On mutualism, models, and masting: the effects of seed-dispersing animals on the plants they disperse

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Contents

1   Abstract

- Species interactions are context dependent, in that their direction and magnitude can vary across ecological conditions. For seed-dispersal interactions—especially plant-seed-caching-animal interactions—the direction of the interactions is often obscured because of seed mortality inherent in seed handling and the delayed effects of fitness benefits received by plants. It is therefore an open question in ecology to understand the ecological contexts under which seed-dispersal interactions are facilitative, antagonistic, or null.

- We review the fitness benefits of animal-mediated seed dispersal, extend a recently-published model to include negative density-dependent effects, and review the feedback between seed production (with a focus on masting) and animal populations.

- Negative density-dependent effects are pervasive and strongly affect the direction of plant-seed-disperser interactions, and including them into models will give a more accurate understanding of the direction of the interaction. Including negative density-dependent effects also makes the interpretation of interaction more mutualistic since seed dispersers decrease seed densities. Additionally, seed production varies greatly, and the lags between seed-production and seed-disperser population sizes complicate and limit inferences made about the direction of interactions in any given short-term field study.

- **Synthesis** If we wish to know the direction of species interactions in real ecological communities, we minimally need models that are biologically realistic. For complex and long-term phenomena, like context-dependent species interactions, we should embrace a multifaceted approach of short-term field research, long-term field research, simple models, and complex models to form a more robust understanding of the ecological problem of context dependency.

Keywords: animal-mediated seed dispersal, context-dependency, granivory, modeling, mutualism, seed caching, seed dispersal, species interactions, synzoochory

2   Introduction

Species interactions are complex, and understanding them is pressing and of paramount importance in ecology. They are important to understand because they are central to both basic ecology, like theories of coexistence (Chesson, 2000), community ecology (Vellend, 2016), and biodiveristy (Bascompte and Jordano, 2007), and central to applied ecology, like conservation (Janzen, 1971; Dirzo et al., 2014), restoration (Palmer et al., 1997; Shaver and Silliman, 2017), and how ecosystems will respond to environmental changes (Suttle et al., 2007; Tylianakis et al., 2008). The complexity of species interactions arises because species interact with many other species, and the magnitude and direction of the interactions are commonly dependent on ecological context (Thompson, 1988; Bronstein, 1994), whether the interactions are competitive (Gurevitch et al., 1992), enemy-victim (Sih et al., 1985), or mutualistic (Chamberlain et al., 2014).

To identify the direction of pairwise species interactions as facilitative, antagonistic, or null, we must reduce the complex interactions within communities into pairwise parts and study interactions across different contexts. One common type of species interaction whose direction is seemingly not entirely clear to many ecologists is seed-dispersal mutualisms between plants and animals. Animals and plants on both sides of the seed-dispersal mutualism respectively benefit from a nutriment reward and a dispersal service. Two of the main reasons that the direction of this interaction is not fully clear is because (i) the dispersal service is often difficult to quantify and (ii) the reward for animals often includes consuming the embryo of the plant, which is ultimately a mortality event. A recent paper in *Journal of Ecology* by Bogdziewicz et al. (2019) aimed to identify the direction of a particular type of plant-seed-disperser interaction that is often presumed to be mutualistic, synzoochory, which is the dispersal of seeds by seed-caching animals (*sensu* Gómez et al., 2019). Bogdziewicz et al. (2019) used a combination

of modeling and empirical approaches to conclude that synzoochory does not always benefit plant recruitment and that the interaction should be tested rather than presumed. This work inspired us to write this forum piece, where our intention is to use Bogdziewicz et al. (2019) as the groundwork to more accurately understand the positive and negative effects that seed-dispersing animals have on plants. We provide some background on dispersal in plants, followed by building negative density-dependent effects into the model from Bogdziewicz et al. (2019), a section on how interannual variability obscures our understanding of this interaction, and ending with some remarks on future directions. Our main arguments are largely twofold. First, negative density-dependent effects cannot be overlooked when trying understand the direction of animal-seed-dispersal interactions, and we show how incorporating them into a model of seed survival makes the interpretation of the interaction mutualistic and therefore in agreement with our observations in nature. Second, interannual variability in seed production obscures inferences made on short-term empirical studies about the direction of the interaction and conclusions drawn from such studies should be interpreted with caution.

