

Granivore abundance shapes mutualism quality in plant–scatterhoarder interactions

Rafał Zwolak¹ , Dale Clement² , Andrew Sih³  and Sebastian J. Schreiber³ 

¹Department of Systematic Zoology, Institute of Environmental Biology, Adam Mickiewicz University, Umultowska 89, Poznań, 61-614, Poland; ²School of Biological Sciences, Washington State University, Pullman, WA 99164-4236, USA; ³Center of Population Biology, University of California, One Shields Avenue, Davis, CA 95616, USA

Summary

Author for correspondence:
Rafał Zwolak
Email: rafal.zwolak@gmail.com

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- Conditional mutualisms involve costs and benefits that vary with environmental factors, but mechanisms driving these dynamics remain poorly understood. Scatterhoarder–plant interactions are a prime example of this phenomenon, as scatterhoarders can either increase or reduce plant recruitment depending on the balance between seed dispersal and predation.
- We explored factors that drive the magnitude of net benefits for plants in this interaction using a mathematical model, with parameter values based on European beech (*Fagus sylvatica*) and yellow-necked mice (*Apodemus flavicollis*). We measured benefits as the percentage of germinating seeds, and examined how varying rodent survival (reflecting, e.g. changes in predation pressure), the rate of seed loss to other granivores, the abundance of alternative food resources, and changes in masting patterns affect the quality of mutualism.
- We found that increasing granivore abundance can degrade the quality of plant–scatterhoarder mutualism due to increased cache pilferage. Scatterhoarders are predicted to respond by increasing immediate consumption of gathered seeds, leading to higher costs and reduced benefits for plants.
- Thus, biotic changes that are detrimental to rodent populations can be beneficial for tree recruitment due to adaptive behavior of rodents. When scatterhoarder populations decline too drastically (< 5 individuals ha^{-1}); however, tree recruitment may also suffer.

Introduction

Because both species in a mutualism benefit from the interaction, a decline in the abundance of one mutualistic partner should be detrimental for the other. Empirical evidence often supports this assumption; for example, in the relationship between ants and sap-feeding insects, the benefits of protection increase with ant abundance (Abbott & Green, 2007; Harmon & Andow, 2007). Similarly, in interactions between trees and frugivorous birds, plants often benefit more when more fruits are removed (Rehling *et al.*, 2023). As a result, there is a widespread concern that the loss in abundance of one mutualistic partner will destabilize the interaction, resulting in chains of extinctions (Kiers *et al.*, 2010; Gilarranz *et al.*, 2015; Hays *et al.*, 2022; Weinbach *et al.*, 2022). Yet, mutualisms have inherent costs, and while sometimes they offer mutual benefits, in other situations they can reveal conflicting interests between species (Bronstein, 2001; Chamberlain *et al.*, 2014; Chomicki *et al.*, 2020). For instance, in symbiotic corals, the burden of nurturing algal mutualists increases sharply when they become overabundant (Falkowski *et al.*, 1993; Xiang *et al.*, 2020). Thus, in some situations, factors that reduce the abundance of a mutualist can make the interaction more beneficial to its partner (Bronstein, 1994). An important goal is thus to better understand mechanisms dictating these shifts between mutualism and antagonism.

We explored the connection between variation in ecological context and changes in the magnitude of benefits in mutualism using a model of plant–scatterhoarder interactions. Scatterhoarders are defined as granivorous animals that hide seeds in numerous, undefended caches for future use (Lichti *et al.*, 2017; Gómez *et al.*, 2019; Zhang *et al.*, 2022). These animals play a crucial, but dual role in the reproduction of numerous plants world-wide because they cache seeds in places that seeds could not otherwise reach, yet destroy many in the process (Bronstein, 2001; Briggs *et al.*, 2009). Thus, they act both as seed dispersers and seed predators (Gómez *et al.*, 2019). Benefits from the caching exceed the costs of seed consumption in most, but not all circumstances (e.g. compare Beck & Vander Wall, 2010 with Bogdziewicz *et al.*, 2020). Therefore, the relationship between plants and scatterhoarders is a prominent example of a ‘conditional mutualism’.

The outcome of plant–scatterhoarder interactions varies with prevailing ecological conditions (Jorge & Howe, 2009; Aliyu *et al.*, 2018) and the species involved (Gómez *et al.*, 2019). Although field studies illuminate the factors that prompt scatterhoarders to adjust their foraging tactics in ecological time (reviewed in Lichti *et al.*, 2017), the evolutionary drivers of costs and benefits in such conditional interactions remain elusive. Mathematical modeling offers a solution to this challenge

(e.g. Holland & DeAngelis, 2010; Cao *et al.*, 2022; Gómez *et al.*, 2023), but it has been underutilized in this domain.

Our research addresses this shortfall. The model that we used is based on the interaction between a masting tree and a scatterhoarding rodent (Zwolak *et al.*, 2021). Masting plants are characterized by synchronous and highly variable seed production among years (Pearse *et al.*, 2016). In the model, the scatterhoarders forage on seeds over years that differ in the magnitude of seed fall and abundance of the rodents. Previously, we used a similar model to explore factors that promote the evolution of scatterhoarding (Zwolak *et al.*, 2021). Rodents can consume encountered seeds (which is deleterious from the plant perspective) or cache them. Later, cached seeds can be consumed by cache owners or pilferers, which is again costly for plants, or left unrecovered, which benefits plants by facilitating germination (Zwolak & Crone, 2012).

Broadly in such systems, the fate of these seeds – whether they are consumed, pilfered, or left in caches – depends on the relative densities of seeds and scatterhoarders (Theimer, 2005). When rodents are abundant, the risk of pilferage is high (Dittel & Vander Wall, 2018). In our previous model, we demonstrated that this risk causes rodents to cache less (Zwolak *et al.*, 2021) and can harm plant recruitment. Empirical data indicate that mast seeding causes rodent populations to increase, but with several years between masts, rodent density can drop quite low by the next masting event (Falls *et al.*, 2007; Bergeron *et al.*, 2011; Selonen *et al.*, 2015; Zwolak *et al.*, 2018). Our model suggested that this change reduces pilfering risk, increases caching, and is ultimately beneficial for plants (Zwolak *et al.*, 2021).

