Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice

Article *in* Journal of Ecology · October 2019

DOI: 10.1111/1365-2745.13307

3 authors, including:

Michał Bogdziewicz
Adam Mickiewicz University

Rafał Zwolak
Adam Mickiewicz University

Received: 13 May 2019 | Accepted: 7 October 2019

DOI: 10.1111/1365-2745.13307

RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice

Michał Bogdziewicz[1] | Elizabeth E. Crone[2] | Rafał Zwolak[1]

[1]Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland

[2]Department of Biology, Tufts University, Medford, MA, USA

Correspondence
Michał Bogdziewicz
Email: michalbogdziewicz@gmail.com

Funding information
Polish National Science Centre, Grant/Award Number: 2015/17/N/NZ8/01565

Handling Editor: Mark Rees

Abstract

1. Numerous interactions between plants and animals vary in their outcome between antagonism and mutualism. Interactions between plants and scatter-hoarding animals provide a prime example of this phenomenon. Scatterhoarders consume large quantities of seeds (potentially reducing plant establishment), yet also disperse seeds and bury them in shallow caches (potentially improving recruitment). Despite intense work on mechanisms that cause these interactions to shift along an antagonism–mutualism continuum, it remains difficult to quantify their final outcomes.
2. We demonstrate how readily available field data can be used to reach this goal, with interactions between rodents and two oaks species (sessile oak *Quercus petraea*, and red oak *Q. rubra*) as an empirical example. Our approach consists of quantifying the net outcome of the interaction through collecting data on different vital rates (e.g. probability that cached seeds survive to germination, probability of seedling recruitment with and without rodents; near and far from conspecific trees; with and without seed pilferage) and assembling them in a simple mathematical model.
3. We found that during the period of the study, interactions between scatter-hoarding rodents and both focal oaks were antagonistic. Even though caching increased the likelihood of seedling establishment, this effect was not strong enough to compensate for the costs of seed predation. Furthermore, there was no evidence that the short-distance transportation that is usually provided by small mammals benefited early oak recruitment.
4. *Synthesis*. Our empirical results demonstrated that certain common assumptions – that caching by rodents invariably benefits plant recruitment; that improved seedling establishment after seed burial is sufficient to make plant–scatterhoarder interactions mutualistic; that transportation away from maternal plants is highly beneficial—do not always hold and should be tested rather than taken for granted.

KEYWORDS

Apodemus flavicollis, conditional mutualism, seed dispersal, seed predation, synzoochory, yellow-necked mouse

1 | INTRODUCTION

Numerous interactions between plants and animals vary in their outcome between antagonism and mutualism (Bronstein, 1994; Palmer et al., 2010). Interactions between plants and scatter-hoarding animals, such as rodents or corvids, are a prime example of this phenomenon because scatterhoarders play a dual role in plant regeneration. On the one hand, they consume large quantities of seeds and reduce plant establishment (Howe & Brown, 2001; Larios, Pearson, & Maron, 2017; Zwolak, Pearson, Ortega, & Crone, 2010). On the other hand, they disperse seeds and bury them in shallow caches, which for some plant species provides the only means of successful recruitment (Asquith, Terborgh, Arnold, & Riveros, 1999; Muñoz & Bonal, 2011; Pesendorfer, Sillett, Koenig, & Morrison, 2016; Vander Wall, 1992). Scatterhoarding is evolutionarily favoured (otherwise, it would not be such a common strategy of seed dispersal: Gómez, Schupp, & Jordano, 2019), but ecologically it can have negative net impacts on plants (Zwolak & Crone, 2012). This disagreement between ecological and evolutionary perspectives deserves resolution. The most promising way to address this dilemma is to understand the mechanisms that determine when scatterhoarding is and is not favourable.

Whether seed dispersal and caching by granivores are beneficial or detrimental for plant populations depends on whether recruitment with granivores is greater or less than recruitment without granivores (Jansen & Forget, 2001; Longland, Jenkins, Vander Wall, Veech, & Pyare, 2001; Schupp, Jordano, & Gómez, 2010; Theimer, 2005; Zwolak & Crone, 2012). This principle is simple, but evaluating it in the field is challenging. One approach is to build up the net outcome from separately measured components (Zwolak & Crone, 2012). This kind of approach is similar to predicting population dynamics from separately measured vital rates (e.g. Morris & Doak, 2002) but has been used less often to evaluate species interactions. Intuitively, when the benefits provided by seed dispersal are high, plants can bear higher costs in the form of seed consumption. Following on this notion, the benefits of scatterhoarding outweigh the costs of seed predation when the probability of caching and not retrieving cached seeds exceeds the ratio of seedling emergence from surface to seedling emergence from caches.

To briefly review our past use of this approach (Zwolak & Crone, 2012), we started from the premise that granivores are beneficial when plant recruitment in the presence of granivores is greater than plant recruitment in the absence of granivores. This inequality is written in mathematical terms as follows:

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

where e_S is the seedling emergence from surface, p_H is the proportion of seeds harvested by granivores, p_C is the probability that seeds will be cached and left uneaten, and e_C is the seedling emergence from caches. In studies of plant–granivore interactions, it is much easier and more common to measure the seedling emergence rates (e_S and e_C) than the caching rates (p_H and p_C; see Zwolak & Crone, 2012). Therefore, to compare the role of granivores across studies, Zwolak and Crone (2012) rearranged the equation to calculate the minimum value of p_C that would be necessary for granivores to increase plant recruitment:

$$p_c > \frac{e_s}{e_c} \tag{2}$$

Thus, granivores help plant recruitment when the proportion of buried and uneaten seeds exceeds a threshold value (hereafter $\tilde{p}_C$, after Zwolak & Crone, 2012, to distinguish it from empirical p_C values) determined by the seedling emergence ratio, that is, the benefits of seed burial.