3 Seed dispersal increases plant fitness in three main ways

Animal-mediated seed dispersal may be the most common mode of seed dispersal in the world (Jordano, 2000; Moles et al., 2007), has evolved independently many dozens of times across all major vascular plant taxa (Herrera, 2002; Dunn et al., 2007), and has been shown to influence rates of speciation in plants (Lengyel et al., 2010; Onstein et al., 2017). In other words, animal-mediated seed dispersal is an interaction that, at sufficiently large scales, persists as mutualistic through space and time. To be mutualistic, seed dispersing animals and the plants whose seeds they disperse share an increase in fitness in each other's presence (Bronstein, 2015). Within these interactions there is often a clear increase in fitness of the animal dispersing seeds, often through a resource reward, such as fruit pulp or nut endosperm. The increase in plant fitness, however, is less apparent and less feasible to study because the vast majority of plants species engaged in this mutualism are woody and thus longer-lived where measuring effects on fitness would take years-to-decades. Notwithstanding the empirical obstacles of measuring fitness in plants, conceptual and theoretical developments have identified mechanistically how dispersal increases plant fitness (Howe and Smallwood, 1982):

1. **Escape from negative density-dependent effects at the seed and seedling stages**. Animals disperse seeds away from parent plants, which increases seed fitness relative to remaining under the parent plant by reducing negative density-dependent effects of enemies on seeds (Janzen, 1970; Connell, 1971).

2. **Colonization of new sites**. Animals deliver seeds to new sites, which increases fitness relative to remaining under parent plants because spatial spread makes populations more robust to disturbance (which tends to be strongly spatially correlated) and, because conditions and resources vary across space and time, spatial spread allows populations to be more robust to changing conditions (e.g., Grinnell, 1936; Gadgil, 1971; Comins et al., 1980).

Most bodies of thought and studies of animal-mediated seed dispersal begin and end at the seed or seedling stage, but survival of seeds and seedlings have relatively small effects on fitness. In structured populations—like woody plants that do not reproduce during early life stages, have low survival rates during early life stages, and are highly fecund during later life stages—contributions to fitness (population persistence) are strongest in the latest life stages (Caswell, 2006). These later stages of the seed dispersal loop (*sensu* Wang and Smith, 2002) are influenced by the seed dispersal process, but are not often considered conceptually and are not often measured empirically—the latter being especially true for plants that are dispersed by animals because they tend to be long-lived. Beyond plant fitness being increased by seeds and seedlings escaping negative density-dependent effects at the seed and seedling stages (e.g., escaping pathogenic, parasitic, and frugivorous and granivorous enemies), therefore, an additional way that dispersal increases plant fitness is through:

3. **Reduction of intraspecific competition at later stages**. Animals disperse seeds away from parent plants, which increases fitness relative to remaining under the parent plant by reducing intraspecific competition at later stages (e.g., sapling and adult stages).

These are the three categorical ways in which animals can increase plant fitness through dispersal. Like all species interactions, however, there are fitness decreasing and increasing behaviors that ultimately result in a net fitness effect. Predators bear costs and benefits of attacking prey, but predator-prey interactions are generally understood as being net positive and negative respectively for predators and prey; competitive interactions bear costs to both species, but are generally understood as being net negative for both species involved unless one is driven to extinction; and mutualistic interactions include both species bearing costs and receiving benefits, but are generally understood as being net positive for both species involved. Nevertheless, given that net effect of costs and benefits of mutualistic seed dispersal interactions can have a degree of context dependency like all other species interactions (Chamberlain et al., 2014), it is important to understand the conditions under which we expect the interactions to have a net increase or decrease in fitness. To that end, a mathematical model with parameters that can be measured by empirical ecologists can reveal non- or counter-intuitive ideas of what we observe—this is the underlying beauty and power of mathematical models in ecology.

4 Modeling the net effect of animals on plant fitness

For models examining the effects of seed-dispersing animals (hereafter, 'animals') on the plants whose seeds they disperse (hereafter, 'plants') to be accurate, they must include the three ways that animals increase plant fitness through dispersal: (i) seed and seedling escape from negative density-dependent effects, (ii) colonization benefit, and (iii) reduction of intraspecific competition. In a recent paper, Bogdziewicz et al. (2019) used a mathematical model developed by Zwolak and Crone (2012) as a basis to empirically determine the direction of the effects of seed-dispersing animals on the plants whose seeds they disperse (specifically synzoochorous (Gómez et al., 2019) animals and nut-bearing plants). Broadly, the model is an inequality relating the proportion of seeds that germinate in the absence of animals (left-hand side) to the proportion of seeds that germinate in the presence of animals (right-hand side). If the proportion of seeds that germinate in the absence of animals is less that the proportion of seeds that germinate in the presence of animals, then the animals could be considered mutualistic; if not, they could be considered antagonists.