In this study, we explored factors that affect these overall dynamics. Specifically, we varied (1) rodent survival (reflecting, e.g. variation in predator pressure), (2) the rate of seed loss (reflecting, e.g. variation in interspecific competition with other granivores), (3) the abundance of alternative food resources, and (4) masting patterns (i.e. masting intensity and the interval between mast years). These factors collectively provide a comprehensive view of the biotic challenges and opportunities faced by scatterhoarders.

We found that under a broad range of conditions, due to the adaptive behavior of rodents (evolutionary changes in caching strategies), changes in these factors that are detrimental for rodent populations can be beneficial for tree recruitment. However, when the negative effects on rodents are too strong, there are large declines in scatterhoarder populations, and tree recruitment is reduced.

Description

Natural history of the modeled system

The yellow-necked mouse (*Apodemus flavicollis* Melchior) is an omnivore, favoring seeds but also incorporating arthropods, fruits, and green parts of plants (Drózdź, 1966). Mast from deciduous trees like beech, oaks (*Quercus* spp.), or hornbeam (*Carpinus betulus*) – depending on the region – can represent over 80% of its diet (Selva *et al.*, 2012). Predation is the leading cause

of mortality for this species (Jędrzejewski & Jędrzejewska, 1993; Pucek *et al.*, 1993). Owls (notably the tawny owl, *Strix aluco*: Jędrzejewski *et al.*, 1996) and mustelids like the weasel (*Mustela nivalis*), and the pine marten, (*Martes martes*) are among its primary predators (Jędrzejewski *et al.*, 1995; Zalewski *et al.*, 1995).

Beech (*Fagus sylvatica* L.), a prevalent broad-leaved tree species, is widespread across temperate Europe and is often the dominant species in forests (Packham *et al.*, 2012). Its masting interval ranges from 2 to 15 yr, though typically between 4 and 8 (Packham *et al.*, 2012). Each beech seed weighs *c.* 0.2–0.3 g, offering *c.* 5.7 kJ of energy (Grodziński & Sawicka Kapusta, 1970). These seeds are available during autumn (most seeds fall in October and November) and persist throughout winter before germinating or decaying in spring. Besides the yellow-necked mouse, other vertebrates such as the wild boar (*Sus scrofa*), birds like the Eurasian jay (*Garulus glandarius*) and Eurasian nuthatch (*Sitta europaea*), and other rodents like the bank vole (*Myodes glareolus*), also feed on beech seeds (Nilsson, 1985). We emphasize that while other seed predators exist, our primary objective is not to provide an exhaustive analysis of the fate of beech seeds, but rather to explain variation in the impact of our focal scatterhoarder species on tree reproductive outcomes.

Modeling approach

We use a modification of a mathematical model introduced by Zwolak *et al.* (2021). Here, we provide a summary of the model and highlight the main modifications necessary to address how the evolution of caching in scatterhoarders impacts the fates of the seeds produced by the predominant masting plant species. We assume timescale separation between scatterhoarder ecology, the evolution of scatterhoarder caching, and tree population dynamics (which are not modeled). At the ecological time scale, the model describes the population dynamics of scatterhoarders and their gathering, consumption, and caching of seeds. At the evolutionary time scale, we use adaptive dynamics to identify the evolutionarily stable strategies for caching. For scatterhoarders playing the evolutionarily stable strategy (ESS) for caching, we recorded key model outputs relating to scatterhoarder densities and the fates of seeds throughout the masting cycle. We then calculate the benefit of the plant–scatterhoarder interaction to the plant, measured as the proportion of produced seeds that germinate, when the scatterhoarders are at their stationary population state and caching ESS. The present model differs from that of Zwolak *et al.* (2021) by explicitly tracking the fate of seeds throughout the year.

The ecological dynamics The model considers a population of scatterhoarders that experience three distinct periods of seed availability in each year: fall, winter/spring, and summer. During the fall of year t , $S(t)$ seeds become available. Scatterhoarders with fall density $n_1(t)$ gather these seeds at a fixed per-capita seed harvest rate a_1 . Seeds are also lost to other seed predators at a per-capita rate of L_1 . The fate of seeds gathered by an individual scatterhoarder depends on its threshold T for caching. If an individual gathers less than T seeds, they consume all their gathered

seeds, else they cache the remaining seeds beyond the first T seeds. We assume that seeds have a negligible probability of surviving and germinating without being cached, so all seeds are either gathered by the scatterhoarder or lost due to seed predation by other species (Zwolak *et al.*, 2016). At the end of the fall period, scatterhoarders reproduce with a type II numerical response with respect to the number of seeds they consumed and with a maximum of b offspring and a half saturation constant h . These offspring and their surviving parents, who survive with probability s_1 , determine the density $n_2(t)$ of scatterhoarders entering the winter/spring period (in short-lived species such as yellow-necked mice, researchers typically do not emphasize age-specific survival rates: Krebs, 2019).

During the winter/spring period, the primary resource for the scatterhoarders is the cached seeds. Owners of cached seed who survived gather their cached seed with a per-capita rediscovery rate a_2 . All other individuals are assumed to pilfer seed from others' caches at a per-capita rate a_{pil} . Simultaneously with this gathering of cached seeds, cached seeds germinate at a rate g and are consumed by other seed predators at rate c . At the end of the winter/spring period, scatterhoarders reproduce with a type II numerical response based on the amount of gathered and consumed cached seeds. The resulting offspring and their surviving parents (survival probability s_2) determine the density $n_3(t)$ of scatterhoarders entering the summer period.

During this final period of the year (summer), individuals rely on other resources to reproduce and survive with probability s_3 . Per-capita reproduction during this period is modeled using a Beverton–Holt function $\frac{\beta}{1+\alpha n_3(t)}$ where β is the maximal summer fecundity and α determines the strength of intraspecific competition. These offspring and their surviving parents determine the density $n_1(t+1)$ of scatterhoarders entering the first period (the fall) of the next year $t+1$.

