


RESEARCH ARTICLE

Scatterhoarder abundance and advantages of seed burial drive dynamics of a tree–rodent interaction

Rafał Zwolak¹  | Paulina Celebias¹  | Milena Zduniak¹ | Michał Bogdziewicz²  | Aleksandra Wróbel³ 

¹Department of Systematic Zoology, Adam Mickiewicz University, Poznań, Poland

²Forest Biology Center, Adam Mickiewicz University, Poznań, Poland

³Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland

Correspondence

Rafał Zwolak

Email: rzwolak@amu.edu.pl and rafal.zwolak@gmail.com

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Abstract

1. Theoretical models suggest that species abundance plays a crucial role in mutualism; high densities can lead to overexploitation. Additionally, mutualistic benefits are expected to increase under abiotic stress.
2. We investigated the interplay between density dependence and abiotic factors in conditional mutualism, focussing on the interactions between yellow-necked mice (*Apodemus flavicollis*) and common oaks (*Quercus robur*) across 3 years. We controlled for seed abundance, while mouse densities varied. Our approach included monitoring mouse abundance, measuring seed removal, determining the fate of harvested seeds and conducting seedling emergence trials to assess the advantages of seeds caching.
3. We found that mouse abundance exerted a strong influence on all studied aspects of seed dispersal. Higher densities led to increased seed removal and greater dispersal distances. However, they also decreased the probability of seed caching and increased seed consumption, degrading dispersal quality and shifting the interaction towards antagonism. Furthermore, the reliance of seedling recruitment on burial varied over time, likely becoming more critical during dry conditions. This indicates that plants face the worst conditions when high abundance of mice coincides with abiotic stress.
4. *Synthesis:* Our results supports the notion that increased rodent abundance reduces plant recruitment, revealing the conflicting interests of the interacting species. However, the dynamics of rodent–oak interactions are shaped not only by the density-dependent foraging decisions of rodents, but also by the benefits of seed burial under stress. These findings illustrate how the interplay between population density and abiotic factors jointly dictate the costs and benefits of mutualistic interactions.

KEYWORDS

conditional mutualism, drought, Poland, seed dispersal, seed predation, synzoochory

1 | INTRODUCTION

Many interactions between species can shift along a mutualism–antagonism spectrum, contingent upon the interplay between biotic and abiotic conditions (Catford et al., 2022; Chamberlain et al., 2014; Maron et al., 2014). According to the stress-gradient hypothesis, stressful conditions nudge context-dependent interactions towards mutualism (Callaway et al., 2002; He et al., 2013; Karban & Agrawal, 2023). Furthermore, several theoretical frameworks emphasize the crucial role of species abundance in shaping the balance between costs and benefits in interspecific interactions (Holland et al., 2002; Holland & DeAngelis, 2010; Wolin & Lawlor, 1984). Consumer-resource models predict that high densities of mutualists can lead to overexploitation, potentially shifting the dynamics from mutualism to a predator–prey relationship, thus blurring the distinction between these interactions (Holland & DeAngelis, 2010). Despite the implications, empirical research focussing on how mutualism changes with population density is limited (Muñoz-Gallego et al., 2023), and studies exploring the combined effects of abundance and abiotic factors are even rarer.

This shortage of empirical data is notably present in plant–scatterhoarder interactions, a prime example of conditional mutualism (Gómez et al., 2019; van Leeuwen et al., 2022). Scatterhoarders, primarily rodents and corvids, bury nuts in shallow, dispersed caches within topsoil or litter (Vander Wall, 2001). These animals, interacting with over 1200 plant species (Gómez et al., 2019), play a pivotal role in the population dynamics of dispersed plants (Elwood et al., 2018). Scatterhoarders can either promote or hinder plant reproduction, depending on the balance of costs and benefits (Bogdziewicz et al., 2020; Gómez et al., 2019). The costs include seed predation, while the benefits involve seed dispersal and caching. The caching protects seeds from adverse conditions, preventing desiccation and enhancing seedling emergence. These benefits are so important that in some situations, plants do not germinate unless their seeds are buried (e.g. Borchert, 2006). However, in most cases, the interaction between plants and scatterhoarders is facultative because seed burial improves rather than enables germination (Zwolak & Crone, 2012). The magnitude of its benefits depends on abiotic factors such as soil types, prevailing temperatures and precipitation levels (Loayza et al., 2020). The latter is crucial because seeds on the ground lose moisture while cached seeds gain it, even in non-arid temperate forests (Perea et al., 2012). Climate change, which affects the duration of snow cover and disrupts rainfall patterns (Ombadi et al., 2023), is likely to further complicate these interactions.

Plants can endure greater costs of seed predation when benefits from seed caching are substantial. Zwolak and Crone (2012) used a theoretical model to show that the interaction is mutualistic when the probability of caching and not retrieving cached seeds exceeds the ratio of seedling emergence from surface (e_s) to seedling emergence from caches (e_c). In other words, granivores help plant recruitment when the proportion of cached and uneaten seeds exceeds a threshold value (hereafter ' \tilde{p}_c ', after Zwolak & Crone, 2012) determined by the emergence ratio:

$$\tilde{p}_c > \frac{e_s}{e_c}$$

Thus, scatterhoarder behaviour interacts with benefits of seed burial to determine whether the plant–scatterhoarder relationship is mutualistic or antagonistic (Bogdziewicz et al., 2020; Sawaya et al., 2018; Theimer, 2005; Zwolak & Crone, 2012).

The profits gained from mutualistic interactions also change with the abundance of interacting partners (Abbott & Green 2007; Cushman & Whitham, 1989; Harmon & Andow, 2007). For example, in many plant–animal interactions, benefits such as enhanced seed dispersal, improved protection or increased food provisions rise with the number of mutualists (Morales & Carlo, 2006; Rehling et al., 2023). However, interactions between plants and rodent scatterhoarders may diverge from this pattern. Theoretical models suggest that benefits to plants actually increase as the number of rodent declines (up to a tipping point at critically low levels of rodent abundance: Zwolak et al., 2024). This happens because, with less competition, these animals are more likely to cache seeds instead of consuming them, which increases plant benefits (Zwolak et al., 2021, 2024). Despite these theoretical propositions, empirical validation is required to fully understand how variation in scatterhoarder density and the advantages of seed burial affect the outcomes of plant–scatterhoarder interactions.