The left-hand side of the equation is the proportion of seeds that emerge (i.e., germinate) in the absence of animals from the surface of the soil, e_S. The right-hand side of the equation is, in the presence of animals, the proportion of seeds that germinate, which is comprised of the proportion of seeds that emerge after being handled by animals and the proportion of seeds that emerge that are not handled by animals. The proportion of seeds handled by animals is composed of three factors: the proportion of seeds harvested by animals, p_H; the proportion of those seeds cached by animals and unrecovered, p_C; and the proportion of those that emerge from animal caches e_C. The second term on the right-hand side is the proportion of seeds that are not handled by animals, $(1 - p_H)$ multiplied by proportion of the seeds that emerge from the surface of the soil, e_S. Together, the equation is:

$$e_S < p_H p_C e_C + (1 - p_H) e_S . \tag{1}$$

Algebraic rearrangement reveals a simple representation to determine if the animals are mutualists or antagonists:

$$\frac{e_S}{e_C} < p_C . \tag{2}$$

That is, if the ratio of proportions of seeds that emerge from the surface to seeds emerging from caches is less than the proportion of unrecovered cached seeds following removal, then the interaction is mutualistic; if not, it is antagonistic. This threshold of the isolated variable on the right-hand side of the equation is the fixed value against which e_S and e_C are evaluated, and designated as $\tilde{p}_C$. This outcome of this simple inequality is that hypothetically empirical

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ecologists could measure these three variables and determine the effect of animals on plant populations.

Implicit in eqn. 1 is that there is only a single benefit conferred by animals: the benefit of burial. Although seed burial generally confers a large germination benefit, Bogdziewicz et al. (2019) and Zwolak and Crone (2012) argue, it must be placed in the context of the proportion of seeds that animals harvest and consume to understand if the interaction is net mutualistic or antagonistic. We strongly agree with with this argument, but contend that it needs to be further extended to more realistically and generally understand the net effect of seed-dispersing animals on the plants whose seeds they disperse. More specifically, the fitness benefits described in section 3 must be considered to make ecologically-meaningful inferences about the direction of the interaction. Of the three benefits conferred by animals, two are not able to be tested with the Bogdziewicz et al. (2019) and Zwolak and Crone (2012) frameworks. That is, despite the importance of the benefits of colonization (sec. 3, benefit 2) and reducing intraspecific competition (sec. 3, benefit 3), they cannot be applied within this framework because it was created for empirical ecologists to collect data on short spatial and temporal scales to approximate if animals are mutualists or antagonists. Nevertheless, the benefit that animals provide plants by reducing negative density-dependent effects (sec. 3, benefit 1) needs to and can be incorporated into this framework. Burying seeds is one benefit conferred by animal, but reducing seed densities around the parent plant reduces mortality imposed by seed predators may be at least, if not more beneficial to seeds than the benefit of burial itself. The evidence for this claim being that in the vast majority of communities where negative density-dependent effects on seed has been studied (including tropical and temperate ecosystems), they have been found to strongly influence seed, seedling, and sapling survival (e.g., Janzen, 1970; Connell, 1971; Harms et al., 2000; Peters, 2003; Packer and Clay, 2000; Hirsch et al., 2012; Terborgh, 2012). Therefore, negative density-dependent effects should be a part of any seed or seedling survival model.

We propose two ways to incorporate negative density-dependent effects into the Bogdziewicz et al. (2019) and Zwolak and Crone (2012) frameworks:

1. Whether or not animals are present, seedling emergence from the surface is reduced from negative density-dependent effects

2. Where there are no animals, seedling emergence from the surface is reduced from negative density-dependent effects

The first scenario is somewhat trivial, but illuminating. Here, seedling emergence is reduced implicitly as part of eqn. 1. But to make it explicit, we can multiply the terms for germination from the surface, e_S, by a negative density-dependent term, which we will call δ_1, with 1 corresponding to the first scenario. As δ_1 approaches 1, survival on the surface is high; as δ_1 approaches 0, survival on the surface is low. Adding it to eqn. 1 gives us

$$e_S \delta_1 < p_H p_C e_C + (1 - p_H) e_S \delta_1 \ . \tag{3}$$

Algebraic rearrangement yields a simple representation to determine if the animals are mutualists or antagonists:

$$\frac{e_S \delta_1}{e_C} < p_C \ . \tag{4}$$

This shows that any increased mortality of the seeds on the surface will result in smaller value on the left-hand side; thus setting the threshold for the interaction to be mutualistic, $\tilde{p}_C$, lower.

The second scenario is both more substantive and realistic. Because animals reduce the density of seeds on the surface, in the absence of animals, predators, pathogens, and other enemies inflict greater mortality on the undispersed seeds because they are accessible on the surface and in higher densities. If we add the negative density-dependent effect, δ_2, with 2 corresponding to the second scenario, in the absence of animals on the left-hand side of the equation, it would be:

$$e_S \delta_2 < p_H p_C e_C + (1 - p_H) e_S \ . \tag{5}$$

Rearrangement yields:

$$\frac{e_S}{e_C}\left(\frac{\delta_2 - 1}{p_H} + 1\right) < p_C \ . \tag{6}$$

Let us make the biologically-reasonable assumption that p_H is high (near 1) because most seeds are dispersed and forest floors are not saturated with the accumulation of hundreds-to-hundreds of thousands of seeds produced per plant per year. Because δ_2 is bounded between 0 and 1, we can see that when negative density-dependent effects are weak, as $\delta_2 \to 1$, the parenthetical factor is slightly less than 1, which will slightly lower the threshold for the interaction to be mutualistic, $\tilde{p}_C$. If negative density-dependent effects are strong, as $\delta_2 \to 0$, the parenthetical factor is considerably less than 1, which will considerably lower $\tilde{p}_C$. In sum, any incorporation of the omnipresent and, in many cases of paramount importance, negative density-dependent effects will lower the threshold to make the interaction more mutualistic. Lowering the mutualism threshold is a consequence of adding a missing, biologically relevant component to eqn. 1. It is not important to lower the threshold per se, but for a model to be empirically accurate for determining the direction of the plant-animal interaction, it must also include all substantive and realistic aspects of the system's ecology.

