



RESEARCH PAPER

Quantifying the mutualism-antagonism continuum for seed removal by a granivorous disperser

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ABSTRACT

Seeds removed by animals have one of two mutually exclusive fates – they are either predated or dispersed and still alive. The quality of seed dispersal by animals and the number of predated seeds will therefore determine net interaction outcomes for plants. Yet, it is poorly understood what proportion of removed seeds animals can predate before benefits of dispersal no longer outweigh costs of seed loss.

Here, we calculated the mutualism-antagonism continuum for seed removal of the fleshy-fruited tree *Frangula alnus* by the seed-predating bird *Coccothraustes coccothraustes* in Białowieża Forest. We integrated effects of the bird during seed dispersal (fruit handling, seed predation, and seed deposition) into microhabitat-structured tree population models.

Results of our models showed that the probability of a seed of *F. alnus* reaching maturity after seed removal by *C. coccothraustes* decreased from 0.0028% to 0% as seed predation increased from 0% to 100%. Seed removal was beneficial when less than 63.7% of seeds were predated, and antagonistic when more than 72.0% of seeds were predated. Modifying key model parameters (here, the negative effect of fruit pulp on seedling recruitment and the frequency of forest gaps) decreased and increased rates of seed predation, at which costs of seed loss outweighed benefits of seed dispersal (from 37.9% to 80.7%).

Our findings highlight that benefits of animal seed dispersal can largely outweigh costs of seed predation in a fleshy-fruited tree. Yet, the mutualism-antagonism continuum of seed removal depends on intrinsic factors (e.g. variation in interactions among individuals) and extrinsic factors (e.g. the environment) of seed dispersal and plant demography. Because *C. coccothraustes* was observed predated at least 80% of removed seeds, it appears to be an antagonist of animal-dispersed plants and exploiter of the seed dispersal mutualism.

Introduction

Plants provide nutritious fruits to animals which in exchange remove, and potentially disperse, the seeds of plants (Beckman & Sullivan, 2023; Farwig & Berens, 2012; Howe & Smallwood, 1982). After being removed by animals, seeds undergo one of two contrasting fates: the seeds will either be dispersed alive to new, potentially favourable locations (García-Rodríguez et al., 2022; Rehling, Schlautmann, Jaroszewicz, Schabo, & Farwig, 2022; Wenny & Levey, 1998), or they are predated (Gómez, Schupp, & Jordano, 2019; Hulme & Benkman, 2002). Whether seed removal by animals will be beneficial to plants will

depend on the quality of their seed dispersal and the quantity of seeds they predate (Gómez et al., 2019; Schupp, Jordano, & Gómez, 2017). If animals predate too many seeds, the costs of seed predation outweigh the benefits of seed dispersal and render their seed removal antagonistic (Zwolak et al., 2020). As a consequence, plants with high rates of seed predation after removal regenerate poorly (Bogdziewicz et al., 2020), and their populations might consequently decline (Ticktin et al., 2023).

Seed predation thresholds at which seed removal changes from a net mutualism into a net antagonism help to better understand ecological principles of species interactions. In addition, they might be of relevance for conservation because they could indicate diminishing plant

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populations and degraded ecosystems (Ticktin et al., 2023; Zwolak et al., 2020). Transitions from mutualism to antagonism have mostly been addressed conceptually (Leeuwen et al., 2022) or indirectly calculated from the ratio of mutualistic to antagonistic seed removal results (Brehm & Mortelliti, 2022; Draxler & Kissling, 2022; Gómez et al., 2019). Seldom have the costs of seed predation and the advantages of seed dispersal for plant populations been combined in research (Bogdziewicz et al., 2020; Elwood et al., 2018). This is due to the difficulties in quantifying all processes that can affect the population outcome of seed removal interactions (Abrams, 1987; Rehling et al., 2023b; Wang & Smith, 2002). Even for interactions between individuals of the same two species, population outcomes of seed removal may vary as a consequence of within-species trait variation and different environmental contexts (Schupp et al., 2019; Zwolak et al., 2024). Therefore, little is known at what levels of seed predation interactions with seed-removing animals become antagonistic for the dispersed plants, and how strongly these transitions are context-dependent.