To address this gap, we have conducted a comprehensive exploration of the dynamics of plant–scatterhoarder interactions, aiming to bridge theoretical models with empirical data and validate the mechanisms proposed in recent theories (Zwolak et al., 2024) within natural settings. We tracked the interactions between yellow-necked mice (*Apodemus flavicollis*) and common oaks (*Quercus robur*) over 3 years and varying mouse densities, while keeping the seed abundance constant. We monitored mouse abundance, measured seed removal, determined the fate of harvested seeds and conducted seedling emergence trials to assess the advantages of seed caching. This approach allowed us to evaluate how fluctuations in mouse populations and changes in the benefits of seed burial impact the outcome of oak–rodent interaction.

We expected that elevated densities of mice would result in increased seed removal. Additionally, we predicted that an increase in mouse abundance, an indicator of the risk of seed pilferage, would be associated with decreased seed caching and increased seed consumption. Furthermore, as mouse abundance is a marker of competition for seeds, we predicted a higher incidence of seeds being fully rather than partially eaten, a decrease in seeds left on surface after dispersal, and seeds being transported farther at higher mouse densities. Consequently, we predict a decline in positive interactions and an increase in negative (consumptive) interactions as mouse numbers rise. Additionally, we expected that adverse environmental conditions (drought) will increase the benefits of seed caching. Acorns are recalcitrant (do not survive drying) and become nonviable when their moisture content is too low (less than 40% in *Q. robur*: Suszka & Tylkowski, 1980). Caching mitigates, and dry weather exacerbates this risk. Overall,

our predictions suggest that the dynamics of oak–rodent interactions hinge on the interplay between mouse foraging behaviour, dictated by their population size and the fluctuating benefits of caching, influenced by abiotic factors.

2 | MATERIALS AND METHODS

2.1 | Natural history

The yellow-necked mouse, a small rodent weighing between 15 and 60 g, is both abundant and prevalent in European woodlands (Marsh et al., 2001; Pucek, 1984). This species is omnivorous but specializes in seeds from trees such as beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*) and oaks (*Quercus robur* and *Q. petraea*), which constitute over 80% of its diet (Selva et al., 2012). Its seed storage behaviours include scatterhoarding—concealing individual or few seeds in shallow litter or topsoil caches—and larderhoarding—storing large seed quantities in underground tunnels (Jensen, 1985).

Reproduction of the yellow-necked mouse is characterized by a 26-day gestation period and typical litter sizes of 4–6 offspring (AnAge database: de Magalhaes & Costa, 2009). The species commonly produces of 2–4 litters each year (Pucek, 1984), facilitating rapid population growth, particularly after mast-seeding events. Periods of high abundance are often followed by steep declines, attributed to several factors: a scarcity of seeds post-mast year (Zwolak, Bogdziewicz, & Rychlik, 2016), predation or parasitism pressures (Jędrzejewski & Jędrzejewska, 1993; Pedersen & Greives, 2008) and density-dependent reproductive inhibition (Montgomery et al., 1997).

The common oak is a large broad-leaved tree, common throughout European temperate forests. Its value lies both in timber production and its ecological role as a supporter of diverse biota (Mitchell et al., 2019). Oak seed production exhibits masting, characterized by high interannual variation and interindividual synchronization. Acorns are large (usually 1–6 g) and consumed by a broad spectrum of animals. They are dispersed primarily by Eurasian jays, *Garrulus glandarius* (Bossema, 1979; Wróbel et al., 2022), while rodents serve a dual role as both dispersers and predators (Bogdziewicz et al., 2020; Gómez et al., 2008). The vulnerability of acorns to drought stress is a major factor in the failure of viable oak seedling production (Bobiec et al., 2018; Gómez, 2004).

2.2 | Study sites and small mammal trapping

The research was conducted in Zielonka Forest Landscape Park, located in the Greater Poland Voivodeship, Poland. The area has a temperate climate, with average temperatures ranging from -2.5°C in January to 18.2°C in July, and annual rainfall around 520 mm. We chose six study sites in managed hardwood stands, dominated by European beech (*Fagus sylvatica*) and oaks (*Quercus robur* and *Q. petraea*), with some Scots pine (*Pinus sylvestris*) and European larch

(*Larix decidua*). The most recent mast seeding event for beech occurred in 2018 and for oak in 2019.

At each site, we established a trapping grid of 100 'dziekanówka' traps (16.5×8×9.5 cm, produced by PPUH A. Marcinkiewicz, Rajgród, Poland) in a 10×10 arrangement with 10-m spacing. The traps, baited with oat flakes and sunflower seeds, were checked twice-daily. We divided the study sites into three pairs and trapped small mammals simultaneously at sites within each pair. We conducted five 4-day trapping sessions every 3 weeks from June to September over 2020, 2021 and 2022, with total trapping effort of 36,000 trap-nights. We measured body mass and determined species, sex and reproductive status of all captured small mammals. All individuals were marked with unique ear tags and yellow-necked mice received additional marking with passive integrated transponder (PIT) tags. The Local Ethical Committee in Poznań approved all fieldwork (Permits No. 24/2018 and 19/2020).

In 2020, yellow-necked mice at three of the six sites received an anti-ectoparasitic treatment using Frontline Combo Spot-on™, a broad-spectrum topical agent applied to the neck region of adult mice. However, this procedure did not influence seed dispersal patterns (Wróbel et al., submitted).

2.3 | Seed tracking experiment

We purchased fully grown oak acorns from a forest nursery, which were collected the previous autumn. To ensure quality, we used a water floatation test and discarded any acorns that were mouldy, hollow, or pest-infested. Theoretically, using stored acorns could affect their attractiveness to foragers. However, our observations did not show any reduced willingness to harvest these acorns. To definitively evaluate this, we would need to compare removal rates between stored and fresh acorns; unfortunately, fresh acorns were not available during our experimental period in the summer (refer to the rationale below).