5   Masting and inferences about seed-dispersal mutualisms

Masting, from the seed perspective, is the intermittent synchronous production of large seed crops typically followed by a period of below-average seed crop production. Ultimately, the reasons why plants mast is still not fully understood (Kelly and Sork, 2002; Burns, 2012; Pearse et al., 2016), but regardless of the evolutionary processes that led to masting, we know that masting has strong effects on seed-consuming populations, especially highly-specialized guilds like granivorous rodents (McShea, 2000; Ostfeld and Keesing, 2000). Rodent populations largely track seed production with an increase in populations occurring shortly after (1–2 years) mast events (Selås et al., 2002; Schnurr et al., 2002; Clotfelter et al., 2007; Li and Zhang, 2007; Elias et al., 2004). The opposite is true during non-mast years, often times creating a significant drop in the populations of rodents that rely on the seed crop as a primary food source (Wolff, 1996; Clotfelter et al., 2007). The variation in the ratio of rodents-to-seeds is likely an important factor in determining the direction and strength of the interaction, as discussed in the subsequent two paragraphs, and is particularly true where predator satiation is presumed to be the primary driver of masting. Scatter-hoarding rodents continue to cache seeds in preparation for food-scarcity, even if they are currently satiated and have enough food to survive the period of food scarcity (Vander Wall, 2010). We expect p_{CO} (probability that a seed is cached and not retrieved, explicitly accounting for pilferage; Bogdziewicz et al. 2019) to be generally higher during mast years than non-mast years. The opposite would be expected after mast years, when rodent abundances are high and seed production is low, with p_{CO} approaching zero resulting in a strongly antagonistic interaction. As a result, p_{CO} values would tend to be intermittent across a masting plant population based on mast strength and rodent population size.

In masting species, it has been found repeatedly that seed and seedling survival increase during mast years (Xiao et al., 2005; Vander Wall, 2002; Perez-Ramos and Maranon, 2008; López-Barrera et al., 2005; Yang et al., 2019). An increase in seed survival during mast years is often attributed to decreased post-dispersal predation due to a decrease in the number of times a seed is recached and/or pilfered (Vander Wall, 2002; Perez-Ramos and Maranon, 2008). Essentially, more seeds are being cached than rodents need for periods of food scarcity (i.e., p_{CO} increases). Additionally, seed harvest rates increase during mast years (Vander Wall, 2002; Xiao et al., 2005) which means more seeds are being cached in the ground during mast years than non-mast years (i.e., $p_H p_{CO}$ increases). This decreases the effects of negative density-dependent factors (δ_i) which we argue are important when looking at the seed-dispersal relationship (section 4).

Not all of the effects of masting may be positive for the plant. Dispersal distance also changes during mast years (Vander Wall, 2002; Li and Zhang, 2007; Jansen et al., 2004; Martínez and González-Taboada, 2009; Xiao et al., 2013). In cases where dispersal distance decreases, plants

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may face stronger negative density-dependent effects and experience reduced survival compared to seeds cached at further distances. In another example (e.g., Xiao et al. 2013), seed removal rates decreased which also likely increases negative density-dependent effects at least for the short-term. However, despite lower removal rates, overall proportion of seeds removed (ranging from 62% to 96% in Xiao et al. 2013) did not change during masting and non-masting years. Overall, there is evidence that masting has a net positive effect on plant reproduction (Jensen, 1985; Watt, 1923). Jensen (1985) was able to show that despite high seed predation during mast years, sapling age structure showed most individuals germinated the years following a mast year. This supports the hypothesis that mast years cause plant-animal relationships to surpass $\tilde{p}_{CO}$ by either decreasing surface survival ($e_S\delta_i$), increasing the number of seeds cached and not retrieved or pilfered ($p_H p_{CO}$), or increasing survival in caches (e_C). Thus we believe that it is incorrect to assume the overall interaction from a temporally-limited sample (Bogdziewicz et al., 2019; Hoshizaki and Hulme, 2002; Theimer, 2005; Klinger and Rejmánek, 2010), and would argue masting may in fact be the reason the interaction can be mutualistic.