Here, we studied the mutualism-antagonism continuum of interactions between the seed-removing Hawfinch *Coccothraustes coccothraustes* (Fig. 1) and the population of the fleshy-fruited Glossy buckthorn *Frangula alnus* in Białowieża forest, Poland. This study is based on a recent animal-tree population model (Rehling et al., 2023b) in which we linked the behavior of 20 animal species during seed removal (fruit handling and removal, seed deposition and germination) along a forest canopy gradient to their effects on the demography of *F. alnus*. We quantified the benefits and costs of seed removal by *C. coccothraustes* more explicitly, and determined at which rate of seed predation the role of the bird shifted from mutualist to antagonist. In addition, we quantified how strongly the mutualism-antagonism continuum is affected by environmental conditions that increase the benefits of seed dispersal (here, the frequency of forest gaps and the dependence of plant populations on seed dispersal by animals to colonize forest gaps), and other model parameters (fruit pulp effect on seedling recruitment).

Materials and methods

Study area

Our research was conducted in the Białowieża Forest, which covers an area of about 1500 km² at the border of Poland and Belarus. Currently, the 630 km² of forest in Poland is divided among the Białowieża National Park (105 km²) and state-managed forests. Human influence has been negligible for almost half a millennium in the Białowieża National Park, which makes it the best-preserved lowland



Fig. 1. The Hawfinch *Coccothraustes coccothraustes* removing a fleshy fruit (here, from *Prunus*). *Coccothraustes coccothraustes* is the main seed predator of fleshy-fruited plant communities in ash-alder forests of Białowieża Forest (Albrecht et al., 2013; Farwig et al., 2017) and throughout Europe (Simmons et al., 2018). Photo by S. Rösner.

forest in Europe (Jaroszewicz et al., 2019). In contrast, commercial logging has changed more than 80% of the Polish part of forest after World War I which is not part of the national park (Jaroszewicz et al., 2019; Mikusiński et al., 2018). Alder dominates up to 20% of the Białowieża forest, and the ash-alder forests support a rich community of at least 15 woody, fleshy-fruited plant species and 41 seed-removing animal species (Albrecht et al., 2015).

Study species

Frangula alnus ('Glossy buckthorn', Rhamnaceae) is found from Morocco, Europe to Western Asia (Hampe et al., 2003). The deciduous tree species is associated with ash-alder forests in Białowieża Forest where it reaches to at least 9 m in height. Forest gaps and open canopies promote *F. alnus* regeneration, whereas shade-tolerant plants outcompete the tree in late-successional forests (Rehling et al., 2023b). From late July to October, *F. alnus* produces black, fleshy fruits with a diameter of 6.2–11.3 mm and up to three seeds (Rehling et al., 2021). Fruits are dispersed mostly by birds or small mammals (Albrecht et al., 2013; Schlautmann et al., 2021), and secondarily by ants, gravity or water (Hampe, 2004). Light and cold stratification increase seed germination as seeds are physiologically dormant (Godwin, 1943).

Coccothraustes coccothraustes ('Hawfinch', Fringillidae) is distributed from North Africa throughout most of Europe to Eastern Asia. It is the largest among the European finches (body mass = 56.6 g), and has a strong conical beak, which enables the bird to predate seeds faster than other seed-predating finches (Perea, Gil, & L, 2014). This forest specialist commonly occurs in deciduous forests (Rehling et al., 2023a) and is very frequent in lime-oak-hornbeam stands in Białowieża Forest (Tomiałojć, 2004). *Coccothraustes coccothraustes* is the main seed predator in ash-alder forests in Białowieża Forest (6.5% of plant community-wide seed removal interactions), and predates seeds of especially *Prunus padus* and *F. alnus* (Fig. 1, Albrecht et al., 2013; Farwig et al., 2017).