Intraspecific variation in seed mass can influence the probability of seed removal, dispersal distances and germination rates (Jansen et al., 2004; Schupp et al., 2019; Wróbel & Zwolak, 2017; but see Chen et al., 2022). However, our experimental design did not specifically aim to isolate seed mass as a variable. Instead, we used a representative sample of acorns that reflects the natural variability in size and mass found in the field to closely mimic natural conditions.

We uniquely identified acorns for our seed tracking experiments by drilling a 1-mm hole at the base and attaching a red plastic tag (20×40 mm) to a steel wire (100–150 mm long, 0.20–0.25 mm in diameter; Wróbel & Zwolak, 2013; Xiao et al., 2006; Yi et al., 2008). The combined weight of the wire and tag was ~0.14 g.

To separate the influence of small mammal abundance from the confounding effect of fluctuations in natural acorn availability, the seed tracking experiments were performed from June to mid-September, before the natural acorn fall (October–November; the only other tree species abundant in these forests that provides seeds consumed by mice is the beech, which also produces seeds

exclusively in the fall). These experiments were conducted at the same locations as the small mammal trapping, immediately followed the trapping sessions. Similarly to trapping, we organized the study areas into three pairs, tracking the seeds in 5 four-day intervals, each separated by 3 weeks, simultaneously at both sites within each pair.

Around 7 pm at each study site, we arranged four clusters of five individually tagged acorns placed in Petri dishes within the loop of a PIT-tag reader's antenna. The PIT-tag readers were used to gather individual-level data on mice removing seeds for a concurrent study (Celebias et al., 2024). The seed clusters were placed at random but maintained a separation of at least 30 m. Each cluster was monitored with a Reconyx HyperFire PC800 Professional™ camera trap mounted 1 metre above the ground on a tree trunk, which recorded the time of seed removal, the species responsible, and the individual identification number if the animal had a PIT-tag.

Theoretically, this set-up should have resulted in the distribution of up to 2400 acorns per year (5 acorns \times 4 stations \times 6 sites \times 4 nights \times 5 sessions). However, the actual figure was slightly less because we were unable to conduct tracking on several nights in 2021 and 2022 due to unforeseen events. In total, we presented 7054 acorns (Figure S1).

Each morning, beginning at 8 am, we evaluated the acorns' status. 'Removal' included both displacement from the original location and consumption on-site. If any marked acorns were missing, we conducted a 20-min time-constrained search within a 30-m radius of the station. 'Recovery' pertained to acorns taken by mice and later located by researchers. We measured how far each recovered acorn was from its initial position and divided their post-dispersal state into three categories: (i) 'consumed' (only the tag and fragments remained, or over 65% of the acorn eaten; less damaged acorns still have a high probability of germination because scatterhoarders typically spare embryos: Giertych & Suszka, 2011; Perea et al., 2011; Yang & Yi, 2012), (ii) 'cached' (intact or partially consumed and hidden in soil or leaves) or (iii) 'left on surface' (intact or partially consumed and placed on the ground). Acorns in the 'cached' and 'left on surface' categories could be either intact or partially consumed (up to 65% eaten). Acorns that were never found were categorized as "missing".

2.4 | Seedling emergence trials

To assess the benefits of seed caching on oak recruitment, we conducted seedling emergence trials over two distinct periods: 2020/2021 and 2021/2022, which experienced markedly different weather conditions. The year 2021 featured weather typical for this region of Poland, with an average temperature of 9.4°C, warmer by 0.1°C than the 1991–2020 average, and precipitation 539 mm, or 98% of the average (Rocznik Meteorologiczny, 2021). In contrast, 2022 was exceptionally warm and dry, especially in our study area, ranking as one of the driest locales in Poland for that year. The average temperature increased to 10.6°C, while rainfall diminished to 414 mm (77% of the average: Rocznik Meteorologiczny, 2022).

To protect seeds from vertebrates, we used 18 \times 18 \times 18 cm wire mesh cages with a mesh size of 13 mm, burying them 5 cm into the ground at each site. We arranged 24 cages per site in 12 pairs, with each pair spaced 2 m apart and the pairs themselves dispersed at 30-m intervals, approximately 5 m from the edges of each trapping grid.

During October of 2020 and 2021, we sowed five acorns from a forest nursery into each cage, handling them with rubber gloves to prevent scent contamination (Duncan et al., 2002). One cage in each pair was used to simulate rodent caching with acorns buried 1 cm in the soil and covered with a thin layer of leaves, while the other cage represented seeds that had fallen directly from trees, with acorns placed on the litter surface and lightly covered with leaves.

Seedlings were counted in June of the following years (2021 and 2022), which was when their emergence was complete (i.e. no further seedlings appeared). However, some cages were destroyed by animals or humans before the assessment could be completed: 10 out of 144 (6.9%) in the 2020/2021 trial and 28 out of 144 (19.4%) in the 2021/2022 trial. Hereafter, the years mentioned (2021 and 2022) refer to the seedling emergence phase.

2.5 | Statistical analysis

Data analysis was performed in R version 4.2.0 (R Core Team, 2018). We fitted generalized linear mixed models (GLMMs) via the 'glmmTMB' package version 1.1.3 (Brooks et al., 2017) and assessed model performance with the DHARMA package, version 0.4.5 (Hartig, 2022), and 'performance' package, version 0.10.9 (Lüdtke et al., 2021). Our analysis included checks for multicollinearity and model overdispersion, with neither issue being detected.

We analysed the abundance of yellow-necked mice using a negative binomial error distribution (linear parameterization) with a log link function. The response variable was an abundance index, defined as the count of unique mice captured at a given site during a specific trapping session. We opted for this index over a capture-mark-recapture estimator as our prior work in this study system has shown that both methods are nearly perfectly correlated (Zwolak, Bogdziewicz, & Rychlik, 2016). The explanatory variables included year, day and their interaction. We also included site as a random intercept.

When analysing seed dispersal, we tested whether mouse abundance affected: (i) probability of acorn removal, (ii) probability of recovery, given they were removed, (iii) probability of consumption, contingent on removal, (iv) probability of partial versus complete consumption, (v) probability of caching, following removal and (vi) the dispersal distance for all seeds moved from the seed cluster.