Masting species may be poor model species when trying to elucidate the generalized or broad relationships animal-dispersed plants have with their dispersers. In a paper on masting and frugivorous birds, Herrera et al. (1994) eloquently comments on a similar point to ours that "…in recruitment, the whole is not the sum, but the product of parts, and as such, permanently susceptible to the overwhelming influence of some near-to zero operand." In synzoochory, this is primarily due to the fact that the majority of animal-dispersed masting plants are long-lived shrubs and trees (Kelly and Sork, 2002). For a population of synzoochorous plants to persist the growth rate during any generation only needs to be positive during a single season to make the overall interaction with its disperser mutualistic. That is, $p_{CO} > e_S/e_C$ (Bogdziewicz et al., 2019). Here in eastern North America, a common seed-dispersal mutualism is between the eastern gray squirrel (*Sciurus carolinensis*) and oaks (*Quercus* spp.) One species, the red oak (*Q. rubra*), can live several centuries and has been recorded in natural populations at over 250 years old (USDA and NRCS, 2019; Orwig et al., 2001). The average lifespan of the eastern gray squirrel is 6–12 years (Koprowski, 1994) meaning an individual red oak will experience multiple generations and population fluctuations of its mutualist partner during its lifetime. Indeed, most other species of plants that are dispersed by animals, especially synzoochorous animals, have average lifespans of at least decades, but over a century in many cases. These include other oaks (*Quercus* spp.), hickories (*Carya* spp.), walnuts (*Juglans* spp.), beeches (*Fagus* spp.), southern beeches (*Nothofagus* spp.), and pines (*Pinus* spp.); representing a minimum of 1300+ species (Gómez et al., 2019). Furthermore, not all mast years are equal, varying across time (Clotfelter et al., 2007; Wolff, 1996; Herrera et al., 1998) and to a lesser degree spatially (Lázaro et al., 2006; Curran and Leighton, 2000). Masting may in fact only be beneficial under a very specific set of cirumstances (e.g., years with relatively low seed predator abundance and relatively high seed production—see years 1992, 1996, and 1998 in Figure 2 of Elias et al. 2004) and may be infrequent throughout a plant's life. Lastly abiotic factors are also an important factor that can influence the interaction between plants and animals. In the western United States many rodent species in arid and semi-arid environments can only detect and pilfer caches (effecting p_{CO}) under favorable soil moisture conditions (Vander Wall, 1998, 1995, 2000). One could imagine a scenario where a community experiences drier fall months during a mast year being very beneficial to a plant population as the caching rodents would be satiated (i.e., do not retrieve all caches) and cache pilferage would be low as seeds would remain mostly undetectable in the dry soils. Thus, in these years p_{CO} would be exceptionally high. Despite the conditions where mutualism would occur seeming obvious, Price and Jenkins (1986) perspicaciously remark that understanding the overall interaction with and without rodents would be successful in only exceptional circumstances.

6 The strategy of model building to understand the ecology of species interactions

Like other common seed-dispersal modes, across large spatial and temporal scales, seed-caching animals appear to have a net mutualistic effect on plants. There is ample evidence for this claim, including, as examples: an underestimation of synzoochory in seed-producing plants is that it occurs across 641 genera in 157 families, synzoochory is found in all terrestrial biogeographic realms (except for Antarctica), and synzoochorous plants are often ecologically dominant and abundant (Gómez et al., 2019). If those observations are accurate and we observe that synzoochory is pervasively mutualistic, then we must reconcile small-scale ecological studies of context-depdnent antagonism and mutualism (e.g., Sawaya et al., 2018; Elwood et al., 2018; Bogdziewicz et al., 2019) with large-scale observations of net mutualism. Aside from the obvious long-term field studies, we need, in addition to simple heuristic models, more realistic and, consequently, complex models if we are going to make realistic inferences about the directions of synzoochorous and other seed-dispersal interactions.

In *The strategy of model building in population biology*, Levins (1966) identified three orthogonal axes of models: realism, generality, and precision. He argued that it was impossible for a model to maximally satisfy all three, and observed that, in practice, modeling strategies tend to maximize 2 but sacrifice 1 of these axes. Each strategy has its strengths and weaknesses, and ultimately all three collectively contribute to a robust understanding of the biological phenomenon in question, which in this case is the direction of species interactions broadly, and seed-disperser-plant interactions specifically. Bogdziewicz et al. (2019) and Zwolak and Crone (2012)'s models fall into the strategy of sacrificing realism for generality and precision. The models sacrifice realism by excluding many biologically-relevant terms that we know affect the direction and strength of these interactions, such as negative density-dependent effects (e.g., Sugiyama et al., 2018), animal densities (e.g., Zeng et al., 2019), interannual variation in seed densities (e.g., Bell and Clark, 2016), seed-competitor densities (e.g., Masaki et al., 2019), and densities of alternative seeds (e.g., Fricke and Wright, 2017). Their models maximize generality and precision by including a few, simple, linearly-proportional terms that result in a precise quantitative outcome from which a decision about the direction of the interaction could be made.