Seed fall dynamics As in Zwolak *et al.* (2021), seed fall $S(t)$ in the fall was modeled as a periodic function of time where the period P corresponds to the time between high-seed years (hereafter 'masting years'). In the masting years, $S(t) = S_{\text{high}}$, next year $S(t) = S_{\text{min}}$ (typically, seed crops produced after mast years are particularly scant: Pearse *et al.*, 2016, Bogdziewicz *et al.*, 2021), then $S(t) = S_{\text{low}}$ until another mast year. To avoid conflating changes in masting patterns with overall seed production, we simulated a scenario where tree resources are constant, but their distribution can differ between mast and nonmast years. Thus, when varying masting intensity, we assume that the average seed output, $(S(1) + S(2) + \dots + S(P))/P$, is fixed and what varies is the proportion of total seed output in the masting year. Higher intensity of masting means more seeds during the masting year, but concomitantly fewer seeds in other years. Similarly, when we vary the number of years between masting events, the average seed output per year remains the same.

Evolutionary stable strategy for caching For a given set of parameters, an ESS for caching is a threshold caching level T such that any small, mutant population with a different threshold cannot establish. To identify the ESS, Zwolak *et al.* (2021) derived

explicit expressions for the invasion growth rate $s(T, T_m)$ of a mutant population with strategy T_m trying to invade a resident population playing the strategy T , and the fitness gradient $\frac{\partial s}{\partial T_m}(T, T)$ when the resident population is playing threshold strategy T . When the fitness gradient is positive, mutants with a higher threshold strategy than the residents can invade while mutants with a lower threshold strategy fail (Geritz *et al.*, 1997). When the fitness gradient is negative, the opposite occurs. As mutants with larger or smaller thresholds fail when invading a resident population playing the ESS, the fitness gradient must equal zero at an ESS and, generically, have negative second-order derivative with respect to the mutant strategy at an ESS, that is $\frac{\partial^2 s}{\partial T_m^2}(T, T) < 0$. Hence, we identified ESSs by iteratively solving for thresholds T at which the fitness gradient $\frac{\partial s}{\partial T_m}(T, T)$ is zero and verifying graphically that the second-order derivative condition held.

Key model outputs For each model evaluation, we kept track of the density of scatterhoarders in the fall of a masting year. These densities, by in large, determined the fraction of seeds, p_{gather} , gathered by scatterhoarders during a masting cycle. Of these gathered seeds, we calculated the fraction, $p_{\text{cachlgather}}$, that were cached; the remaining fraction was consumed by the scatterhoarders. Of the cached seeds, we calculated what fraction p_{leftcach} , p_{gather} were neither recovered, pilfered, or consumed by other seed predators. These seeds had the potential to germinate with a fixed probability p_{germ} . Taking the product of these conditional probabilities $p_{\text{gather}} \times p_{\text{cachlgather}} \times p_{\text{leftcach,gather}} \times p_{\text{germ}}$ gives us the fraction of all fallen seeds that successfully germinated during a masting cycle. For simplicity, we use the term 'plant recruitment' to describe this outcome. However, it is worth noting that plant recruitment more precisely includes two additional components: seedling survival and growth (Fraaije *et al.*, 2015).

Model scenarios and parameters

We explored how different environmental factors simultaneously impacted densities of scatterhoarders and the fraction of successfully germinating seeds. To represent different environmental effects, we focused on the roles of scatterhoarder survival, s_1 , s_2 , s_3 , interspecific competition with seed predators, L_1 and c , summer resource availability β , masting period P , and masting intensity $S_{\text{high}}/(S(1) + \dots + S(P))$. For each of these factors, we varied them in multiplier manner from the base parameter values.

Our base parameter values, except as described below, come from Zwolak *et al.* (2021); see Supporting Information Table S1. These estimates were based mostly on research on European beech (*Fagus sylvatica*) and yellow-necked mice (*Apodemus flavicollis*). *Apodemus* mice are among the most important seed predators and scatterhoarders in Eurasia (e.g. Muñoz & Bonal, 2011; Shimada *et al.*, 2015; Wróbel & Zwolak, 2019; Yang *et al.*, 2020). Zwolak *et al.* (2021) assume that seed masting occurs every fourth year (a 4-yr masting period) with a fall seed loss rate L_1 of 5.59. Because Zwolak *et al.* (2021) were not concerned with seed germination, they treated the germination rate g of cached seeds and the interspecific seed predation rate c as a