In models (i–v), we used a binomial error distribution with a logit link function. For model (vi), we used a gamma error distribution with a log link to analyse seed dispersal distances, characterized by non-negative, strongly right-skewed values. Each model included two explanatory variables: the abundance of yellow-necked mice, defined as the number of unique individuals

captured per trapping session at a given trapping grid, and the day of the experiment, a numerical variable reflecting potential temporal shifts in mouse foraging behaviour (Sunyer et al., 2014). This latter effect was important to verify because our experiments occurred before the natural seedfall. We also explored potential nonlinear effects of abundance by including its quadratic term, but retained it only when it was statistically significant. The variable 'Year' was excluded to avoid confounding effects, as years exhibited substantial differences in mouse abundance, likely due to fluctuating beech and oak seed production. Finally, the models incorporated random intercepts for study sites and seed clusters (nested within study sites).

To provide a synthetic measure of positive and negative (from the plant's perspective) foraging decisions, we calculated an interaction score as the proportion of seeds receiving positive effects to the proportion of seeds receiving negative effects (Gómez et al., 2019). Positive effects included seeds dispersed and subsequently cached or deposited intact, while negative effects included seeds that were eaten (either immediately or after dispersal) or missing, with the assumption that missing seeds likely signify larderhoarding in deep burrows, where germination is unlikely (Brehm & Mortelliti, 2022). We then used a binomial model with a logit link to examine how the ratio of positive versus negative events changed with rodent abundance and over time (day of the experiment). The model included study site as a random intercept.

Seedling emergence probability was analysed with a binomial error distribution and a logit link function. Fixed effects included treatment (buried or sowed on surface), year (2021 or 2022) and their interaction. Random intercepts included site and cage pair, nested within plot.

The \tilde{p}_C threshold was calculated as a ratio of emergence from seeds sown on surface versus emergence from buried seeds (Zwolak & Crone, 2012). Confidence intervals were obtained with parametric bootstrapping, that is sampling from the distributions defined by the mean and standard error of each coefficient to obtain a joint distribution for the derived variables.

3 | RESULTS

3.1 | Small mammal trapping

Yellow-necked mice dominated the small mammal community, comprising 61.0% of the captured individuals. Bank voles (*Myodes glareolus*) were also common (36.8% of individuals). Other, rarely captured small mammal species included striped mice (*Apodemus agrarius*), voles (*Microtus* sp.), shrews (*Sorex* sp.), and house mice (*Mus musculus*).

Yellow-necked mouse abundances varied over the years ($\chi^2 = 373.9$, $df = 2$, $p < 0.001$; Figure 1). Specifically, the abundance was very high in 2020, decreased to a low in 2021, and stabilized at an intermediate level in 2022. In addition, we observed a pattern of increasing abundance throughout the summer ('Day' effect: $\chi^2 = 43.2$,

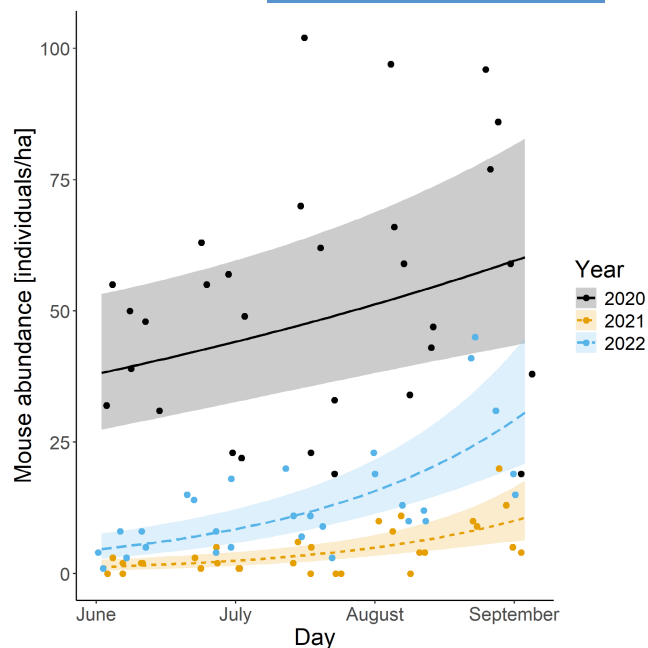


FIGURE 1 Yearly and seasonal variation in yellow-necked mouse (*Apodemus flavicollis*) abundance. Dots indicate data points, that is abundances across six sites during five trapping sessions per year ($n = 90$ site/trapping session/year combinations), lines represent estimated average abundances for each year derived from negative binomial mixed model, and shading corresponds to 95% confidence intervals. Colours and line styles differentiate years.

$df = 1$, $p < 0.001$). This seasonal increase was more pronounced in 2021 and 2022 compared to 2020, the year with the highest overall abundance ('Day \times Year' effect: $\chi^2 = 28.6$, $df = 2$, $p < 0.001$).

3.2 | Seed removal and the probability of recovering seeds

Rodents removed 42.5% of the seeds offered ($n = 2999$ out of 7054; Figure S1). A major proportion (85%) of the unremoved seeds were located at stations where no seeds were taken. Camera trap data confirmed that all removed acorns were harvested by yellow-necked mice, with the exception of 13 acorns, which were removed by bank voles. This represents 0.18% of seeds offered and 0.43% of those removed.

The probability of seed removal increased with mouse abundance, peaking at approximately 75 individuals per ha, beyond which the relationship between seed removal probability and mouse abundance levelled off (quadratic 'Abundance' effect in Table 1a; Figure 2a). Furthermore, the probability of seed removal by mice increased as the season progressed, from June to September each year ('Day' effect in Table 1a).

We found 58.4% ($n = 1743$; Figure S1) of the seeds removed by mice. The probability of recovering removed seeds declined with the abundance of mice, and increased within seasons ('Abundance' and 'Day' effects in Table 1b; Figure 2b).