Scatterhoarders not only bury the seeds in the topsoil but also move them away from the parent plant. This behaviour also modifies recruitment probability, with effects that are usually thought to be positive, due to colonization of ephemeral microsites or escape from distance- and density-dependent mortality ('Janzen-Conell effect'; Comita, Muller-Landau, Aguilar, & Hubbell, 2010; Fricke, Tewksbury, & Rogers, 2014; Jansen, Bongers, & Van Der Meer, 2008; Johnson, Beaulieu, Bever, & Clay, 2012). However, the effects can also be negative, for example, when habitat quality is autocorrelated, it often declines with distance from maternal plants (Condit, Engelbrecht, Pino, Perez, & Turner, 2013; John et al., 2007). Furthermore, distance to the seed source may alter rodent foraging activity and seed predation rates through changes in local seed availability (Gálvez, Kranstauber, Kays, & Jansen, 2009; Stapanian & Smith, 1984). Nonetheless, even though factors shaping dispersal distance by scatterhoarders, especially by rodents, are extensively studied (Jansen, Bongers, & Hemerik, 2004; Lichti, Steele, & Swihart, 2017; Moore, McEuen, Swihart, Contreras, & Steele, 2007; Sunyer, Espelta, Bonal, & Muñoz, 2014; Xiao, Zhang, & Wang, 2005), the actual influence of dispersal distance on recruitment probability is seldom quantified. The intertwined benefits of burial and transportation constrain our ability to understand mechanisms that drive the ecological interactions between plants and scatterhoarders.

Here, we use empirical data to illustrate an approach for separating benefits of burial and benefits of transportation by scatterhoarders on plant recruitment (note that we do not address here the benefits of seed transport that do not translate into increased recruitment, such as providing gene flow: Gelmi-Candusso, Heymann, & Heer, 2017). We used two oak species as a model system: sessile oak (*Quercus petraea*) and northern red oak (*Quercus rubra*). *Quercus petraea* is the dominant native oak in Central European forests. *Q. rubra* was introduced to European forests from North America in the 17th century as an ornamental species (Bogdziewicz et al., 2018; Woziwoda, Kopec, & Witkowski, 1998; Woziwoda, Potocki, et al., 2014). For both oaks, the primary means of reproduction is thought to be abandonment of seed caches made by scatter-hoarding rodents and birds (den Ouden, Jansen, & Smit, 2005; Kurek, Dobrowolska, & Wiatrowska, 2019;

Myczko, Dylewski, Zduniak, Sparks, & Tryjanowski, 2014; Steele, 2008). Nonetheless, whether benefits of burial and transportation exceed the costs imposed by seed predation has never been experimentally evaluated (and in fact, experimental approaches are rarely used to address this issue in scatter-hoarding systems). We conduct this evaluation using the estimates of caching probability, probability of seed survival in the caches, and seedling establishment probability obtained in field experiments and the modelling framework developed by Zwolak and Crone (2012) to place the focal interactions at the antagonism–mutualism continuum. However, the original model did not include the potential changes in caching benefits driven by seed pilferage (Steele et al., 2013; Sunyer, Boixadera, Muñoz, Bonal, & Espelta, 2015; Zwolak, Bogdziewicz, Wróbel, & Crone, 2016). Therefore, as part of this paper, we extend the logic of the $\tilde{p}_C$ calculation to include pilferage.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

We established four study sites in *Q. petrea*–*Q. rubra* mixed forests in Drawieńska Forest (longitude: 52.931, latitude: 15.988), western Poland. The sites were spaced 1–15 km from each other. This area is located in the temperate climate zone, with average annual precipitation of 592 mm and mean monthly temperature ranging from 17°C in July to −2°C in January. These mixed forests are comprised almost exclusively of the two oak species (*Q. petraea* and *Q. rubra*), with occasional individuals of *Q. robur*, *Carpinus betulus* and *Fagus sylvatica*. The understory is poorly developed, with some patches of *Rubus* sp. and *Urtica dioica*, and seedlings of oaks and beech. Oak acorns are relatively large (average mass; *Q. petraea* 1.26 g., *Q. rubra*: 2.85 g.) and are readily dispersed and eaten by small mammals (Bogdziewicz, Lichti, & Zwolak, 2019; den Ouden et al., 2005). As revealed by camera traps, small mammals at our study sites were dominated by *Apodemus* sp., most likely *A. flavicollis*, a seed specialist (Gasperini, Bonacchi, Bartolommei, Manzo, & Cozzolino, 2017; Selva, Hobson, Cortés-Avizanda, Zalewski, & Donázar, 2012).

To quantify effects of acorn burial on seedling emergence, we conducted seed addition experiments. We fully crossed three treatments: rodent exclusion/rodent access, seed buried/seed sown on surface and distance from the adult plant. To do so, we randomly chose 12 *Q. petraea* trees (3 per site) and 12 *Q. rubra* trees (3 per site). We added acorns of the focal species in 20 × 20 × 20 cm wire mesh cages (five acorns per cage). Cages were buried ~5 cm into the ground in sets of four. In half of the cages we buried acorns 1–2 cm into the ground and in the other half we placed acorns at the top of the litter layer and covered them with leaves to mimic autumn leaf fall. This treatment (burial/sowing on surface) was crossed with rodent exclusion: in half of the cages, we cut 8 × 8 cm holes to allow rodent access; the other half remained closed to exclude rodent foraging. A comparison of seedling recruitment from acorns that were buried versus placed on surface allowed us to estimate burial-dependent benefits of rodent seed dispersal. Rodent exclusion allowed us to estimate seed pilferage by comparing recruitment of buried acorns in open versus closed cages.