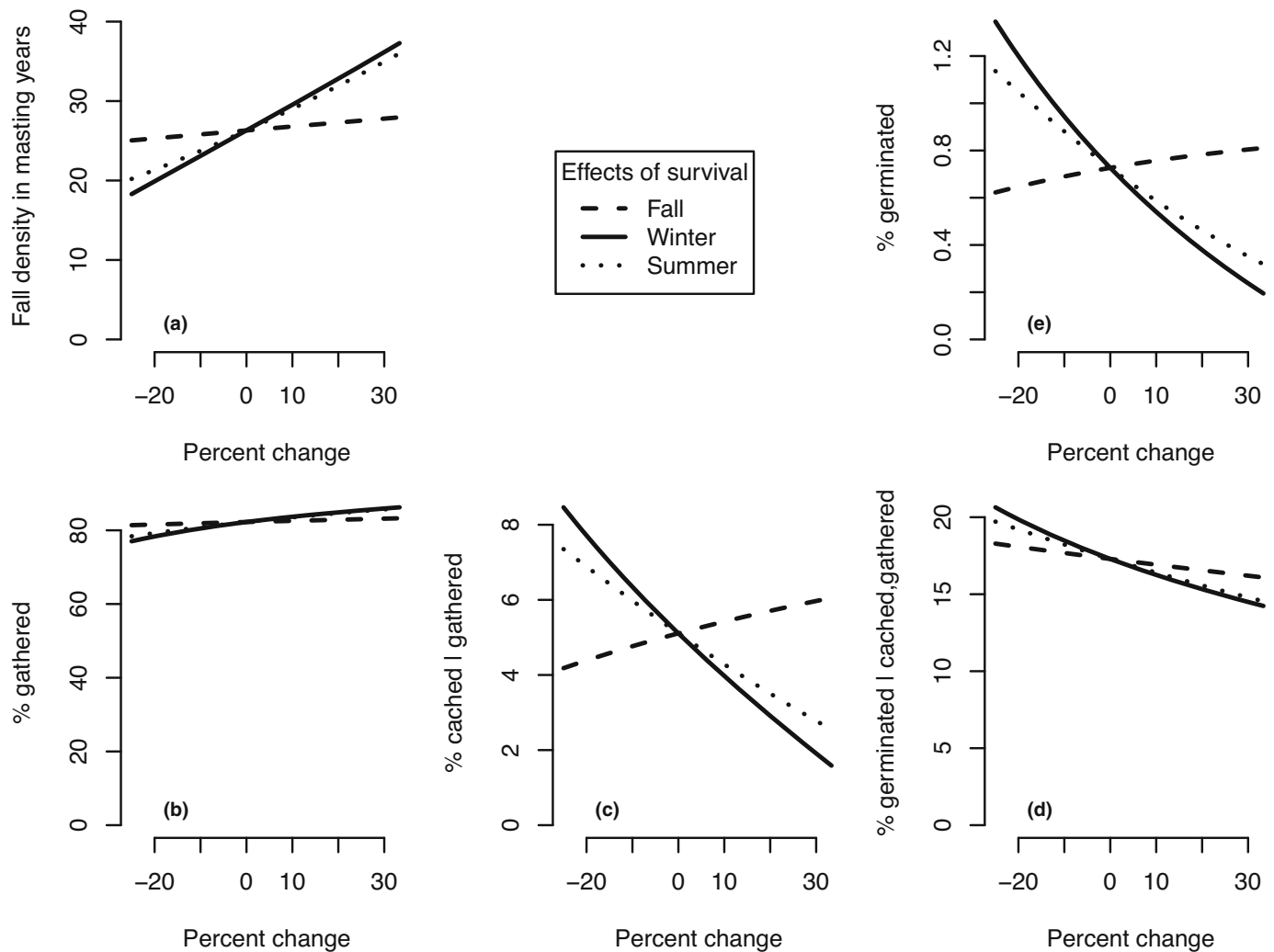


Fig. 1 Increasing summer and winter scatterhoarder survival is disadvantageous for plants; increasing fall survival benefits plants. Effects of changes in scatterhoarder survival on (a) most year autumn population density of scatterhoarders in individuals ha^{-1} , (b) proportion of seed crop that is gathered by scatterhoarders, (c) proportion of gathered seeds that is cached, (d) proportion of cached seeds that germinate, and (e) proportion of germinating seeds. Dashed, solid, and dotted lines represent seasons (fall, winter, and summer). All dependent variables are given at the evolutionary stable caching strategy and its associated periodic population dynamics. The model simulates interactions between yellow-necked mice (*Apodemus flavicollis*) and European beech (*Fagus sylvatica*).

single composite parameter, the winter/spring loss rate $L_2 = g + c$. They estimated L_2 to be between 15.1 and 336.3 and used a value in the upper end of this range (300) for their analysis. We, however, choose the winter/spring seed loss rate to equal the fall seed loss rate ($L_2 = L_1 = 5.59$) and assume 46% of unrecovered cached seeds germinate, on average (Zwolak *et al.*, 2016). This yields $g = 2.57$ and $c = 3.02$ for our base values.

Results

The impact of changes in rodent survival on beech benefits (specifically, the percentage of germinating seeds) varies with season. Increasing summer and winter survival of the scatterhoarders has a strong negative effect on the benefits for the plants. The mechanism underlying these changes is as follows. High summer and winter survival of mice increases their population density (dotted and solid curves in Fig. 1a). While this results in a higher

percentage of gathered seeds (Fig. 1b), a lower proportion of these seeds are cached (Fig. 1c), and, due to higher cache recovery by the scatterhoarders, a lower proportion of cached seeds germinate (Fig. 1d), with a net negative impact on the recruitment of the plants (Fig. 1e). Conversely, decreasing summer and winter survival of the scatterhoarders benefits the plants.

Increasing fall survival has positive, but weak effects on the scatterhoarder population density (dashed line in Fig. 1a), the proportion of seeds gathered, and the percentage of cached seeds that germinate (Fig. 1b,d). However, increases in fall survival positively affect the proportion of gathered seeds that are cached (Fig. 1c), because the animals have a higher chance of using their caches in the following winter. The net result of increasing fall survival is a positive, but relatively small effect on the plant recruitment (Fig. 1e).

Increasing levels of competition between the scatterhoarders and other granivores negatively affect beech recruitment