Modeling

The effect of animal seed dispersal on the life cycle of *F. alnus* along the canopy gradient in the forest was studied using integral projection models (IPMs) (Easterling et al., 2000; Ellner et al., 2016; Merow et al., 2014). The IPMs amalgamated data from ten years of research in one ecosystem: in the first step, the removal of fruits and fruit handling behavior (i.e., removing or dropping fruits and crushing seeds) by animal species was observed on 52 reproductive individuals of *F. alnus* over 936 h. In a second step, we quantified animal species-specific seed deposition by DNA barcoding of 1729 scat samples containing 9590 seeds, including *F. alnus* and other fleshy-fruited plants, collected across the forest canopy gradient. In a third step, we included an estimate for the reduced recruitment of seedlings if a fruit was not consumed by an animal and seedlings recruited from seeds in fruits instead (−71%) from a recent meta-analysis (Rogers et al., 2021) into our models. In a fourth step, we investigated seedling recruitment by sowing 2500 seeds in the forest. In a fifth step, we documented growth, survival, and reproduction of 938 *F. alnus* individuals over three years across the canopy gradient. We analyzed these vital rates in relation to size and location along the canopy cover gradient using GLMMs (R-package *glmmTMB*) (Brooks et al., 2017) in R (R Core Team, 2023). To synthesize these datasets, we developed animal species-specific microhabitat-structured integral projection models, where the state of the *F. alnus* population was simultaneously depicted by the size distribution of plants and the locations of plants along the canopy gradient (Rehling et al., 2023b).

In this study, we used the same demography model and calculated the probability of a seed of *F. alnus* to reach maturity $f_{maturity}$ after being dispersed by the seed-predating bird *C. coccothraustes* under different rates of seed predation. $f_{maturity}$ is a surrogate for the quality of seed

dispersal over the full life cycle of a plant and is given by:

$$f_{maturity}(z_0, c) = \int_L^U \int_L^U f_{nocrush} f_{consumed} f_{deposition}(c) f_{recruit1} l_{(\bar{a}_{repr})}(z_0, c) dz_0 dc \quad (1a)$$

$$+ \int_L^U \int_L^U f_{nocrush} f_{1-consumed}(c) f_{recruit1} f_{recfruit} l_{(\bar{a}_{repr})}(z_0, c) dz_0 dc \quad (1b)$$

It is the sum of the probability of seeds in consumed fruits (Eq. (1a)) and dropped fruits (Eq. (1b)) reaching maturity conditional on seed dispersal (benefits) and seed predation (costs) by *C. coccothraustes*, the initial size distribution of seedlings z_0 and the canopy cover distribution c in the forest. Here, $f_{nocrush}$ is the probability of not being crushed and therefore not predated, $f_{consumed}$ is the probability of a fruit being consumed conditional on not being crushed, $1 - f_{consumed}(c)$ is equivalent to the probability of a fruit being dropped beneath a conspecific adult in environment c conditional on not being crushed, $f_{deposition}(c)$ is the probability of a seed being deposited somewhere along the canopy gradient c within the forest, $f_{recruit1}$ is the probability of recruitment of seedlings, $f_{recfruit}$ is the factor by which $f_{recruit1}$ is inhibited if seedlings are recruiting from seeds in fruits (−71%, Rogers et al., 2021), and $l_{(\bar{a}_{repr})}$ describes the probability of a seedling surviving until it has produced fruits at least once. $l_{(\bar{a}_{repr})}$ is a function of growth, survival and reproduction of *F. alnus*, and a modification of formulas presented in Ellner et al. (2016). For more information on the underlying methods, on the IPM of *F. alnus* or on parameter definition, see Rehling et al. (2023b).