To address the benefits of seed transportation, the above-described cage sets were placed along transects. Under each tree, we established a transect along one cardinal direction, aiming to maximize the distance of the transect to other conspecifics. This was done assuming that rodents tend to carry and cache seeds towards areas of lower conspecific seed density (Hirsch, Kays, Pereira, & Jansen, 2012; Stapanian & Smith, 1984; Steele et al., 2013; Yang, Zhang, & Yi, 2016). Thus, our estimates of transportation benefits may be overly positive, if such directed dispersal does not occur in our system. We placed five sets of cages at each transect. We used tree crown as a reference point and buried one set of cages directly underneath the crown border, another set 5 m towards the tree trunk (underneath the crown), and the remaining three sets every 5 m in the opposite direction. We used 25 m as the maximum evaluated distance because acorn-tracking experiments report that the vast majority of acorns transported by rodents are cached within that radius (Bogdziewicz, Crone, Steele, & Zwolak, 2017; den Ouden et al., 2005; Muñoz & Bonal, 2011; Xiao et al., 2005). This includes our preliminary tracking studies at the same forest, where the mean dispersal distance by rodents for both focal oaks is <3 m. We set up experimental cages in October 2016 and quantified seedling establishment in August 2017. Seeds for the experiment were locally collected. The overall sample size equalled 2,400 acorns (480 seedling cages).

2.2 | Statistical analysis

To test how acorn burial, distance from the tree and rodent foraging affect seedling establishment, we built a separate generalized linear mixed model (GLMM) for each oak species. We used nested random effects of cage set, tree, study site, logit link and binomial family error distribution, and implemented the models via lme4 package in R (Bates, Maechler, Bolker, & Walker, 2015). In each model, we used proportion of established seedlings as the response variable, and burial (surface vs. sowed), rodent access (excluded vs. allowed) and distance from the tree as fixed effects. We also included all possible two-way interaction terms between fixed effects, and the three-way interaction (which was removed when non-significant). We calculated marginal (i.e. the proportion of variance explained by fixed effects) and conditional (i.e. the proportion of variance explained by fixed and random effects) R^2 for GLMMs using the 'MuMIn' package (Bartoń, 2016; Nakagawa & Schielzeth, 2013).

2.3 | Calculating the $\tilde{p}_C$ threshold and the effects of seed pilferage

We evaluated how the interactions between rodents and oaks are placed along the antagonism–mutualism continuum (Zwolak & Crone, 2012). The $\tilde{p}_C$ threshold was calculated as a ratio of emergence from seeds sown on surface versus emergence from buried seeds, both with rodents excluded. Seed pilferage was gauged as the ratio of seedling recruitment from buried seeds in open versus closed cages. Implicitly, the original definition of the proportion of

seeds buried and uneaten (p_c) combined three processes (Zwolak & Crone, 2012): the probability that a seed is buried, the probability it is eaten by the cache owner and the probability it is pilfered:

$$p_C = p_{\text{cached}} \times (1 - p_{\text{eaten by cache owner}}) \times (1 - p_{\text{pilfered}}) \quad (3)$$

where p_{cached} is the probability a seed is buried by a rodent, p_{eaten} by cache owner is the probability of retrieval by individuals responsible for seed burial and p_{pilfered} is the probability of retrieval by pilferers. The $\tilde{p}_C$ threshold is the minimum value of p_c when the benefits for plants balance the costs of seed consumption. Thus, if the threshold is determined by the proportion of seedling emergence from surface-placed acorns, e_s (estimated with data on seedling emergence from seeds sown on surface in closed cages) to emergence from caches, e_c (i.e. by benefits of burial, estimated with data on seedling emergence from seeds buried in closed cages), that is,

$$\tilde{p}_C = \frac{e_S}{e_C}$$

then the equation can be expanded to show the effects of pilferage:

$$p_{\text{cached}} \times (1 - p_{\text{eaten by cache owner}}) \times (1 - p_{\text{pilfered}}) = \frac{e_S}{e_C}$$

and rearranged to include only the unknown proportion of seeds buried and uneaten by the cache owner:

$$\tilde{p}_{CO} = p_{\text{cached}} \times (1 - p_{\text{eaten by cache owner}}) = \frac{e_S}{e_C(1 - p_{\text{pilfered}})} \quad (4)$$

In the above equation, $\tilde{p}_{CO}$ is the minimum beneficial proportion of seeds buried and uneaten by the *cache owner*, and all other parameters are as defined above. In other words, the $\tilde{p}_{CO}$ threshold defines the burial benefits while taking into account cache pilferage by other granivores in the community. The pilfered seeds can be consumed or re-cached and possibly pilfered again (Jansen et al., 2012; Vander Wall & Joyner, 1998); thus, our model does not assume that their survival rate is 0, but that a constant fraction is consumed after pilferage (see Online Supplement).

Confidence intervals for these parameters (e_s, e_c and $\tilde{p}_C$) 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. We repeated the calculations of $\tilde{p}_C$ and $\tilde{p}_{CO}$ for both near the conspecific probability of seedling establishment, that is, seedling establishment rate estimated at 0 m distance, and far at 25m distance. Estimated probabilities of establishment were derived from the above-described GLMMs.

The empirical p_{CO} value (the ultimate probability that an acorn will be cached and not retrieved, accounting for retrieval by the entire granivore community) for both oak species was derived from a parallel study investigating rodent seed dispersal of the focal oaks, that is, 17% for *Q. rubra* and 2% for *Q. petrea* (Bogdziewicz et al., 2019).

