitrifying microorganisms. Defaunation of large, terrestrial mammals and the accompanying loss of dung resources may also reduce dung beetle abundance, species richness, and average size (Kurten 2013), in turn reducing secondary dispersal and nutrient cycling (Feer & Boissier 2015). Global defaunation and deforestation may thus impact nutrient cycles and productivity, although further investigations are needed from other ecosystems before general conclusions can be drawn.

7. REVERSING DEFAUNATION: CONSERVATION APPROACHES TO RESTORE SEED DISPERSAL

Ecosystem service: a benefit to humans that is provided by the natural environment

Surrogate species: species introduced as proxies for extinct native species to restore ecological function

Ecosystem restoration is one of the main priorities for biodiversity conservation. Restoring seed dispersers must be a key component of ecosystem restoration in order to maintain plant diversity and the multiple ecosystem functions derived from seed dispersal. Dispersal also contributes to human welfare through regulating and cultural avenues (Brauman et al. 2020), although it has only recently been considered as an ecosystem service. Seed dispersal contributes directly to human well-being for any plant species for which dispersal affects plant population persistence and for which the product is, for example, directly collected from the wild for human use (e.g., timber, fruit, nut) (de Freitas Chagas et al. 2020). A recent study provided the first empirical evidence of how frugivore loss is linked to decline of an economically and culturally valued plant, the chili pepper (Egerer et al. 2018). Preserving or restoring seed dispersers can support climate regulation through increased carbon storage (Osuri et al. 2016) and might help plant species track climate change (González-Varo et al. 2021). Here, we present promising strategies for reversing the impacts of frugivore defaunation.

In areas where frugivores persist but some plant species are limited by dispersal, dispersers may be manipulated to promote dispersal of select species. In Hawaii, bird vocalizations were played near endangered plants in a large patch of attractive non-native shrubs, which attracted more frugivores and increased seed dispersal of the endangered plant (MacDonald et al. 2019). Another strategy, called Induced Seed Dispersal, takes advantage of generalist seed dispersers by placing seeds of desirable plant species within the flesh of readily accessible and attractive fruits (Silva et al. 2020). Natural or artificial perching structures can be used to direct the dispersal of native seeds to suitable recruitment sites (Robinson & Handel 2010).

When functionally important frugivores have been extirpated from a system, strategic rewilding may be the best approach. This could involve reintroducing lost native frugivores, as was done with howler monkeys in the Atlantic Forest (Genes et al. 2019). Alternatively, if the native frugivores are extinct or unable to be reintroduced, surrogate species may be used (Seddon et al. 2014). Tortoises have been introduced to the Brazilian Atlantic Forest (Sobral-Souza et al. 2017) and to the Mascarene Islands (Falcón & Hansen 2018) to restore lost seed dispersal services. In some locations, non-native species may be functionally important dispersers and therefore the target of conservation rather than control (Gawel et al. 2018). Even when dispersers are still available for a plant population, reintroductions may be necessary to restore particular phenotypes. In Brazil, where loss of large-bodied frugivores caused a reduction in seed size for the palm, *Euterpe edulis*, models have shown that reintroduction of large-bodied dispersers would restore large-seeded phenotypes more efficiently than direct reintroduction of large-seeded phenotypes (Carvalho et al. 2020).

Finally, while gardening natural systems is inefficient and unsustainable, some plants deemed valuable to humans may benefit from human-aided dispersal for the purposes of agroforestry. The aforementioned *E. edulis* in Brazil is valued for its fruit and palm heart, and it is overharvested in protected areas, but agroforestry may provide a sustainable harvest and persistence of *E. edulis* populations (de Freitas Chagas et al. 2020).

The preservation of the seed dispersal process and of seed dispersers themselves is a valuable tool for low-cost ecological restoration (Howe & Miriti 2004). Maintaining and increasing remnant trees within a deforested matrix can accelerate secondary succession by attracting seed dispersers (Schlawin & Zahawi 2008). Some empirical and simulation studies have found that fruit removal rates and mean dispersal distances are strongly affected by fruiting plant neighborhoods and frugivore identity (Donoso et al. 2017a, Thierry & Rogers 2020). Plants in denser neighborhoods had greater fruit removal and shorter mean dispersal distances than more isolated plants. The interplay between frugivore habitat use, feeding, and movement decisions and the spatial distribution of adult plants could have consequences for the spatial dynamics of plant recruitment and should be considered in a restoration program.