The turnover from mutualistic to antagonistic interactions of *F. alnus* with *C. coccothraustes* was defined by the value at which seed dispersal of *F. alnus* without the bird (here, gravity-dispersal) contributed more to the population growth than with bird seed removal. $f_{maturity}$ for seeds dispersed by gravity was calculated as:

$$f_{maturity}(z_0, c) = \int_L^U \int_L^U f_{recruit1} f_{recfruit} l_{(\bar{a}_{repr})}(z_0, c) dz_0 dc \quad (2)$$

As fruits dispersed by gravity (Eq. (2)) do not change their position along the canopy gradient, the canopy c also refers to the environment of seeds of gravity-dispersed fruits (i.e., $c' = c$). Similar to our approach of modeling gravity dispersal in Rehling et al. (2023b), we calculated the probability of a seed of *F. alnus* to reach maturity after being dispersed by gravity for two dispersal scenarios. In the first scenario, we assumed that *F. alnus* occurred along the whole gradient of canopy cover, as observed in the studied forest. In the second scenario, we assumed that *F. alnus* only occurred in the closed forest and relied on seed dispersal by animals to reach the 50%-brightest microhabitats. Because adult plants only occurred in the closed forest, values of the probability of seeds to reach maturity after being dispersed by gravity were reduced in the second scenario.

Sensitivity analyses

To quantify how model parameters affected the quality of seed dispersal by either *C. coccothraustes* or without the bird (here, gravity), and thus the interaction continuum from mutualism to antagonisms and its turnover, we modified two parameters of the model independent of each other: Firstly, we varied the factor for the reduced recruitment of seedlings if seedlings recruit in fruits (i.e. $f_{recfruit}$) from −80% to −50%. $f_{recfruit}$ was the factor with the strongest effect on seed dispersal quality in our original model. $f_{recfruit}$ is equivalent to $-1 \times$ bird gut passage effects on recruitment, as the positive effect of a bird gut passage on seed germination is mostly due to the removal of pulp during fruit consumption (Rogers et al., 2021). This parameter will usually not vary strongly between interactions of the same two species (such as those between *C. coccothraustes* and *F. alnus*). However, $f_{recfruit}$ can vary with

plant-animal interactions due to differences in traits of interacting species (e.g. differences in seed size between plant species, or differences in gut passages between animal taxa), or due to differences in the location where the interaction takes place (temperate/subtropical vs. tropical, mainland vs. island, see Rogers et al., 2021). Changing values of $f_{recfruit}$ had minimal influence on the quality of seeds dispersed by *C. coccothraustes*, but strongly influenced the quality of seeds that were not dispersed by the bird (here, gravity), and therefore affected the value for the transition from mutualism to antagonism.

Secondly, we varied the relative availability of forest gaps (i.e. the 50%-brightest environments, 9.2% of available microhabitats) from 0% to 20%. As we increased the frequency of forest gaps in the model, we decreased the relative abundance of the 50%-darkest environments such that values added up to 1. Because changes in the frequency of forest gaps will also affect the deposition of seeds by *C. coccothraustes* therein, we varied the proportion of seeds deposited along the forest canopy gradient by *C. coccothraustes* similar to those in the frequencies of forest gaps and closed forests (i.e. 0–20% in forest gaps, 80–100% in closed forest). We changed values for the frequency of forest gaps and the seed deposition of *C. coccothraustes* to a similar extent, as the seed deposition of *C. coccothraustes* along the forest canopy gradient was similar to patterns of random seed deposition (Rehling et al., 2022; Rehling et al., 2023b). These changes in model parameters affected the slope of the relationship between seed dispersal quality and seed predation for *C. coccothraustes*, and the quality of gravity-dispersed seeds (i.e. the value for the transition from mutualism to antagonism).