Category ^a	Variable ^b	Estimate (SE)	z-value	p
(a) Removal	Intercept	-2.242 (0.262)	-8.55	<0.0001
	Abundance	66.509 (3.870)	17.19	<0.0001
	Abundance ²	-21.016 (3.523)	-5.97	<0.0001
	Day	0.035 (0.002)	20.71	<0.0001
(b) Recovery	Intercept	0.956 (0.134)	-7.15	<0.0001
	Abundance	-0.008 (0.002)	4.47	<0.0001
	Day	-0.006 (0.002)	2.90	0.0037
(c) Caching	Intercept	-0.596 (0.211)	-2.83	0.0047
	Abundance	-0.011 (0.003)	-3.99	<0.0001
	Day	0.000 (0.003)	-0.08	0.9362
(d) Consumption	Intercept	-0.468 (0.197)	-2.38	0.0172
	Abundance	0.018 (0.003)	7.14	<0.0001
	Day	-0.001 (0.003)	-0.31	0.7555
(e) Partial consumption	Intercept	-1.229 (0.240)	-5.13	<0.0001
	Abundance	-0.008 (0.003)	-2.68	0.0074
	Day	0.004 (0.004)	1.06	0.2986
(f) Left on surface	Intercept	-1.384 (0.202)	-6.83	<0.0001
	Abundance	-0.017 (0.003)	-5.04	<0.0001
	Day	0.002 (0.004)	0.66	0.5120
(g) Dispersal distance	Intercept	1.649 (0.084)	19.60	<0.0001
	Abundance	12.243 (1.152)	10.63	<0.0001
	Abundance ²	-3.720 (1.152)	-3.30	0.0012
	Day	0.007 (0.001)	5.80	<0.0001
	Seed status: consumed	-0.320 (0.054)	-5.92	<0.0001
	Seed status: left on surface	-0.407 (0.069)	-5.90	<0.0001

Note: Bold indicate statistically significant values.

^a'Removal' refers to both the displacement of acorns from seed stations and their consumption at the station. 'Recovery' refers to the acorns removed by mice and found by an experimenter. If an acorn was buried in topsoil or leaves, it was labelled as 'cached'. When an acorn was mostly eaten (>65% of the acorn destroyed), it was labelled as 'consumed'. When parts of an acorn were eaten (≤65% of the acorn destroyed), it was labelled as 'partially consumed'. 'Dispersal distance' refers to the distance between the seed station and the location where acorns (excluding consumed) were found. Seed status is a categorical variable with three levels: 'cached' (reference level), 'consumed' and 'left on surface'.

^bThe mouse abundance was measured as the number of individuals captured per trapping session at each of six 1-ha grids, and temporal changes in foraging were represented by the numerical variable 'Day'.

3.3 | Seed caching, consumption, and seeds left on surface

Overall, as mouse abundance increased, the proportion of positive seed dispersal events decreased while the proportion of negative events escalated (Figure 3). Mice cached 32.1% ($n=559$), ate 51.3% ($n=894$; note that this category includes only cases where >65% of the cotyledon was consumed) and left on surface 16.6% ($n=290$) of the seeds that we found. As mouse abundance increased, the probability of seed caching declined (Table 1c, Figure 2c), and probability of seed consumption increased (Table 1d, Figure 2d). Additionally,

TABLE 1 Effects of yellow-necked mouse (*Apodemus flavicollis*) abundance and temporal shifts in their foraging behaviour on the fate of *Quercus robur* acorns.

the chance of seeds being partially rather than completely consumed decreased with mouse abundance (Table 1e, Figure 2e). Finally, the likelihood that dispersed seeds were left on forest floor also declined as mouse abundance grew (Table 1f, Figure 2f). The variable 'Day' had no impact on these probabilities (Table 1c-f).

3.4 | Distance of dispersal

Seeds were typically found less than 10m from the seed station, but the distance was highly left-skewed and the longest recorded