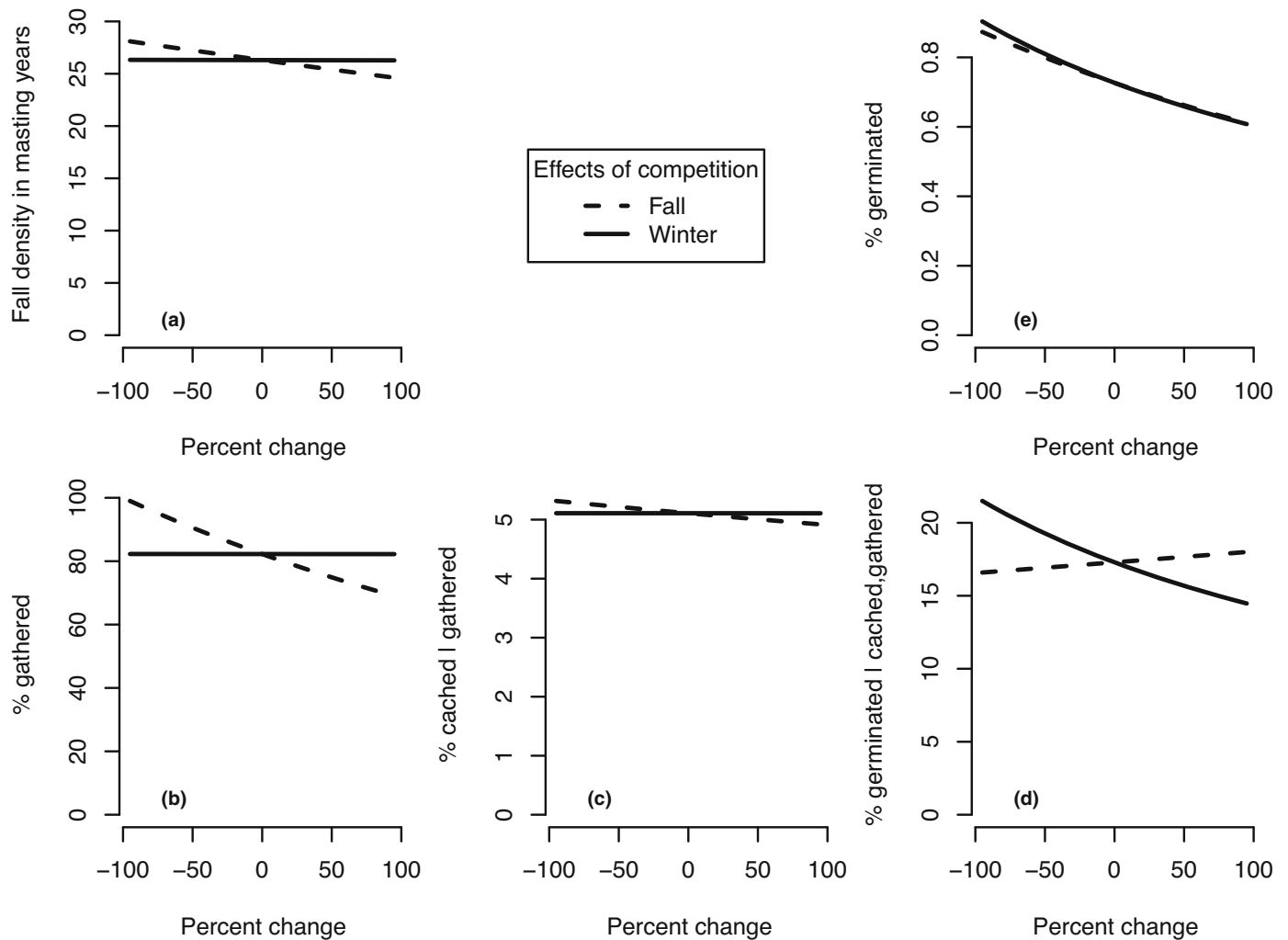


Fig. 2 High levels of interspecific competition in the fall (for seeds on the ground) and winter (for cached seeds) negatively affect plant recruitment. Effects of changes in competition on (a) mast year autumn population density of scatterhoarders in individuals ha^{-1} , (b) proportion of seed crop that is gathered by scatterhoarders, (c) proportion of gathered seeds that is cached, (d) proportion of cached seeds that germinate, and (e) proportion of germinating seeds. Solid and dashed lines represent seasons (fall and winter). All dependent variables are given at the evolutionary stable caching strategy and its associated periodic population dynamics. The model simulates interactions between yellow-necked mice (*Apodemus flavicollis*) and European beech (*Fagus sylvatica*).

(Fig. 2a–e). Mechanisms underlying these changes are season-dependent. High levels of competition in the fall (for seeds on the ground) reduce the percentage of seeds gathered by the scatterhoarders, with weak effects on other processes; high levels of competition in the winter (for cached seeds) reduce the chances that seeds cached and unrecovered by rodents survive to germinate, with weak effects on other variables (Fig. 2a–e).

Increased abundance of alternative foods available to the scatterhoarders in the summer is detrimental for the plants (Fig. 3e). High levels of nonseed food resources increase fall density of the scatterhoarders (Fig. 3a), which increases seed gathering (Fig. 3b), but decreases caching of gathered seeds (Fig. 3c) and seed survival in caches (Fig. 3d), because high population abundance increases the risk of cache pilferage.

Increasing intensity of masting and longer intervals between mast events improve beech recruitment, with changes in mast intensity producing relatively stronger responses (Fig. 4). This

beneficial effect is a consequence of reduced fall density of the scatterhoarders (Fig. 4a). Despite this translating into a lower percentage of seeds gathered (Fig. 4b), low scatterhoarder density increases the proportion of gathered seeds that are cached (Fig. 4c), and the proportion of cached seeds that germinate (Fig. 4d). The net result of these changes is improved recruitment (Fig. 4e), at least until the changes are so extreme that granivores reach very low densities between mast events (*c.* 5 individuals ha^{-1} ; Fig. S1).

In general, most factors that are negative for the scatterhoarders (decrease their abundance), benefit the dispersed plants (Table 1).

Discussion

Mutualisms are highly dynamic, with costs and benefits fluctuating in space and time (Song *et al.*, 2020). Framing mutualisms as