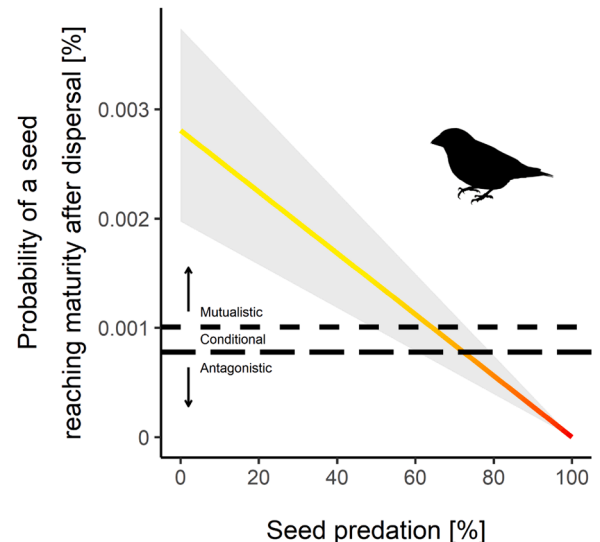


Fig. 2. The mutualism-antagonism continuum of the seed removal of *Frangula alnus* by *Coccothraustes coccothraustes*, which acts as disperser and predator of seeds. Here, the interaction quality is defined by the probability of a seed reaching maturity after dispersal by *C. coccothraustes*, i.e. a surrogate for the lifelong quality of seed dispersal by animals (Rehling et al. 2023b). The horizontal dashed lines display the transition from mutualistic to conditional to antagonistic interactions, and are defined by values for the quality of seed dispersal without animals (here, gravity dispersal). We modelled the quality of seed dispersal by gravity under two dispersal scenarios; in the first scenario, the plant populations of *F. alnus* were fully established along the canopy cover gradient in Białowieża forest (upper, short-dashed). In the second scenario, the plant populations of *F. alnus* only occurred in the closed forest and depended on animal seed dispersal to colonize forest gaps (lower, long-dashed). As plant establishment and growth is reduced under a closed canopy, the quality of seed dispersal by gravity was reduced in the second scenario, and therefore seed removal more tolerant towards seed predation.

Results

We found that even at considerably high levels of seed predation (up to 63.7–72.0%, Fig. 2), the quality of seed removal by *C. coccothraustes* was sufficiently higher than the quality of dispersal without their interactions (here, gravity dispersal), and still outweighed the costs of seed loss due to predation. When more than 72.0% of seeds were predated, the net effect of seed removal by *C. coccothraustes* was always worse than that of gravity dispersal. The intermediate state of seed removal by *C. coccothraustes* depended on the seed dispersal by gravity and, therefore, on the distribution of plants of *F. alnus* along the canopy gradient. When individuals of *F. alnus* were present in forest gaps, the quality of gravity dispersal was increased through improved plant regeneration, and interactions with *C. coccothraustes* became antagonistic already at a rate of 63.7% seed predation. However, when individuals of *F. alnus* were only present in closed forest, and the population therefore depended on animal seed dispersal to colonize forest gaps, interactions with *C. coccothraustes* became antagonistic at a rate of 72.0% seed predation (Fig. 2).

When we reduced the negative impact of fruit pulp on seedling recruitment in the models (from –80% to –50%), the quality of seeds dispersed by gravity improved, and seed removal by *C. coccothraustes* became antagonistic at rates of 37.9%, 56.4% and 75.1% seed predation when *F. alnus* was present in forest gaps, and at rates of 52.0%, 66.3% and 80.7% seed predation when *F. alnus* was only present in closed forest (Fig. 3A).

When we changed the frequency of forest gaps, and similarly the seed deposition of *C. coccothraustes* in those forest gaps, from 0% to 20%, the transition from mutualism to antagonism of *C. coccothraustes* was affected only to a small extent when *F. alnus* was present in forest gaps (rates between 62.6% and 66.8%, Fig. 3B). However, when *F. alnus* was only present in the closed forest, rates towards antagonism of *C. coccothraustes* gradually increased from rates of 62.6% seed predation when there were no forest gaps to rates of 79.3% seed predation when the forest included 20% forest gaps.