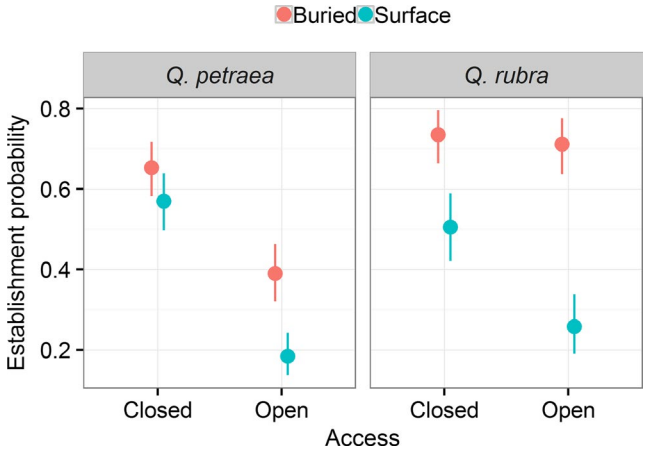

FIGURE 1 Probability of seedling establishment of *Quercus petraea* and *Quercus rubra* in closed (rodent access excluded), and open (rodent access allowed) cages. 'Sowed' indicates acorns buried 1–2 cm in the soil, while 'surface' indicates acorns placed on soil surface and covered with leaves to mimic autumn leaf fall. Whiskers indicate standard errors

3 | RESULTS

3.1 | Effects of acorn burial

Acorn burial enhanced seedling establishment in both species, although it was less beneficial for *Q petraea* than for *Q. rubra* (Figure 1). In *Q. petraea*, when rodents had access, acorn burial increased establishment probability two-fold (open cages, surface vs. buried acorns: 18% vs. 39%). This effect was considerably weaker when rodents were excluded (closed cages, 57% for acorns on the surface vs. 65% for buried acorns; rodent exclusion × burial interaction in Table 1a, Figure 1). Similarly, burial increased establishment probability almost three-fold in *Q. rubra* (open cages: 25% vs. 71%, Figure 1). This effect was weaker when rodents were excluded (50% vs. 73%; rodent exclusion × burial interaction in Table 1b). The finding that the difference between seedling establishment from buried and surface acorns was larger in the rodent access treatment than in the rodent exclusion treatment indicates that burial enhanced establishment mainly through reducing acorn removal.

3.2 | Pilferage rates

Pilferage rates were higher in *Q. petraea* than in *Q. rubra*. In *Q. petraea*, seedling establishment from buried acorns was 1.5 times higher when rodents were excluded (39% in open vs. 65% in closed cages). In *Q. rubra*, burial provided almost complete protection from pilferage (open vs. closed cages: 71% vs. 73%). Note that the percentage estimates are the model intercepts and decreased with distance from the tree in some treatments (see below).

3.3 | Effects of transportation

We did not detect any transportation-related benefits of seed dispersal and the oak species did not differ in this regard. In fact, seedling

TABLE 1 Effects of burial, distance from the parent tree and rodent access on the seedling establishment probability of focal oaks

Fixed effect	Estimate	*SE*	*z*	*p*
(A) Sessile oak *Quercus petraea*				
Intercept (rodent access allowed, burial: surface)	−1.49	0.35	−4.23	<.001
Rodents excluded	1.77	0.33	5.31	<.001
Burial: cached	1.04	0.33	3.10	.001
Distance	−0.06	0.02	−2.16	.03
Rodents excluded × Burial: cached	−0.67	0.31	−2.19	.03
Rodent excluded × Distance	0.04	0.02	1.82	.07
Burial: cached × Distance	0.04	0.02	2.03	.04
(B) Northern red oak *Quercus rubra*				
Intercept (rodent access allowed, burial: surface)	−1.06	0.39	−2.71	.006
Rodents excluded	1.09	0.37	2.95	.003
Burial: cached	1.97	0.36	5.36	<.001
Distance	−0.10	0.03	−3.75	<.001
Rodents excluded × Burial: cached	−0.97	0.33	−2.94	.003
Rodent excluded × Distance	0.06	0.02	2.88	.004
Burial: cached × Distance	0.03	0.02	1.21	.22

Note: The marginal R^2 of the model for *Quercus petraea* was 0.28 and the conditional value was 0.34. For *Q. rubra*, the marginal R^2 of the model was 0.33 and the conditional value was 0.38

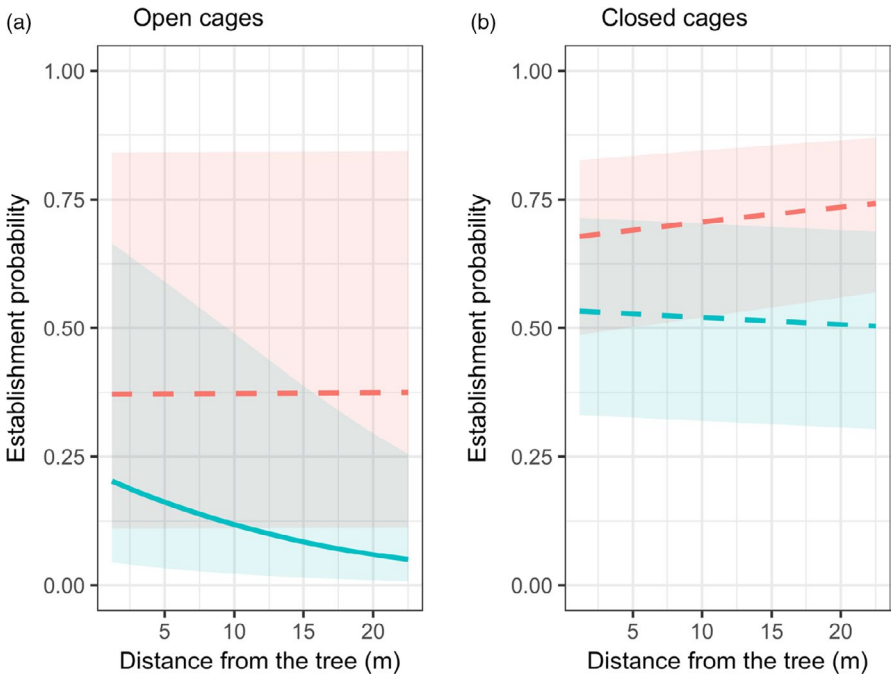

FIGURE 2 Probability of seedling establishment of *Quercus petraea* as a function of distance from the mother tree. Open cages indicate rodent access and closed cages indicate rodent exclusion. Red lines indicate acorns buried in topsoil and blue lines indicate those placed on soil surface. The solid line indicates a relationship significantly different from 0 and the dashed lines indicate a non-significant relationship. Shaded areas indicate 95% confidence intervals

establishment probability decreased with distance from the focal tree (Table 1, Figures 2 and 3). This phenomenon was caused by an increase in acorn removal, as we detected distance-related decrease in seedling establishment only in open cages. In *Q. petraea*, increased removal was apparent only when acorns were sown on the surface (Table 1a, Figure 2). Pilferage of buried acorns did not differ with distance from the tree in this species (Figure 2). In *Q. rubra*, this effect occurred both for acorns that were buried and those that were left on the surface (Figure 3).