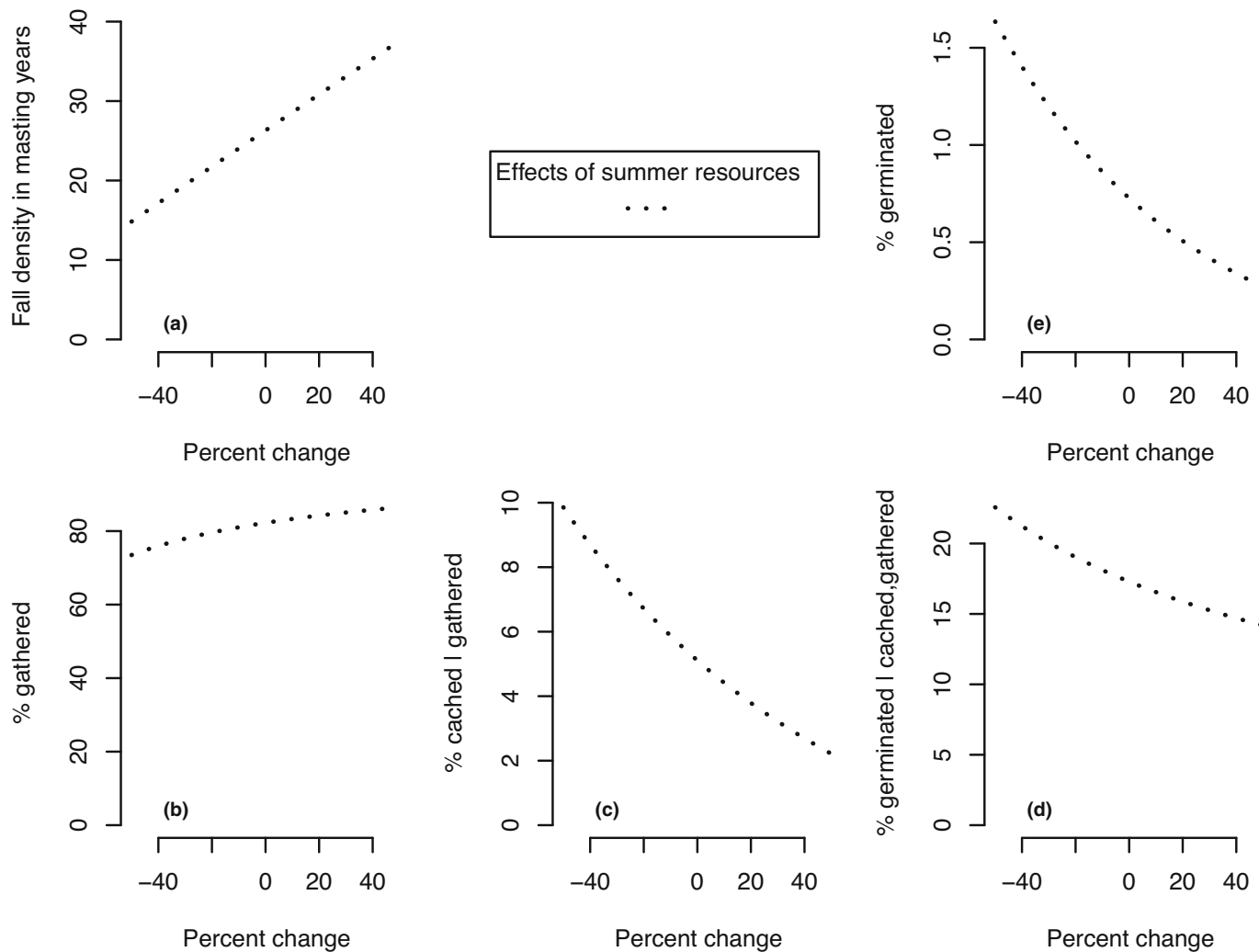


Fig. 3 High levels of nonseed food resources, in the summer, negatively affect plants. Effects of changes in nonseed food resources on (a) mast year autumn population density of scatterhoarders in individuals ha^{-1} , (b) proportion of seed crop that is gathered by scatterhoarders, (c) proportion of gathered seeds that is cached, (d) proportion of cached seeds that germinate, and (e) proportion of germinating seeds. All dependent variables are given at the evolutionary stable caching strategy and its associated periodic population dynamics. The model simulates interactions between yellow-necked mice (*Apodemus flavicollis*) and European beech (*Fagus sylvatica*).

either one-way or two-way consumer–resource relationships has been a powerful tool for studying how mutualist abundance impacts the interaction (Holland & DeAngelis, 2010). If the incremental gains (‘marginal benefits’) of resource provisioning by one partner decrease as the other partner’s population grows, while the marginal costs do not, then the ‘overabundant’ population of the consuming partner will eventually become detrimental to the provisioning partner (Holland *et al.*, 2002). Our results on beech–rodent interactions illustrate that this tipping point may be reached at much lower population levels than previously thought (Bronstein, 1994): per-capita benefits for plants decrease rather than increase with the increase in scatterhoarder abundance over most of the parameter range we examined (Table 1). Thus, scatterhoarder ‘overabundance’ might actually occur under a wide range of conditions.

The mechanism behind this phenomenon was that high density of the scatterhoarder population led to increased pilferage of caches. Scatterhoarders adapt to this risk by increasing immediate

consumption of gathered seeds at expense of caching. This evolved response increases costs and reduces benefits gained by plants. Thus, seeds fare best when scatterhoarder populations are relatively low. Plants can either create such conditions via the satiation–starvation cycle induced by masting or capitalize on conditions set by other drivers.

However, there are two specific deviations from the general pattern of the negative association between scatterhoarder abundance and plant benefits (Table 1): increased fall survival and decreased fall competition, both of which increase scatterhoarder abundance, also inherently select for more caching. These special cases suggest that certain factors can override the importance of population density in driving the adaptive changes in scatterhoarder behavior. More generally, our results illustrate how factors that trigger changes in the abundance of a mutualistic partner can have varying impacts on the quality of the interaction, depending on the precise mechanism of the underlying costs and benefits. In the following sections, we provide further details on