Discussion

This study showcases the mutualism-antagonism continuum of a species interaction and its context dependency, exemplified by seed removal of the fleshy-fruited tree *F. alnus* by the seed-predating bird *C. coccothraustes*. Seed removal of *C. coccothraustes* shifted from mutualism to antagonism at seed predation rates of 63.7–72.0%. If plants rely on animal seed dispersal to colonize environments favourable for plant regeneration, the tolerance of plants towards predation was higher (72.0%). Varying model parameters that are linked to intrinsic and extrinsic drivers of seed dispersal and plant demography affected the mutualism-antagonism continuum of seed removal. For example, reducing the negative impact of fruit pulp on seedling recruitment in the models (from –80% to –50%) improved the quality of seeds dispersed by gravity, and seed removal by *C. coccothraustes* became antagonistic at lower rates of seed predation. Increasing the frequency of forest gaps in the model improved the quality of seed dispersal by both, *C. coccothraustes* and gravity if *F. alnus* was present along the entire canopy gradient, and the transition from mutualism to antagonism was influenced only to a small extent ($\pm 4.2\%$). However, if *F. alnus* was present only in the closed forest and depended on animal seed dispersal to reach forest gaps, rates of seed predation at which seed removal by *C. coccothraustes* became antagonistic, increased from 62.6% to 79.3% with an increase in the proportion of forest gaps from 0% to 20%. The sensitivity of the mutualism-antagonism continuum towards the negative effect of fruit pulp on seedling recruitment, the dependence of plant populations on animal seed dispersal to colonize forest gaps, and the frequency of forest gaps underlines the strong context dependency of mutualistic and antagonistic plant-frugivore interactions, and that of ecological interactions more broadly (Bronstein, 1994; 2001; Chamberlain et al., 2014; Gómez et al., 2023).

Our findings hint towards the antagonistic role of potential seed dispersers, when more than 63.7–72.0% of seeds are predated. Frugivorous birds, bats, and large mammals which only occasionally predate seeds (less than 40% of seeds in c. 76% of pair-wise species interactions, Gómez et al., 2019; Perea et al., 2013) will thus often improve plant