3.4 | Combining the effects to estimate the net outcome

Estimated $\tilde{p}_{CO}$ values (the minimum beneficial proportion of seeds buried and uneaten *by cache owners*, i.e. those taking into account loses due to cache pilferage) equalled 1.21 (95% CI: 0.86–1.79) for *Q. petraea* (both near and far from the tree), and 0.69 (95% CI: 0.46–0.97) in *Q. rubra* near, and 1.24 (95% CI: 0.77–1.99) in *Q. rubra*

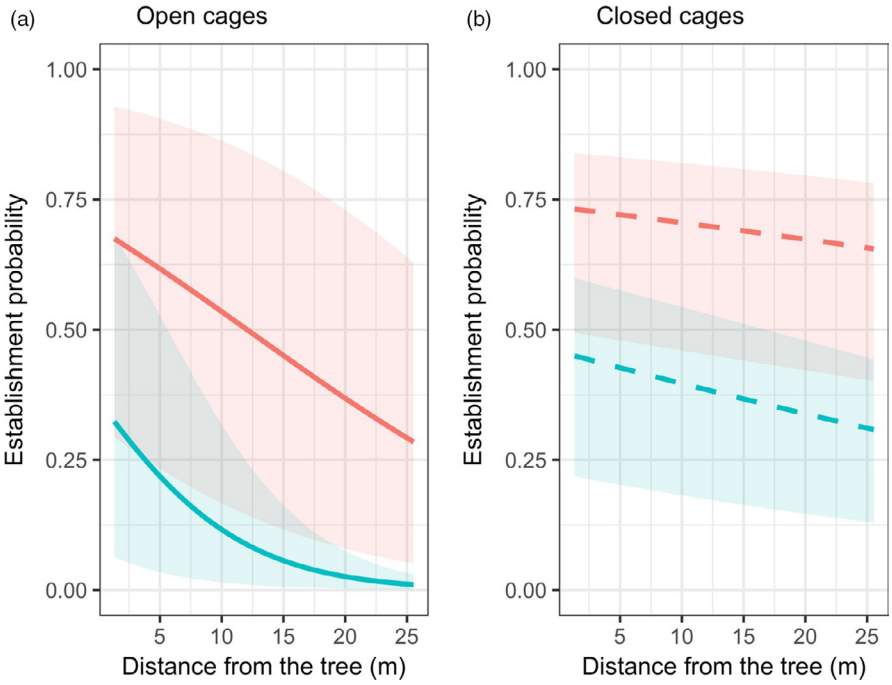

FIGURE 3 Probability of seedling establishment of *Quercus rubra* as a function of distance from the mother tree. Symbols, lines and shading are the same as in Figure 2

far from the tree (Figure 4). Note that the $\tilde{p}_{CO}$ value for *Q. petraea* does not differ with distance because the pilferage rates were distance-independent (Figure 2a). These values are either impossible to reach (when they exceed 1) or would require almost all cached acorns to be never retrieved to approach the mutualism parameter space of the interaction (Figure 4). Thus, observed interactions between scatterhoarders and oaks in our study system were antagonistic.

A fraction of pilfered acorns could be re-cached rather than consumed (Jansen et al., 2004; Perea, San Miguel, & Gil, 2011). If once a seed is pilfered its fate in terms whether it is eaten or re-cached is similar to the fate of seeds collected for the first time (Jansen et al., 2004), then the consequences of seed burial depend on the number of rounds of re-caching (see Figure S1). Nonetheless, for the parameters observed in our system, re-caching of pilfered acorns would not affect the conclusion that scatterhoarders acted antagonistically in their interactions with oaks (Figure S1).

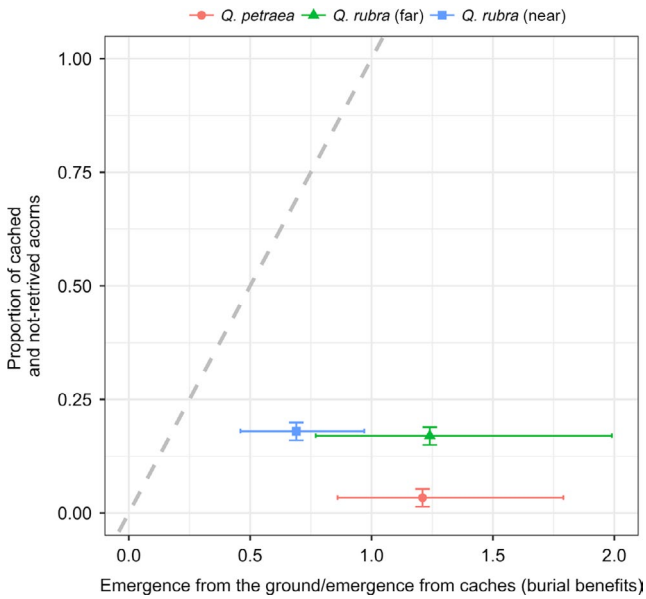

FIGURE 4 Classification of oak–granivore interactions based on the probability of caching and not retrieving seeds, and the ratio of seedling emergence from the ground to emergence from caches. The net effect of granivores is beneficial at any point above the dotted grey line and antagonistic at any point below it. The 'far' and 'near' categories indicate the establishment ratio calculated based on the seedling establishment rate estimated at distances of 0 m (near) and 25 m (far). For *Quercus petrea*, the ratio components did not differ with the distance from the seed source tree (see Figure 2). The values on *y*-axis (proportion of acorns cached and not retrieved) are derived from another study conducted in the same forest (Bogdziewicz et al., 2019)

4 | DISCUSSION

Our study is the first to separate and directly quantify the two of the most important services provided to plants by their rodent partners: seed transportation away from parent plants and seed burial in topsoil. Our results suggest that widely accepted distance-dependent benefits of transportation can be smaller than expected. Moreover, they demonstrate that even relatively large improvements in seedling establishment after seed burial do not necessarily outweigh the costs of seed predation. Finally, and most generally, our study illustrates a straightforward empirical approach that can be used to evaluate the ambiguous role of scatter-hoarding granivores in plant recruitment.