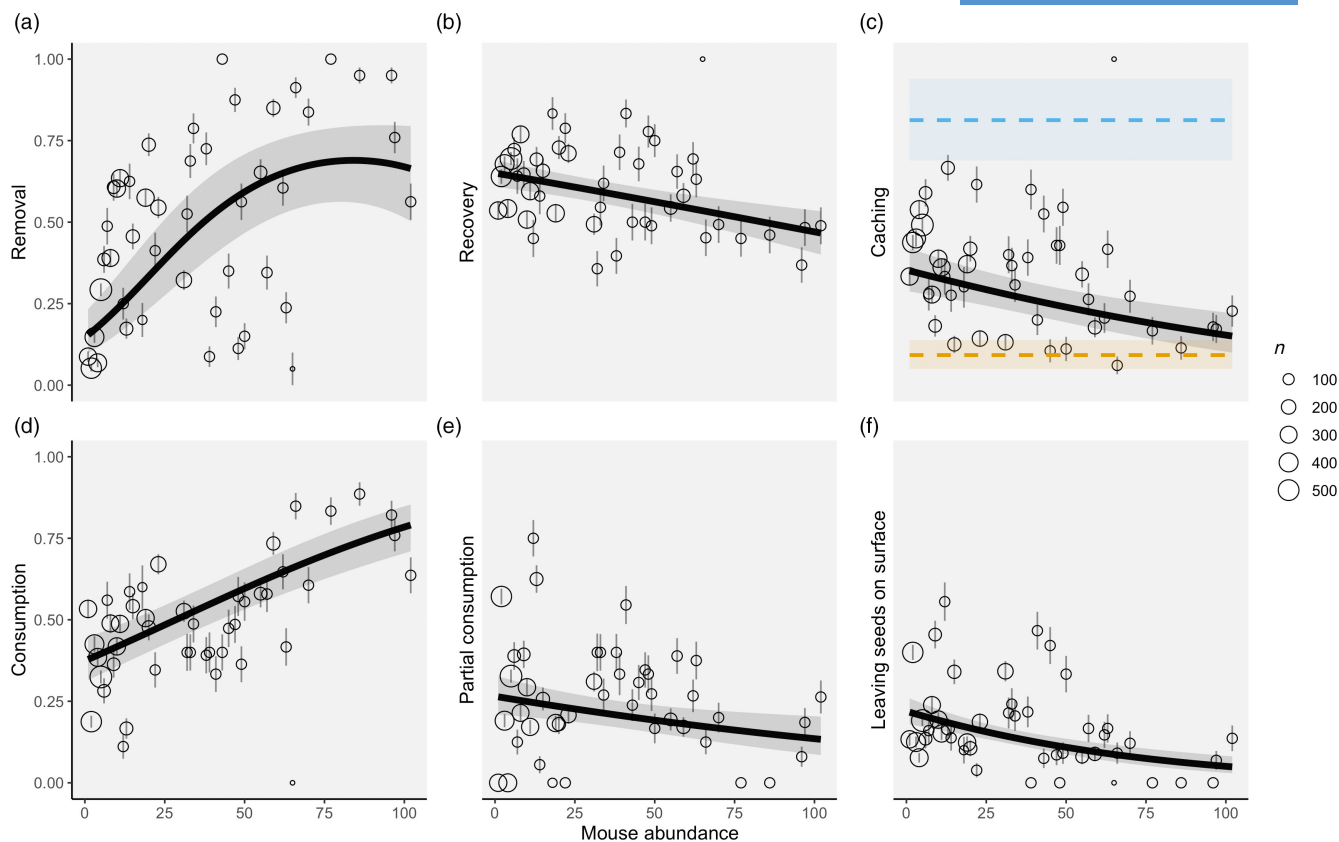


FIGURE 2 Association between the abundance of yellow-necked mice (*Apodemus flavicollis*) and the probability of (a) seed removal, (b) recovering removed seeds, (c) seed caching, (d) seed consumption, (e) partial seed consumption (vs. complete seed consumption), and (f) leaving dispersed seeds on the forest floor. Black lines represent estimates from generalized linear mixed models and grey shading corresponds to 95% confidence intervals. Points are means per given level of mouse abundance, error bars are associated standard errors, and points are scaled to the sample size (number of seed fate recordings) per abundance level. On panel (c), blue line and shading correspond to the \bar{p}_C threshold in 2021 (estimate and 95% confidence intervals), and orange to the \bar{p}_C threshold in 2022.

dispersal distance was 52.2 m. Seed dispersal distance increased with mouse abundance in a nonlinear fashion, more steeply at low and moderate abundances and less steeply at high abundances (Table 1g, Figure 4). In addition, seed dispersal distance increased over time ('Day' effect in Table 1g) and was associated with seed fate. Cached seeds were transported farther relatively to seeds that were left on surface or found eaten (Figure 4).

3.5 | Seedling emergence

Treatment effects (seeds buried vs. on the surface) significantly influenced seedling emergence ($\chi^2=86.5$, $df=1$, $p<0.001$), as did the year of experiment (2021 vs. 2022: $\chi^2=45.3$, $df=1$, $p<0.001$), and the interaction between these factors ($\chi^2=78.6$, $df=1$, $p<0.001$). The advantage of burial was considerably stronger in 2022 than in 2021. Specifically, in 2021, 71% of buried and 58% of surface seeds produced seedlings, whereas in 2022, the seedling emergence rates were 66% for buried seeds and a mere 6% for surface seeds (Figure 5). The estimated mutualism threshold, \bar{p}_C was 0.809 (95% CI: 0.689–0.940) in 2021, but only 0.083 (95% CI: 0.050–0.138) in 2022 (Figure 2c).

4 | DISCUSSION

All aspects of seed fate strongly and predictably shifted with mouse abundance. As the population of scatterhoarders grew, more seeds were harvested and moved farther away, but interactions with seeds became more consumptive and antagonistic. These changes align with our predictions, and with theoretical models emphasizing conspecific abundance as key to scatterhoarder foraging choices (Theimer, 2005; Zwolak et al., 2021, 2024). However, seedling emergence trials showed substantial variability in caching benefits, most likely driven by contrasting weather conditions over 2 years of the experiments. Consequently, both rodent behaviour and environmental factors influenced the patterns of plant–scatterhoarder interactions.

Previous studies of density-dependent dynamics in plant–scatterhoarder interactions focused mostly on the seed-to-rodent ratio, suggested by Theimer (2005) as potentially the ultimate index of competition for seeds. Analytically, however, it is advantageous to separate the seed-to-rodent ratio into its individual elements. Doing so gives a clearer understanding of their influence because both variables simultaneously fluctuate, confounding their impacts. Moreover, each presents inherent measurement challenges, which

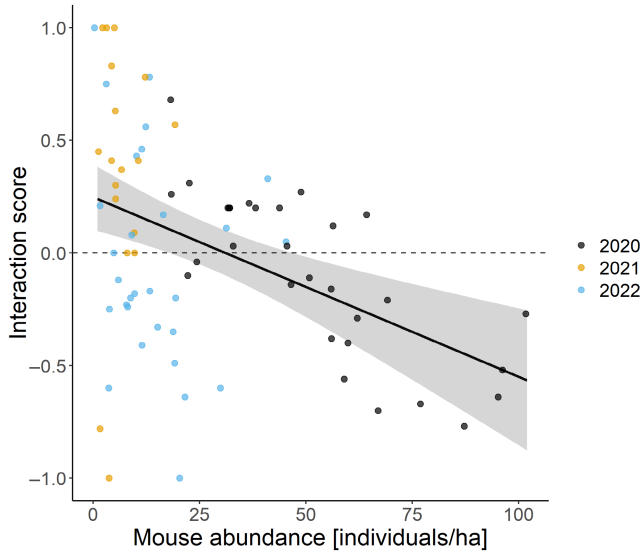


FIGURE 3 Decline in positive interaction events with rodent abundance. The interaction score, plotted on the y-axis, was calculated as the difference between the proportion of positive events (where the seed is deposited alive on the ground or in shallow caches) minus the proportion of negative events (where the seed is consumed or not found, suggesting deep burial in burrows that hinders germination). Each point corresponds to the interaction score obtained from individual trapping sessions ($n=90$ site/trapping session/year combinations), with colours indicating years of occurrence. The prediction line is derived from a binomial family mixed model, and the shading indicates 95% confidence intervals.

are particularly obvious with the involvement of multiple, ecologically diverse rodent species and various seed types with differing sizes and nutritional content. This complexity often leads to convoluted results (e.g. note the conflicting outcomes in Xiao et al., 2013 vs. Theimer, 2001; Yi et al., 2011). In our study, we simplified the system to one predominant granivore and a single seed species. Our experiments, conducted before natural seedfall, varied only in rodent abundance. This set-up provided clear insights into the density dependence of rodent foraging behaviour.