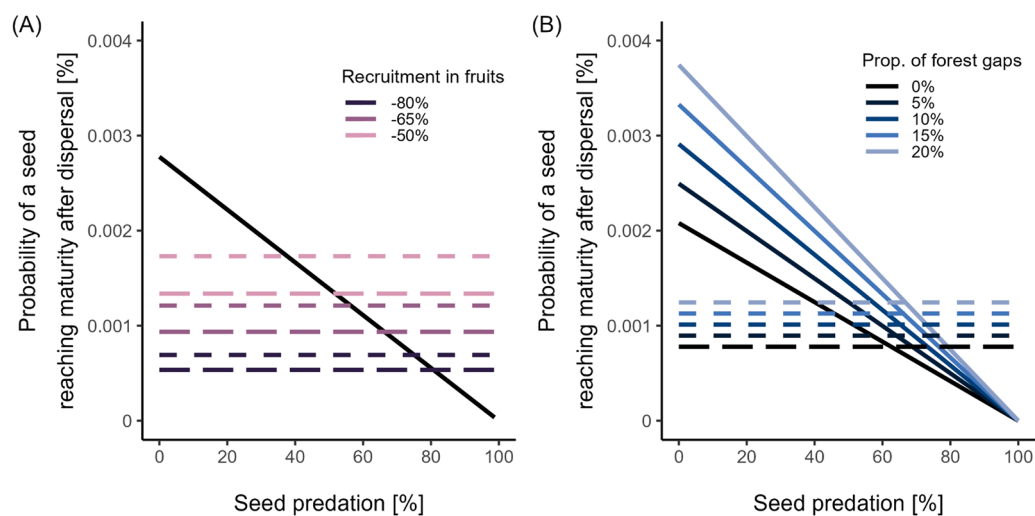


Fig. 3. Sensitivity of the mutualism-antagonism continuum of seed removal of *F. alnus* by *C. coccothraustes* to changes in key model parameters, as depicted by changes in (A) the recruitment of seedlings in fruits, and (B) the proportion of forest gaps (i.e. the 50%-brightest environments along the canopy gradient). In (A) and (B), the horizontal dashed lines represent the two dispersal scenarios, where either the plant population of *F. alnus* was fully established along the canopy cover gradient in Białowieża forest (upper, short-dashed), or only occurred in the closed forest and depended on animal seed dispersal to colonize forest gaps (lower, long-dashed). (A) As the negative effect of fruit pulp on seedling recruitment decreases, the quality of seed dispersal by gravity (but not that of *C. coccothraustes*) increased and seed removal became antagonistic at lower rates of seed predation. (B) As forest gaps become more frequent, the quality of seed dispersal by gravity and by *C. coccothraustes* increased to a similar extent if *F. alnus* occurred along the entire canopy gradient. Consequently, the transition from mutualism to antagonism of seed removal was affected only to a small extent by forest gap frequency. However, if the population of *F. alnus* only occurred in the closed forest and depended on animal seed dispersal to reach forest gaps, seed removal became more tolerant towards seed predation as the proportion of forest gaps increased.

performance and act as mutualists of the plants they disperse (Aziz et al., 2021; Leeuwen et al., 2022; Rehling et al., 2023b). Animals that regularly predate seeds, such as scatter-hoarding rodents, will be mutualistic only if their predation rates are low (e.g., 50% or less in agoutis) (Jansen et al., 2012; Mittelman et al., 2020). In contrast, granivorous animals that predate most seeds may often negatively influence the growth of plant populations (Montesinos-Navarro et al., 2017; Simmons et al., 2018), including the studied *C. coccothraustes*, chipmunks (86% in *Pinus jeffreyi*, Wall & Joyner, 1998) or parrots (at least 78.5% in *Araucaria angustifolia*, Tella et al., 2016). In line with this, a recent study found that the costs of seed predation by *Apodemus flavicollis* in two *Quercus* species outweighed the benefits of seed dispersal for early plant recruitment (Bogdziewicz et al., 2020). Seed dispersal by different granivorous animals (including chipmunks) was antagonistic for a plant population of *Castanea dentata* when the proportion of predated seeds was modelled similar to field conditions (Elwood et al., 2018). Seed predation rates of more than 72% might thus also indicate declining tree populations (Ticktin et al., 2023), especially for tree species associated with early forest succession stages, such as *F. alnus* in Białowieża Forest.

However, the estimated turnover from mutualistic to antagonistic interactions could occur at even higher levels of seed predation, as animal seed dispersal has more versatile advantages for populations of *F. alnus* beyond those studied in our animal-tree population model (Green et al., 2022). These advantages include the increased importance of animal seed dispersal for plant populations in dynamic environments (Metcalf et al., 2009) (please note that although we included a canopy gradient, the environment in our demography model was static over time). Likewise, animal seed dispersal might be beneficial for other population processes than local population growth, for instance, range expansion (Ando et al., 2022; Szweczyk et al., 2019), gene flow (Browne et al., 2018), or plant migration in response to climate change (Fricke et al., 2022; González-Varo et al., 2021). In fact, the relative importance of interacting animals can change for plant species when the focus of researchers is shifted from local population dynamics to spread (Marchetto et al., 2014; Shea et al., 2010). We look forward to more studies that aim at quantifying values of turnovers of interaction continua, not only for the mutualism-antagonism continuum of seed removal, but for other types of ecological interactions as well.

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Data archiving statement

The original datasets and the R code generated during the current study are available in the Dryad Digital Repository, [10.5061/dryad.h44j0zpmq](https://doi.org/10.5061/dryad.h44j0zpmq).

CRedit authorship contribution statement

Finn Rehling: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Eelke Jongejans:** Conceptualization, Writing – review & editing, Supervision. **Nina Farwig:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Dana G. Schabo:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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