This approach consists of quantifying the net outcome of an interaction through assembling different parameters piecewise with a simple mathematical model. This method, although used

here to a specific plant-scatterhoarder dataset, is very general: in fact, it is analogous to building population models with separately measured vital rates (e.g. Caswell, 2001; Morris & Doak, 2002). Similarly, just like other ecological models, it is a simplification that can be made more realistic by adding additional information (see, e.g., Maron & Crone, 2006; Ehrlén, Morris, von Euler, & Dahlgren, 2016 in a demographic context). Here we used data on probability of seedling recruitment with and without rodents (through rodent exclusion); near and far from adult conspecifics (through evaluating seedling establishment near and far from parent trees); with and without seed pilferage (through including fate of pilferage seeds into the model, and estimating the probability of pilferage). Possible future extensions of our seed-scatterhoarder model include, for example, effects of temporal variability, comparisons of long-term seedling survival near and far from the parent tree or effects of directed dispersal of seeds into particularly favourable microsites (see below).

Scatter-hoarding rodents reduced recruitment of focal oak species during the period of our study. Acorn burial increased the likelihood of seedling establishment, but seedling establishment of unburied acorns in the absence of small mammal foraging was high for both species. Finally, burial benefits were too small to override the costs of seed predation (Zwolak & Crone, 2012). In fact, even if the probability of seedling establishment of buried acorns were 100%, the p_{CO} value would be 0.57 for *Q. petraea* and 0.50 for *Q. rubra*. This level of survival of buried acorns appears unlikely, as reported values commonly range from 1% to 20% (Bogdziewicz, Crone, et al., 2017; Gómez, Puerta-Pinero, & Schupp, 2008; Vander Wall & Joyner, 1998; Vander Wall, 2002; Wróbel & Zwolak, 2017; Xiao, Zhang, & Krebs, 2013). Therefore, while it is still best for an acorn to be buried and forgotten, presence of small mammals did not help recruitment of oaks in our system.

We note that the balance of benefits and costs in conditional mutualisms typically changes over time (Klinger & Rejmánek, 2010; Theimer, 2005; Zwolak et al., 2016) and our study was conducted during a relatively short time frame (1 year). It is possible that fluctuating environmental conditions (e.g. years with droughts or severe winters) increase the benefits of acorn burial and shift the oak–rodent relationship towards mutualism. This possibility is supported by previous studies that have reported higher benefits of burial in oaks (García, Bañuelos, & Houle, 2002; Kollmann & Schill, 1996; Sawaya, Goldberg, Steele, & Dalgleish, 2018; Xia, Tan, Turkington, Hu, & Zhou, 2016). Indeed, both oak species in our study exhibit mast years (Bogdziewicz, Szymkowiak, et al., 2017; Sork, Bramble, & Sexton, 1993), which, in turn, drive fluctuations in small mammal population abundance and may create satiation effects, both at the source tree and after acorn burial (Kelly, 1994; Xiao et al., 2013; Zwolak et al., 2016). Yet, the potential increase in cache survival caused by the satiation is unlikely to counterbalance the costs of seed predation, unless it is accompanied by environmental changes that increase the benefits of seed burial. Thus, an interesting venue for future studies would be to quantify temporal variation in oak–scatterhoarder interactions.

The patterns of seedling establishment suggest that rodent foraging is a strong filter of oak spatial recruitment at our study site. When rodents were excluded, distance from the tree did not change the probability of seedling establishment in either species. However, when rodent foraging was allowed, the seedling establishment rate was highest near adult trees, indicating that locally dense seed shadows may allow a higher proportion of undispersed seeds to survive and germinate. In addition, distance to adult trees influenced pilferage of buried acorns in a species-specific manner. In *Q. petraea*, the pilferage did not change with distance from the tree, while it decreased with distance in *Q. rubra*. This difference suggests that ambient seed density has a stronger effect on cache pilferage rates in *Q. rubra* than in *Q. petraea* (Gálvez et al., 2009). Because we did not measure seed shadows, however, this pattern might have resulted from other factors such as a larger crop size of *Q. rubra* at the time of our experiments.

Animal dispersers often provide several different services that are not of equal value for their partner plants, and the benefits provided by each are rarely separated. The few studies that have done so demonstrate how distinguishing between types of service can change the way we think about particular interactions. For example, birds that disperse chili peppers (*Capsicum chacoense*) remove pathogens from the dispersed seeds (condition-related benefit) and transport seeds far from parent plants (distance-related benefit). However, only gut passage enhances seed survival (Fricke et al., 2013). A similar situation was reported for Iberian pears (*Pyrus bourgaeana*), where pulp removal was more important than transportation distance for plant recruitment (Fedriani, Żywiec, & Delibes, 2012). By disentangling the role of burial (condition-related benefit) from transportation (distance-related benefit) in oak–scatterhoarders interactions, our study demonstrated that acorn burial was the main benefit of this interaction, at least during the period of our study. The lack of transportation benefits is possibly unsurprising because in locally common plant species, the benefits should disappear when the species become so common that their predator and pathogen communities become functionally uniform across the landscape (Fricke et al., 2013; Garzon-Lopez et al., 2015; Janzen, 1971; Schupp, 1992). This is likely the case in our system because *Q. petrea* and *Q. rubra* dominate forest stands. Our results suggest that the generally greater establishment of some species far from parent plants may be due to distance-independent benefits of burial rather than distance-dependence per se. In other words, intertwined burial and transportation may create a false-positive effect of distance, while it is only burial that helps recruitment (as in our system). This calls for increased attention to condition-dependent benefits of seed dispersal, which have been often overlooked as researchers focused on dispersal distance and final location of seeds (Fricke et al., 2013).