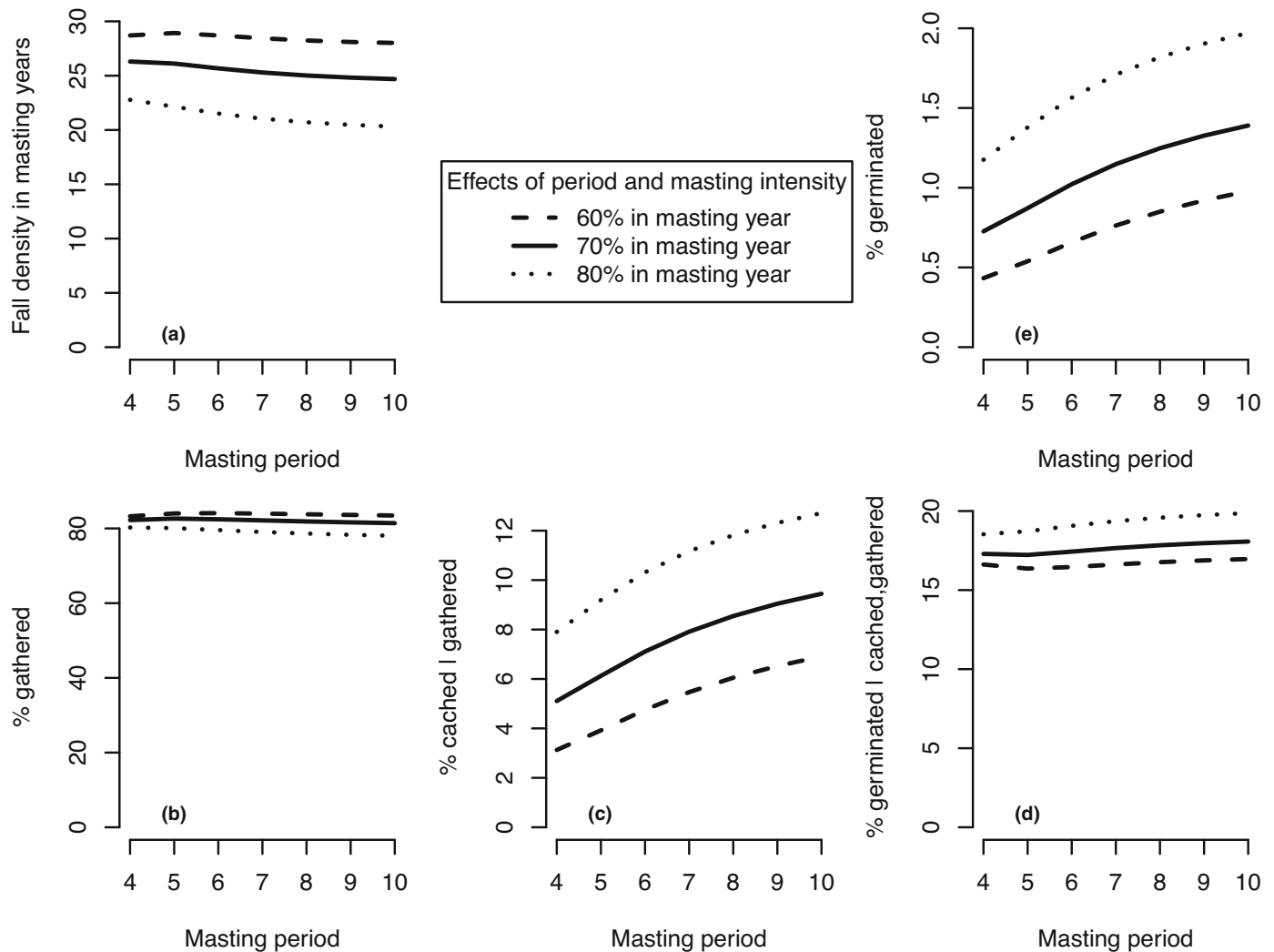


Fig. 4 Increases in masting intensity and interval benefit plant recruitment. Mast year autumn population density of scatterhoarders in individuals ha^{-1} (a), proportion of seed crop that is gathered by scatterhoarders (b), proportion of gathered seeds that is cached (c), proportion of cached seeds that germinate (d), and proportion of germinating seeds (e) as a function of changes in intermast interval. Dashed, solid, and dotted lines represent mast intensity (60, 70, or 80% of total seed production occurring during mast years). All dependent variables are given at the evolutionary stable caching strategy and its associated periodic population dynamics. The model simulates interactions between yellow-necked mice (*Apodemus flavicollis*) and European beech (*Fagus sylvatica*).

the patterns observed in the tree–scatterhoarder interaction that we modeled.

Variation in scatterhoarder survival

The classical model by Andersson & Krebs (1978) suggested that high survival of hoarding animals facilitated the evolution of caching because surviving is an obvious condition of using caches in the future. We found analogous results when fall survival varied: low mortality of scatterhoarders promoted seed caching, which in turn positively affected plant recruitment. However, this pattern was not universal. Winter and summer survival affected caching behavior mostly through positive effects on the population density of scatterhoarders, which decreased the adaptive value of caching. Moreover, varying winter and summer survival of scatterhoarders resulted in stronger effects on plants than did changes in fall survival.

These findings add nuance to the results by Andersson & Krebs (1978). More importantly, they indicate that mortality factors can indirectly increase recruitment of scatterhoarder-dispersed plants (at least until the densities of dispersers were so low that seeds ended up unharvested). Predation is the leading source of mortality for most scatterhoarders (Jędrzejewski & Jędrzejewska, 1993; Aliaga-Rossel *et al.*, 2006). Our findings suggest that the seasonal dynamics of predation might shape its indirect impact on plant dispersal.

While it is widely recognized that predators and pathogens of herbivores can have cascading, positive effects on plants (Schmitz *et al.*, 2000; Morris & Letnic, 2017; Bogdziewicz *et al.*, 2022), our results suggest that mortality agents of scatterhoarders can have similar consequences. Yet, this phenomenon has been largely overlooked.

Our current understanding of the indirect effects of predators on seed caching is based mostly on immediate behavioral

Table 1 Summary of changes in scatterhoarder abundance and plant recruitment in response to variation in selected factors.

Factor	Scatterhoarder abundance	Plant recruitment	Plant vs scatterhoarder interests
Survival			
Fall	+	+	Aligned
Winter	++	--	Opposed
Summer	++	--	Opposed
Competition for seeds			
Fall	–	--	Aligned
Winter	No effect	--	N/A
Alternative food resources			
Summer	++	–	Opposed
Masting			
Intensity	--	++	Opposed
Period	–	+	Opposed

If a given factor positively affects both scatterhoarder abundance and plant recruitment, the interests are classified as 'aligned' (denoted as '+'); if the effects on scatterhoarders and plants differ, the interests are classified as 'opposed' (denoted as '–'). Relatively strong effects are denoted with '++' or '--'.

responses of scatterhoarders to proxies of predation risk, such as olfactory cues or habitat structure (Sunyer *et al.*, 2013; Lichti *et al.*, 2017; Gálvez & Hernández, 2022). In general, cues of predation risk are associated with reduced seed removal, but also reduced cache pilferage. The first effect potentially decreases plant benefits, while the second increases them. However, if predators affect plant–scatterhoarder interactions also through changes in scatterhoarder abundance that trigger adaptive responses of caching behavior, they can create lasting, long-term effects that go beyond the better-known, rapid adjustments in habitat used and time spent on foraging vs vigilance.

Competition with seed predators

High rates of seed loss, which simulated competition with other, noncaching granivores, provided an exception to the trend that what is bad for yellow-necked mice, is good for their plant mutualists. Competition for seeds had weakly negative or no effects on scatterhoarder density because cached seeds represented a small (< 6%) proportion of total seeds consumed, but always reduced the benefits of their plant partners. This was the case both when competition occurred during seed gathering (because interspecific competitors do not cache, but only consume seeds), and when the competitors pilfered seeds that were already cached (because it reduced the chances that seeds will be left abandoned in the caches).

This result is consistent with most field studies that measured short-term, behavioral responses to competition. For example, scatter-hoarding rodents increased seed consumption *in situ* in the presence of wild boars, with potential negative effects on plant recruitment (Sunyer *et al.*, 2015). However, wild boars act not only as competitors, but also as occasional predators of rodents. A majority of studies on the effects of pilferage risk on seed caching indicate

that it increases immediate consumption of seeds and larder-hoarding, at the expense of scatter-hoarding (Zhang *et al.*, 2013; Luo *et al.*, 2014; Zhang *et al.*, 2014; Cao *et al.*, 2018; Niu *et al.*, 2020; see Huang *et al.*, 2011 for an exception). Thus, the increased abundance of competing granivores has the potential to deteriorate the quality of plant–scatterhoarder mutualism.