Seed dispersal interaction networks link frugivores to the fruits they disperse and can be useful in both the restoration planning stage and monitoring restoration effectiveness (Pires 2017). For example, interaction networks can be used to identify keystone mutualists using a measure of centrality that assesses the importance of each species to the structure of the entire network (Mello et al. 2015) and to predict the potential consequences (positive and negative, direct and indirect) of species introductions or species eradication programs (Hansen 2010, Kaiser-Bunbury et al. 2010). Because most plants interact with pollinators and herbivores in addition to dispersers, and dispersers also serve as pollinators and predators, a comprehensive multilayer network approach may be warranted to more accurately assess the impacts of defaunation on plant communities (Hutchinson et al. 2019).

8. CONCLUSIONS

Defaunation due to overharvesting, fragmentation, and invasive species has demonstrated that animal-mediated seed dispersal is a key ecological function affecting plant populations and communities. A majority of plants benefit from seed dispersal by animals, and the strength of this relationship is reflected in life history strategies; plants that require escape from conspecifics, colonization of particular microsites, or changes to the condition of their seeds for germination, and that lack abiotic mechanisms to achieve these outcomes, are dependent upon animal partners. Even species that do not require dispersal for population persistence may benefit from dispersers for migration or gene flow between populations. The importance of endozoochory by large animals in the tropics is well accepted, but dispersal by smaller-bodied frugivores, nonendozoochorus modes of animal-mediated dispersal, and animal dispersal in temperate systems are understudied, and likely underappreciated.

The risk of decline for a plant species is based upon its intrinsic dependence on the interaction combined with the risk of losing all of its dispersers. Defaunation has largely occurred in a size-selective manner, with the largest-bodied dispersers disappearing first. As a result, large-seeded species have been differentially affected by defaunation because they often have relatively few dispersers, leading to shifts in the composition of defaunated forests. The ability of other species to compensate for lost dispersers is still unclear yet critically important for predicting the impacts of defaunation. Small-seeded, fleshy-fruited plant species tend to have many dispersers, which increases the likelihood that they will be adequately dispersed even under moderate levels of defaunation. However, when all dispersers are lost from a system, small-seeded animal-dispersed species will be more strongly affected due to their greater intrinsic dependence on dispersal for escape, colonization, and germination. Changes to dispersal may interact with or cascade to affect other species interactions such as pollination, mycorrhizal associations, and herbivory, yet there are few empirical studies on these cascading impacts. At the ecosystem scale, the loss of seed dispersers also affects succession, carbon storage, and nutrient cycling. It is critical to restore seed dispersal interactions to maintain species diversity and the potential for plants to respond to global change.

FUTURE ISSUES

1. Seed dispersal research has been biased toward studies in tropical systems and on endozoochorous vertebrate dispersers. Future studies of seed dispersal should pay attention to geographic and taxonomic cold spots, including temperate, arctic, aquatic, and desert

systems, and to vectors such as arthropods, small mammals, waterbirds, and fish, which remain largely overlooked.

2. Seed dispersal is but one stage and interaction type in the life cycle of a plant. To understand the full impacts of defaunation on plant populations, studies that simultaneously measure and integrate changes in pollination, dispersal, seed predation, and herbivory are much needed. Future research should move beyond the study of isolated phases of the plant life cycle and integrate the effects across interaction types.
3. The trade-off between depth—understanding a single species well—and breadth—studying dynamics across a community—has limited our ability to scale up to the community and ecosystem levels in seed dispersal ecology. More empirical knowledge generated through collaborative projects together with recent tools (e.g., next-generation sequencing, ecological networks, extinction models, and trait-based approaches) is needed to better predict community and ecosystem-level consequences of seed dispersal loss.
4. Classic studies on the role of biodiversity in ecosystem functions mainly focused on primary productivity. It is time now to investigate the relationship between biodiversity and ecosystem functions such as seed dispersal and those derived from seed dispersal, including succession, carbon storage, and nutrient cycling. Linking species interaction frequencies to the final outcome of seed dispersal, as well as identifying similar or complementary functional contributions among dispersers, is critical to understand the relationship between disperser diversity and ecosystem functioning.
5. We need a clearer understanding of how remaining organisms and different mechanisms may compensate for seed disperser loss. Observational studies along defaunation gradients and rewiring models are promising ways to provide insights into the probability of species coextinctions and the potential of communities and ecosystems to buffer negative defaunation effects.
6. Studies assessing how seed disperser loss leads to declines of economic and cultural values are still scarce but necessary to identify the value of seed dispersers to humans.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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