The changes in seed fate observed in this study can be linked to density-dependent competition. When mice were more abundant, seeds appeared more valued. They were less often left on surface after dispersal. They were also consumed more often, and more thoroughly. The risk of cache pilferage was not measured in this study, but both theoretical (Zwolak et al., 2021, 2024) and empirical studies (Dittel & Vander Wall, 2018; Zwolak, Bogdziewicz, Wróbel, et al., 2016) point out that it increases with rodent abundance. This probably explains the positive association between mouse abundance and seed dispersal distance observed in this study: Transporting seeds farther before caching makes them safer (Galvez et al., 2009; Male & Smulders, 2007; Moore et al., 2007). The risk of pilferage is also the most likely driver of the density-dependent decline in seed caching observed in our study (Zwolak et al., 2024). Overall, these changes led to a marked reduction in interaction quality as rodent numbers grew.

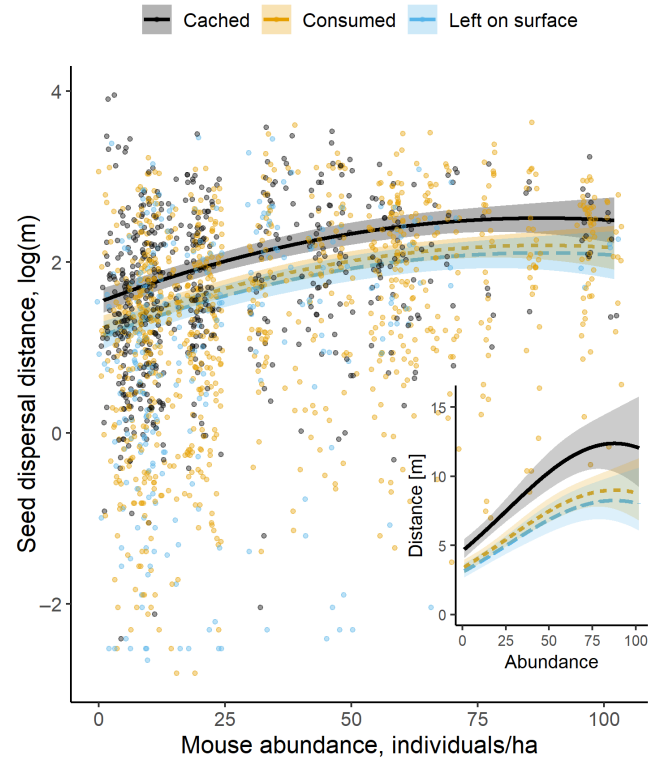


FIGURE 4 Distance of seed dispersal by yellow-necked mice (*Apodemus flavicollis*). Lines represent estimates from generalized linear mixed models for seeds that were found cached, consumed, or left on surface; shading represents 95% confidence intervals; data points are marked by dots. Note log-scaled Y-axis. Back-transformed estimates are presented in the inset.

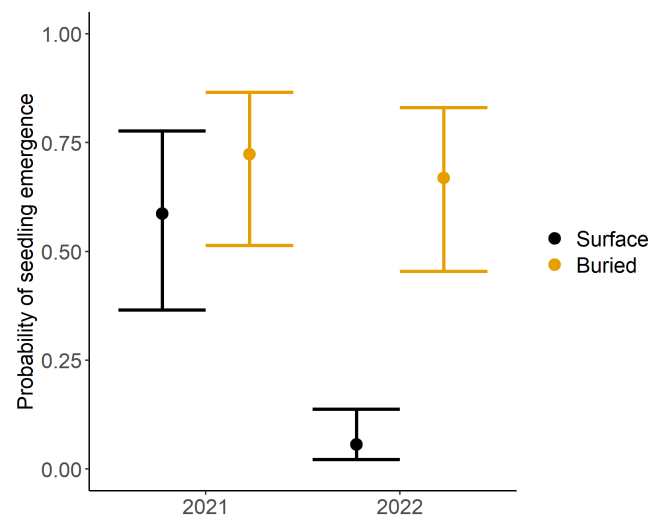


FIGURE 5 Emergence probability of *Quercus robur* seedlings from acorns either buried in shallow caches or left on the litter surface, for the years 2021 and 2022. Estimates are derived from generalized linear mixed models, with whiskers denoting 95% confidence intervals.

The decline in seed recovery rate at higher rodent densities may be due to increased larder-hoarding, driven by greater cache pilferage as rodent numbers rise (Yang & Yi, 2018). Additionally, the

positive correlation between dispersal distances and mouse abundances (Figure 4) could make the recovery more challenging. Such a scenario suggests that our estimates of the association between mouse abundance and seed dispersal distance could be understated. Lastly, with a higher number of seeds being removed when rodents are abundant, finding dispersed seeds becomes more challenging. Labour and time constraints might lead to reduced recovery rates when a large quantity of seeds is removed.

From a plant's perspective, there was one potentially positive side of the high mouse abundance: increased seed dispersal distances. Existing studies on scatterhoarders have established that seed dispersal increases when there are fewer seeds available (Galvez et al., 2009; Jansen et al., 2004; Moore et al., 2007; Puerta-Piñero et al., 2010; Rong et al., 2013 but see Vander Wall, 2002). This increase is a strategic response to reduce the pilferage of scarce, hence more valuable, seeds by minimizing seed clumping (Male & Smulders, 2007; Moore et al., 2007; Wilke et al., 2015). In this study's context, a similar dynamics is likely in play. The high number of potential seed pilferers necessitates greater efforts in seed dispersal, thus increasing the dispersal distance. This expansion in distance could mitigate the negative, distance-dependent seedling mortality known as the Janzen–Connell effect (Connell, 1971; Janzen, 1970). However, this pattern has not been consistently observed in oaks (Bogdziewicz et al., 2020; Deniau et al., 2017; Wróbel et al., 2019). Furthermore, increased seed dispersal distance can be important for colonization of new sites, such as forest gaps, but the direct impact on oak recruitment remains ambiguous. Overall, while the importance of seed dispersal distances is recognized (Spiegel & Nathan, 2007), linking these distances with plant recruitment patterns proved difficult (Schupp et al., 2010).