If we desire to make inferences from real ecological communities about the direction of the interaction between plants and animals that disperse and consume their seeds, then a realistic model is needed. According to Levins (1966), either generality or precision must therefore be sacrificed as a model becomes more realistic. To our knowledge, there is a dearth of realistic models that do this: this is a glaring gap in our knowledge; a gap that can and must be filled. Precise and realistic models, like those by Price and Jenkins (1986) and Price and Mittler (2003, 2006), are more realistic by having full biologically-relevant model terms or parameter values (e.g., 40 parameters in the latter 2 studies), but, despite having relevant terms for determining the direction of plant-animal interactions, are focused on seed fates and animal population persistence and not the effects on plant fitness. General and realistic models focused on the qualitative outcomes of plant-seed-disperser interactions are rare. Lichti et al. (2014) is a step in this direction, as they include meaningful nonlinear terms and most of the biologically-relevant terms. They do not, however, extrapolate over time to determine how their short-term data would affect plant fitness over longer periods of time. Ultimately, we must see the value in all three strategies to form a robust understanding of seed-dispersal and other species interactions. Indeed, because no single strategy or model can give full insight alone, as stated by Levins (1966), "...our truth is the intersection of independent lies."

7 Authors' contributions

Both authors conceived of and wrote the paper.

8 Data availability

No data were used in this manuscript.

References

J. Bascompte and P. Jordano. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 38:567–593, 2007.

D. M. Bell and J. S. Clark. Seed predation and climate impacts on reproductive variation in temperate forests of the southeastern usa. *Oecologia*, 180(4):1223–1234, 2016.

M. Bogdziewicz, E. E. Crone, and R. Zwolak. Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? an example with oaks and yellow-necked mice. *Journal of Ecology*, 2019. doi: 10.1111/1365-2745.13307.

J. L. Bronstein. Conditional outcomes in mutualistic interactions. *Trends in ecology & evolution*, 9(6):214–217, 1994.

J. L. Bronstein. The study of mutualism. In J. L. Bronstein, editor, *Mutualism*, chapter 1. Oxford University Press, 2015.

K. Burns. Masting in a temperate tree: evidence for environmental prediction? *Austral Ecology*, 37(2):175–182, 2012.

H. Caswell. *Matrix population models*. Sinauer Associates, 2 edition, 2006.

S. A. Chamberlain, J. L. Bronstein, and J. A. Rudgers. How context dependent are species interactions? *Ecology letters*, 17(7):881–890, 2014.

P. Chesson. Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, 31(1):343–366, 2000.

E. D. Clotfelter, A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and E. D. Ketterson. Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia*, 154(3):493–503, 2007.

H. N. Comins, W. D. Hamilton, and R. M. May. Evolutionarily stable dispersal strategies. *Journal of theoretical Biology*, 82(2):205–230, 1980.

J. H. Connell. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations*, 298:312, 1971.

L. Curran and M. Leighton. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting dipterocarpaceae. *Ecological Monographs*, 70(1):101–128, 2000.

R. Dirzo, H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen. Defaunation in the anthropocene. *science*, 345(6195):401–406, 2014.

R. R. Dunn, A. D. Gove, T. G. Barraclough, T. J. Givnish, and J. D. Majer. Convergent evolution of an ant–plant mutualism across plant families, continents, and time. *Evolutionary Ecology Research*, 9:1349–1362, 2007.

S. P. Elias, J. W. Witham, and M. L. Hunter. *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. *Journal of Mammalogy*, 85(4):743–747, 2004.

E. C. Elwood, N. I. Lichti, S. F. Fitzsimmons, and H. J. Dalgleish. Scatterhoarders drive long-and short-term population dynamics of a nut-producing tree, while pre-dispersal seed predators and herbivores have little effect. *Journal of Ecology*, 106(3):1191–1203, 2018.

E. C. Fricke and S. J. Wright. Measuring the demographic impact of conspecific negative density dependence. *Oecologia*, 184(1):259–266, 2017.

M. Gadgil. Dispersal: population consequences and evolution. *Ecology*, 52(2):253–261, 1971.

J. M. Gómez, E. W. Schupp, and P. Jordano. Synzoochory: the ecological and evolutionary relevance of a dual interaction. *Biological Reviews*, 94(3):874–902, 2019.

J. Grinnell. Up-hill planters. *The Condor*, 38(2):80–82, 1936.

J. Gurevitch, L. L. Morrow, A. Wallace, and J. S. Walsh. A meta-analysis of competition in field experiments. *The American Naturalist*, 140(4):539–572, 1992.

K. E. Harms, S. J. Wright, O. Calderón, A. Hernandez, and E. A. Herre. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404(6777):493, 2000.

C. M. Herrera. Seed dispersal by vertebrates. *Plant–animal interactions: an evolutionary approach*, pages 185–208, 2002.

C. M. Herrera, P. Jordano, L. Lopez-Soria, and J. A. Amat. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological monographs*, 64(3):315–344, 1994.