Variation in alternative food resources

The connection between alternative food resources, which provide subsistence for yellow-necked mice in the summer, and beech recruitment was again mediated by the resource effects on scatterhoarder abundance. High levels of alternative resources led to high abundance, with generally negative effects on plants; low levels of resources decreased abundance, which promoted seed caching and improved plant recruitment.

An obvious factor that could affect alternative food resources is interspecific competition (e.g. Allen *et al.*, 2022). Other possible causes include changes in weather, occurrence of disturbances, and anthropogenic alterations of habitats. Our model suggests that all these factors can indirectly affect plant recruitment. The direction of change will depend on their impacts on scatterhoarder population density, with negative effects on scatterhoarders improving plant benefits and positive effects decreasing them.

Masting intensity and period

Less frequent and more intense masting reduced the density of scatterhoarders, which experienced longer and more pronounced periods of scarce seed resources. The reduced abundances of mutualistic partners led to higher benefits for plants, at least until the densities were so low that scatterhoarders faced extinction. This finding resembles the predation satiation hypothesis, which states that masting evolved to reduce the proportion of seed crop that is consumed by granivores (Kelly & Sork, 2002). Masting is particularly effective in reducing seed losses when consumers are starved between and satiated during mast years (Zwolak *et al.*, 2022).

Another hypothesis, the predator dispersal hypothesis, states that masting benefits plant recruitment because it stimulates seed dispersal and caching by scatterhoarders (Vander Wall, 2002; Zwolak *et al.*, 2016). According to this idea, consumption is easily satiated, but caching behavior is not (when food is abundant, a loss of appetite occurs much sooner than a loss of motivation to gather and store food: Vander Wall, 2002, 2010). Here, we show that reduction in seed losses to granivores and the stimulation of caching by dispersers can be achieved by the same mechanism, that is by keeping consumer abundance at a low level between mast events. This emphasizes a close connection between the mechanisms behind the predator satiation and predator dispersal effects of masting.

Scope and limitations of the model

Our study primarily applies to situations where the benefits provided by a mutualistic species, such as rodents, decrease with

increasing population density, while the associated costs to its partner remain constant. This is particularly true when the partner species influences the mutualist's population density, for example through resource provisioning.

An important caveat is that we treat seed fall and masting intensity as parameters, without modeling the tree energetics and population dynamics that underly these quantities. This is reasonable in our system given the short lifespan of yellow-necked mice relative to beech trees, but it means that our results may not apply to systems where the mutualist partners have similar lifespans or where the population dynamics of the longer-lived partner is of interest. Such situations are better described by other models (e.g. Holland & DeAngelis, 2010; Revilla, 2015).

Finally, even when applying our findings to other scatterhoarding systems, it is necessary to consider the biology of the species involved. For example, as seeds' ability to germinate without caching improves, their interaction with scatterhoarders leans more toward antagonism (Zwolak & Crone, 2012). In another context, cache pilferage among corvids may depend less on the abundance of their own species and more on rodent numbers (Thayer & Vander Wall, 2005; but see Molina-Morales *et al.*, 2020).

Future studies should validate the mechanisms outlined in our model in natural settings. For instance, scatterhoarder abundance stands out as a key variable affecting interaction dynamics. Our model predicts that high scatterhoarder abundance should increase seed removal and cache pilferage, but reduce caching rates. Some of these links already received a certain degree of support from empirical studies. For instance, Dittel & Vander Wall (2018) documented a positive association between scatterhoarder abundance and cache pilferage. Moreover, emerging research indicates that scatterhoarders provide the most benefits at moderate densities (Mittelman *et al.*, 2021; Zeng *et al.*, 2021). Yet, a comprehensive exploration of how scatterhoarder abundance affects various facets of seed dispersal remains essential, especially when distinguishing its impact from other factors, like seed abundance.

Conclusions

Rapid anthropogenic changes increasingly disrupt interspecific interactions (Tylianakis *et al.*, 2008; Aslan *et al.*, 2013). While the consequences of extinctions and distribution shifts are the most conspicuous, more subtle effects (e.g. on the behavior of interacting species) also exert strong impacts on populations and communities (Hammond *et al.*, 2020). Despite their importance, mechanisms of these effects remain relatively understudied. Our findings highlight the nuanced effects of environmental shifts on mutualisms. Specifically, in our simulated plant–scatterhoarder interaction, increasing scatterhoarder abundance typically led to declining benefits for the plant (Table 1). This phenomenon was mediated mainly by adaptive changes in the caching behavior in response to density-dependent cache pilferage risk. Such changes can switch the interaction from mutualism to antagonism, as scatterhoarders can both increase (as seed dispersers) and decrease (as seed predators) plant recruitment. It remains to be seen how

often a similar dynamic, with factors that depress the abundance of one mutualistic partner increasing the benefits for the other partner, occurs in other mutualistic or conditionally mutualistic interactions. Thus far, positive density dependence has been more often found in mutualisms (Cushman & Whitham, 1989; Morales & Carlo, 2006). However, given that mutualisms often entail substantial costs, we speculate that such dynamics might be more common than currently appreciated.

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Competing interests

None declared.

Author contributions

RZ and SJS conceived the study. SJS and DC developed and analyzed the model with feedback from RZ and AS. RZ wrote the first draft of the manuscript. All authors critically revised the draft and approved the final version of the article.

ORCID

Dale Clement  <https://orcid.org/0000-0001-7327-3323>
 Sebastian J. Schreiber  <https://orcid.org/0000-0002-5481-4822>
 Andrew Sih  <https://orcid.org/0000-0001-6161-1663>
 Rafał Zwolak  <https://orcid.org/0000-0002-7665-5033>

Data availability

The code for the model has been deposited in the Zenodo open depository, doi: [10.5281/zenodo.10052019](https://doi.org/10.5281/zenodo.10052019).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Extremely low winter survival of the scatterhoarder causes the proportion of germinating seeds to decrease.

Table S1 List of names, values, and descriptions for the model parameters.

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