The intensity of removal and the distance of seed dispersal plateau at very high rodent densities. However, unlike some previous studies, we did not observe a hump-shaped relationship between the quality of seed dispersal (often measured by the likelihood of caching or the proportion of positive interactions) and mouse abundance (Mittelman et al., 2021; Zeng et al., 2021; Zhang et al., 2021). This hump-shaped relationship is also predicted by theoretical models (Zwolak et al., 2021, 2024). According to the models, at very low densities of scatterhoarders, the increased probability of caching does not compensate for the low rate of seed removal, and plant recruitment declines (Zwolak et al., 2024). Our study, however, focussed on seed fate rather than plant recruitment. Thus, determining the impact of rodent abundance on plant recruitment remains an important area for future research.

Some aspects of seed dispersal also varied over time. As the season progressed, there was an increase in the probability of seed removal and the dispersal distance, suggesting that rodents may alter their foraging behaviours to prepare for fall (Rusch et al., 2014; Sunyer et al., 2014). Yet, other aspects of seed dispersal, such as the proportion of cached seeds, remained unchanged. Although we incorporated the timing of acorn experiments into our analysis, the overall effect of time on seed dispersal was relatively

minor compared with the influence of rodent abundance. Abiotic conditions strongly affects the benefits of seed burial (Cordeau et al., 2018; Gómez, 2004). Acorns appear to be less reliant on burial than smaller seeds, like those of beech *Fagus sylvatica* (compare Zwolak, Bogdziewicz, Wróbel, et al., 2016 with Bogdziewicz et al., 2020 and this study), probably because they have more resource reserves and are less susceptible to desiccation. However, our findings suggest that under dry conditions, burial, facilitated by rodents, becomes crucial for the survival and germination of acorns. In 2021, a year with typical weather conditions, the benefits of seed caching were relatively low. In contrast, in the warm and dry 2022, seed burial was vital for seedling emergence. Rodent populations were moderate during this period. The most detrimental scenario is one where poor abiotic conditions, such as drought, coincide with high rodent abundance, and therefore a low incidence of seed caching. Emerging evidence suggests that such scenarios might be more common with climate change, as deficits in soil moisture are amplified (Cook et al., 2018), and the abundance of small mammal possibly increases (Czeszczewik et al., 2020). These changes can lead to scenarios where both poor abiotic conditions and high rodent abundance exacerbate the challenge for seed survival.

The benefits of burial determine the \tilde{p}_c threshold, the lowest proportion of removed seeds that have to be cached and unrecovered to foster mutualism. Yet, in 2021, reaching the \tilde{p}_c threshold was clearly impossible. In 2022, caching probability exceeded the \tilde{p}_c threshold at all mouse density levels, but including cache recovery in our analysis would likely reduce this estimate. Nonetheless, achieving the mutualism threshold seemed feasible in 2022, particularly when rodent populations were low. Thus, we surmise that the activity of mice, which is often negative for oaks (see also Bogdziewicz et al., 2020; Gómez et al., 2008) becomes beneficial when abiotic conditions are particularly challenging.

A notable limitation of our study is the short span of seedling emergence data, limited to just 2 years. Long-term data collection is essential to obtain a distribution of caching benefits. With such data, we could quantify the frequency at which rodents potentially enhance plant recruitment and predict future changes in the frequency of years characterized by mutualistic versus antagonistic interactions. However, even with this limited dataset, it is evident that benefits of burial can widely fluctuate, strongly modifying the dynamics of the plant–scatterhoarder interaction.

In conclusion, our study underscores the impact of rodent abundance on their foraging behaviour and, consequently, the fate of tree seeds. As mouse populations grow, their interactions with seeds became increasingly detrimental to trees. These findings support the notion that reduced rodent numbers indirectly aid plant recruitment, thus revealing the divergent interests of the interaction partners (Zwolak et al., 2024). Trees can foster the advantageous situation of low granivore density by alternating years of high and low seed production (the satiation–starvation cycle of masting: Zwolak et al., 2022). Additionally, external factors such as predators, parasites or diseases that reduce rodent numbers can also benefit plants, as long as they do not lead to scatterhoarder extinction. This

dynamic suggests a strong potential for trophic cascades to improve plant recruitment via better seed dispersal quality. However, the dynamics of rodent–oak interactions are governed not only by a combination of rodent foraging decisions, which vary with their density, but also by the benefits of seed burial, which are greater under stressful abiotic conditions. Thus, our findings reveal how density dependence and abiotic factors work together to shape potentially mutualistic interactions.

AUTHOR CONTRIBUTIONS

Rafał Zwolak planned and designed the research; Paulina Celebias, Milena Zduniak and Aleksandra Wróbel conducted fieldwork; Rafał Zwolak analysed data with assistance from Aleksandra Wróbel and Michał Bogdziewicz; Rafał Zwolak wrote the manuscript draft with input from Aleksandra Wróbel, Michał Bogdziewicz and Milena Zduniak.

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CONFLICT OF INTEREST STATEMENT

Michał Bogdziewicz is an associate editor of *Journal of Ecology* but took no part in the peer review and decision-making processes for this paper. The authors have no other conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14356>.

DATA AVAILABILITY STATEMENT

Data are available from the OSF repository: <https://doi.org/10.17605/osf.io/56m2n> (Zwolak, 2024).

ORCID

Rafał Zwolak  <https://orcid.org/0000-0002-7665-5033>

Paulina Celebias  <https://orcid.org/0000-0001-9916-2904>

Michał Bogdziewicz  <https://orcid.org/0000-0002-6777-9034>

Aleksandra Wróbel  <https://orcid.org/0000-0002-0307-4035>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Fates of common oak (*Quercus robur*) acorns placed in Puszcza Zielonka, Poland, and removed by rodents during 2020–2021. The number of seeds offered varied because in 2021 and 2022, logistical constraints prevented experimentation on all planned nights, and some seed placements were compromised. With the exception of eight acorns in 2020 (4 missing, 2 eaten, 1 partially eaten and 1 cached) and five in 2021 (all missing), which were removed by bank voles (*Myodes glareolus*), all other acorns were taken by yellow-necked mice (*Apodemus flavicollis*). Seeds removed by bank voles are included in this figure, but excluded from the statistical analyses.

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