C. M. Herrera, P. Jordano, J. Guitián, and A. Traveset. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *The American Naturalist*, 152(4):576–594, 1998.

B. T. Hirsch, R. Kays, V. E. Pereira, and P. A. Jansen. Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letters*, 15(12):1423–1429, 2012.

K. Hoshizaki and P. E. Hulme. Mast seeding adn predator-mediated indirect interactions in a forest community: evidence from post-dispersal fate of rodent-generated caches. In D. Levey, W. Silva, and M. Galetti, editors, *Seed dispersal and frugivory: ecology, evolution, and conservation*, chapter 15, pages 227–240. CABI Publishing, New York, 2002.

H. F. Howe and J. Smallwood. Ecology of seed dispersal. *Annual review of ecology and systematics*, 13(1):201–228, 1982.

P. A. Jansen, F. Bongers, and L. Hemerik. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs*, 74(4):569–589, 2004.

D. H. Janzen. Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104(940):501–528, 1970.

D. H. Janzen. The deflowering of central america. *Natural History*, (83):48–53, 1971.

T. S. Jensen. Seed-seed predator interactions of european beech, fagus silvatica and forest rodents, clethrionomys glareolus and apodemus flavicollis. *Oikos*, 44(1):149–156, 1985.

P. Jordano. Fruits and frugivory. In M. Fenner, editor, *Seeds: the ecology and regeneration in plant communities*, pages 125–166. CAB International, 2nd edition edition, 2000.

D. Kelly and V. L. Sork. Mast seeding in perennial plants: why, how, where? *Annual review of ecology and systematics*, 33(1):427–447, 2002.

R. Klinger and M. Rejmánek. A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm. *Oecologia*, 162(4):951–963, 2010.

J. L. Koprowski. Sciurus carolinensis. *Mammalian Species*, (480):1–9, 12 1994.

A. Lázaro, A. Traveset, and M. Méndez. Masting in buxus balearica: assessing fruiting patterns and processes at a large spatial scale. *Oikos*, 115(2):229–240, 2006.

S. Lengyel, A. D. Gove, A. M. Latimer, J. D. Majer, and R. R. Dunn. Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. *Perspectives in Plant Ecology, Evolution and Systematics*, 12(1):43–55, 2010.

R. Levins. The strategy of model building in population biology. *American scientist*, 54(4): 421–431, 1966.

H. Li and Z. Zhang. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in prunus armeniaca (rosaceae). *Forest Ecology and Management*, 242 (2-3):511–517, 2007.

N. I. Lichti, M. A. Steele, H. Zhang, and R. K. Swihart. Mast species composition alters seed fate in north american rodent-dispersed hardwoods. *Ecology*, 95(7):1746–1758, 2014.

F. López-Barrera, A. Newton, and R. Manson. Edge effects in a tropical montane forest mosaic: experimental tests of post-dispersal acorn removal. *Ecological Research*, 20(1):31–40, 2005.

I. Martínez and F. González-Taboada. Seed dispersal patterns in a temperate forest during a mast event: performance of alternative dispersal kernels. *Oecologia*, 159(2):389–400, 2009.

T. Masaki, T. Nakashizuka, K. Niiyama, H. Tanaka, S. Iida, J. M. Bullock, and S. Naoe. Impact of the spatial uncertainty of seed dispersal on tree colonization dynamics in a temperate forest. *Oikos*, 128(12):1816–1828, 2019.

W. J. McShea. The influence of acorn crops on annual variation in rodent and bird populations. *Ecology*, 81(1):228–238, 2000.

A. T. Moles, D. D. Ackerly, J. C. Tweddle, J. B. Dickie, R. Smith, M. R. Leishman, M. M. Mayfield, A. Pitman, J. T. Wood, and M. Westoby. Global patterns in seed size. *Global ecology and biogeography*, 16(1):109–116, 2007.

R. E. Onstein, W. J. Baker, T. L. Couvreur, S. Faurby, J.-C. Svenning, and W. D. Kissling. Frugivory-related traits promote speciation of tropical palms. *Nature ecology & evolution*, 1 (12):1903, 2017.

D. A. Orwig, C. V. Cogbill, D. R. Foster, and J. F. O'Keefe. Variations in old-growth structure and definitions: forest dynamics on wachusett mountain, massachusetts. *Ecological Applications*, 11(2):437–452, 2001.

R. S. Ostfeld and F. Keesing. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in ecology & evolution*, 15(6):232–237, 2000.

A. Packer and K. Clay. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, 404(6775):278, 2000.

M. A. Palmer, R. F. Ambrose, and N. L. Poff. Ecological theory and community restoration ecology. *Restoration ecology*, 5(4):291–300, 1997.

I. S. Pearse, W. D. Koenig, and D. Kelly. Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212(3):546–562, 2016.

I. M. Perez-Ramos and T. Maranon. Factors affecting post-dispersal seed predation in two coexisting oak species: microhabitat, burial and exclusion of large herbivores. *Forest Ecology and Management*, 255(8-9):3506–3514, 2008.

H. A. Peters. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology letters*, 6(8):757–765, 2003.

M. Price and S. Jenkins. Rodents as seed consumers and dispersers. In D. R. Murray, editor, *Seed Dispersal*, chapter 5, pages 191–235. Academic Press, Australia, 1986.

M. V. Price and J. E. Mittler. Seed-cache exchange promotes coexistence and coupled consumer oscillations: a model of desert rodents as resource processors. *Journal of Theoretical Biology*, 223(2):215–231, 2003.

M. V. Price and J. E. Mittler. Cachers, scavengers, and thieves: a novel mechanism for desert rodent coexistence. *The American Naturalist*, 168(2):194–206, 2006.

G. M. Sawaya, A. S. Goldberg, M. A. Steele, and H. J. Dalgleish. Environmental variation shifts the relationship between trees and scatterhoarders along the continuum from mutualism to antagonism. *Integrative zoology*, 13(3):319–330, 2018.

J. L. Schnurr, R. S. Ostfeld, and C. D. Canham. Direct and indirect effects of masting on rodent populations and tree seed survival. *Oikos*, 96(3):402–410, 2002.

V. Selås, E. Framstad, and T. K. Spidsø. Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (clethrionomys glareolus) and wood mouse (apodemus sylvaticus) in southern norway. *Journal of Zoology*, 258(4):459–468, 2002.

E. C. Shaver and B. R. Silliman. Time to cash in on positive interactions for coral restoration. *PeerJ*, 5:e3499, 2017.

A. Sih, P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16(1):269–311, 1985.

A. Sugiyama, L. S. Comita, T. Masaki, R. Condit, and S. P. Hubbell. Resolving the paradox of clumped seed dispersal: positive density and distance dependence in a bat-dispersed species. *Ecology*, 99(11):2583–2591, 2018.

K. Suttle, M. A. Thomsen, and M. E. Power. Species interactions reverse grassland responses to changing climate. *science*, 315(5812):640–642, 2007.

J. Terborgh. Enemies maintain hyperdiverse tropical forests. *The American Naturalist*, 179(3): 303–314, 2012.

T. Theimer. Rodent scatterhoarders as conditional mutualists. In J. Lambert, P. Hulme, and S. Vander Wall, editors, *Seed fate: predation, dispersal, and seedling establishment*, chapter 17, pages 283–296. CABI Publishing, New York, 2005.

J. N. Thompson. Variation in interspecific interactions. *Annual review of ecology and systematics*, 19(1):65–87, 1988.

J. M. Tylianakis, R. K. Didham, J. Bascompte, and D. A. Wardle. Global change and species interactions in terrestrial ecosystems. *Ecology letters*, 11(12):1351–1363, 2008.

USDA and NRCS. Northern red oak: *Quercus rubra* L. *The PLANTS Database (http://plants.usda.gov)*, 2019.

S. B. Vander Wall. Influence of substrate water on the ability of rodents to find buried seeds. *Journal of Mammalogy*, 76(3):851–856, 1995.

S. B. Vander Wall. Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. *Ecology*, 79(1):233–241, 1998.

S. B. Vander Wall. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (tamias amoenus) and deer mice (peromyscus maniculatus). *Behavioral ecology*, 11(5):544–549, 2000.

S. B. Vander Wall. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology*, 83(12): 3508–3516, 2002.

S. B. Vander Wall. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1542): 989–997, 2010.

M. Vellend. *The theory of ecological communities (MPB-57)*, volume 75. Princeton University Press, 2016.

B. C. Wang and T. B. Smith. Closing the seed dispersal loop. *Trends in ecology & evolution*, 17 (8):379–386, 2002.

A. S. Watt. On the ecology of british beechwoods with special reference to their regeneration. *Journal of Ecology*, 11(1):1–48, 1923.

J. O. Wolff. Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy*, 77(3):850–856, 1996.

Z. Xiao, Z. Zhang, and Y. Wang. The effects of seed abundance on seed predation and dispersal by rodents in castanopsis fargesii (fagaceae). *Plant Ecology*, 177(2):249–257, 2005.

Z. Xiao, Z. Zhang, and C. J. Krebs. Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. *Journal of Ecology*, 101(5):1256–1264, 2013.

Y. Yang, M. Zhang, and X. Yi. The effects of masting on rodent-mediated seed dispersal interaction of sympatric tree species. *Forest Ecology and Management*, 446:126 – 134, 2019.

D. Zeng, R. K. Swihart, Y. Zhao, X. Si, and P. Ding. Cascading effects of forested area and isolation on seed dispersal effectiveness of rodents on subtropical islands. *Journal of Ecology*, 107(3):1506–1517, 2019.

R. Zwolak and E. E. Crone. Quantifying the outcome of plant-granivore interactions. *Oikos*, 121(1):20–27, 2012.