As a potential caveat, Janzen-Connell effects are stronger at the seedling than seed-to-seedling stage (Comita et al., 2014), which means that benefits of seed transportation by rodents might appear at later stages of a plant's life cycle. However, several studies that evaluated distance-dependent survival rates at the seedling stage in temperate oaks did not find such an effect (Comita et al., 2014; Reinhart, Johnson, & Clay, 2012). Furthermore, directed dispersal increases the likelihood of colonization of microhabitats that are

favourable for germination and establishment (Steele et al., 2013; Yi, Liu, Steele, Shen, & Liu, 2013). Although such effects are not reported for the oaks in this study, our experimental design could underestimate these effects and thus, benefits of acorn transportation by scatter-hoarding rodents. Finally, although rodent dispersal distance is usually short, *Apodemus* mice can carry seeds >100 m (Perea et al., 2011) and tropical rodents can carry seeds even further (Jansen et al., 2012). We do not exclude the possibility that such rare dispersal events could be more beneficial for seedling establishment than the typical short-distance dispersal evaluated here. This could be an interesting avenue for future research.

To conclude, we presented simple means by which the outcomes of conditional plant–scatterhoarder interactions can be classified. The strength of our approach lies in its versatility: it uses mathematics to combine different types of data and can be easily modified to incorporate new information when data on other parameters becomes accessible. Our empirical results demonstrated that certain common assumptions—that scatterhoarding by rodents invariably improves plant recruitment; that improved seedling establishment after seed burial is sufficient to make plant–scatterhoarder interactions mutualistic; that transportation away from maternal plants is highly beneficial—do not always hold and should be tested rather than taken for granted.

ACKNOWLEDGEMENTS

We thank Nadleśnictwo Krzyż Wlkp for the permission to conduct the study. Kinga Stępniak, Agnieszka Amborska-Bogdziewicz and Jan Bogdziewicz helped during the field work, and Anna and Bogusław Bogdziewicz provided logistical assistance. Dawid Manyś provided invaluable assistance during field site selection. Douglas Levey improved the manuscript with helpful comments. The study was supported by the (Polish) National Science Centre grant 'Preludium' no. 2015/17/N/NZ8/01565. The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.B., R.Z. and E.E.C. conceived and designed the study; M.B. collected the data; M.B., R.Z. and E.E.C. analysed the data; M.B. and R.Z. wrote the manuscript, and all authors contributed substantially to the revising of the paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2jm63xsjh (Bogdziewicz et al. 2019).

ORCID

Michał Bogdziewicz https://orcid.org/0000-0002-6777-9034
Elizabeth E. Crone https://orcid.org/0000-0002-5287-221X
Rafał Zwolak https://orcid.org/0000-0002-7665-5033

REFERENCES

Asquith, N. M., Terborgh, J., Arnold, A. E., & Riveros, C. M. (1999). The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. *Journal of Tropical Ecology*, *15*, 229–235.

Bartoń, K. (2016). MuMIn: Multi-Model Inference. R package version, 1.15.6. Retrieved from https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bogdziewicz, M., Bonal, R., Espelta, J. M., Kalemba, E. M., Steele, M. A., & Zwolak, R. (2018). Invasive oaks escape pre-dispersal insect seed predation and trap enemies in their seeds. *Integrative Zoology*, *13*, 228–237. https://doi.org/10.1111/1749-4877.12285

Bogdziewicz, M., Crone, E. E., Steele, M. A., & Zwolak, R. (2017). Effects of nitrogen deposition on reproduction in a masting tree: Benefits of higher seed production are trumped by negative biotic interactions. *Journal of Ecology*, *105*, 310–320. https://doi.org/10.1111/1365-2745.12673

Bogdziewicz, M., Crone, E. E., & Zwolak, R. (2019). Data from: Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? an example with oaks and yellow-necked mice. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.2jm63xsjh

Bogdziewicz, M., Lichti, N. I., & Zwolak, R. (2019). Consumer-mediated indirect interaction with a native plant lowers the fitness of an invasive competitor. *Journal of Ecology*, *107*, 12–22. https://doi.org/10.1111/1365-2745.13023

Bogdziewicz, M., Szymkowiak, J., Kasprzyk, I., Grewling, L., Borowski, Z., Borycka, K., … Ziemianin, M., et al. (2017). Masting in wind-pollinated trees: The role of weather and pollination dynamics in driving seed production. *Ecology*, *98*, 615–2625. https://doi.org/10.1002/ecy.1951

Bronstein, J. L. (1994). Conditional outcomes in mutualistic interactions. *Trends in Ecology & Evolution*, *9*, 214–217. https://doi.org/10.1016/0169-5347(94)90246-1

Caswell, H. (2001). *Matrix Population Models*, 2nd ed.. Sunderland, MA: Sinauer Associates Inc.

Comita, L. S., Muller-Landau, H. C., Aguilar, S., & Hubbell, S. P. (2010). Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, *329*, 330–332. https://doi.org/10.1126/science.1190772

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., … Zhu, Y. (2014). Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance-and density-dependent seed and seedling survival. *Journal of Ecology*, *102*, 845–856. https://doi.org/10.1111/1365-2745.12232

Condit, R., Engelbrecht, B. M. J., Pino, D., Perez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 5064–5068. https://doi.org/10.1073/pnas.1218042110

den Ouden, J., Jansen, P. A., & Smit, R. (2005). Jays, Mice and Oaks: Predation and Dispersal of Quercus robur and Q. petraea in Northwestern Europe. Seed Fate: Predation, dispersal, and seedling establishment: 223.

Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, *104*, 292–305. https://doi.org/10.1111/1365-2745.12523

Fedriani, J. M., Żywiec, M., & Delibes, M. (2012). Thieves or mutualists? Pulp feeders enhance endozoochore local recruitment. *Ecology*, *93*, 575–587. https://doi.org/10.1890/11-0429.1

Fricke, E. C., Simon, M. J., Reagan, K. M., Levey, D. J., Riffell, J. A., Carlo, T. A., & Tewksbury, J. J. (2013). When condition trumps location: Seed

consumption by fruit-eating birds removes pathogens and predator attractants. *Ecology Letters*, *16*, 1031–1036. https://doi.org/10.1111/ele.12134

Fricke, E. C., Tewksbury, J. J., & Rogers, H. S. (2014). Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. *Ecology Letters*, *17*, 593–598. https://doi.org/10.1111/ele.12261

Gálvez, D., Kranstauber, B., Kays, R. W., & Jansen, P. A. (2009). Scatter hoarding by the Central American agouti: A test of optimal cache spacing theory. *Animal Behaviour*, *78*, 1327–1333. https://doi.org/10.1016/j.anbehav.2009.08.015

García, D., Bañuelos, M.-J., & Houle, G. (2002). Differential effects of acorn burial and litter cover on *Quercus rubra* recruitment at the limit of its range in eastern North America. *Canadian Journal of Botany*, *80*, 1115–1120.

Garzon-Lopez, C. X., Ballesteros-Mejia, L., Ordonez, A., Bohlman, S. A., Olff, H., & Jansen, P. A. (2015). Indirect interactions among tropical tree species through shared rodent seed predators: A novel mechanism of tree species coexistence. *Ecology Letters*, *18*, 752–760. https://doi.org/10.1111/ele.12452

Gasperini, S., Bonacchi, A., Bartolommei, P., Manzo, E., & Cozzolino, R. (2017). Seasonal cravings: Plant food preferences of syntopic small mammals. *Ethology Ecology & Evolution*, *14*, 1–4.

Gelmi-Candusso, T. A., Heymann, E. W., & Heer, K. (2017). Effects of zoochory on the spatial genetic structure of plant populations. *Molecular Ecology*, *26*, 5896–5910. https://doi.org/10.1111/mec.14351

Gómez, J. M., Puerta-Pinero, C., & Schupp, E. W. (2008). Effectiveness of rodents as local seed dispersers of Holm oaks. *Oecologia*, *155*, 529–537. https://doi.org/10.1007/s00442-007-0928-3

Gómez, J. M., Schupp, E. W., & Jordano, P. (2019). Synzoochory: The ecological and evolutionary relevance of a dual interaction. *Biological Reviews*, *94*, 874–902. https://doi.org/10.1111/brv.12481

Hirsch, B. T., Kays, R., Pereira, V. E., & Jansen, P. A. (2012). Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letters*, *15*, 1423–1429. https://doi.org/10.1111/ele.12000

Howe, H., & Brown, J. (2001). The ghost of granivory past. *Ecology Letters*, *4*, 371–378. https://doi.org/10.1046/j.1461-0248.2001.00237.x

Jansen, P. A., Bongers, F., & Hemerik, L. (2004). Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs*, *74*, 569–589. https://doi.org/10.1890/03-4042

Jansen, P. A., Bongers, F., & Van Der Meer, P. J. (2008). Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. *Ecography*, *31*, 43–52. https://doi.org/10.1111/j.2007.0906-7590.05156.x

Jansen, P. A., & Forget, P.-M. (2001). *Scatterhoarding rodents and tree regeneration* (pp. 275–288). Nouragues: Springer.

Jansen, P. A., Hirsch, B. T., Emsens, W. J., Zamora-Gutierrez, V., Wikelski, M., & Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences*, *109*, 12610–12615. https://doi.org/10.1073/pnas.1205184109

Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics*, *2*(1), 465–492. https://doi.org/10.1146/annurev.es.02.110171.002341

John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard, R. F., Mirabello, M., … Foster, R. B. (2007). Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 864–869. https://doi.org/10.1073/pnas.0604666104

Johnson, D. J., Beaulieu, W. T., Bever, J. D., & Clay, K. (2012). Conspecific negative density dependence and forest diversity. *Science*, *336*, 904–907. https://doi.org/10.1126/science.1220269

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, *9*, 465–470. https://doi.org/10.1016/0169-5347(94)90310-7

Klinger, R., & Rejmánek, M. (2010). A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm. *Oecologia*, *162*, 951–963. https://doi.org/10.1007/s00442-009-1542-3

Kollmann, J., & Schill, H. P. (1996). Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. *Vegetatio*, *125*, 193–205. https://doi.org/10.1007/BF00044651

Kurek, P., Dobrowolska, D., & Wiatrowska, B. (2019). Dispersal distance and burial mode of acorns in Eurasian Jays *Garrulus glandarius* in European temperate forests. *Acta Ornithologica*, *53*, 155–162. https://doi.org/10.3161/00016454ao2018.53.2.005

Larios, L., Pearson, D. E., & Maron, J. L. (2017). Incorporating the effects of generalist seed predators into plant community theory. *Functional Ecology*, *31*, 1856–1867. https://doi.org/10.1111/1365-2435.12905

Lichti, N. I., Steele, M. A., & Swihart, R. K. (2017). Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Reviews*, *92*(473), 504. https://doi.org/10.1111/brv.12240

Longland, W. S., Jenkins, S. H., Vander Wall, S. B., Veech, J. A., & Pyare, S. (2001). Seedling recruitment in *Oryzopsis hymenoides*: Are desert granivores mutualists or predators? *Ecology*, *82*, 3131–3148. https://doi.org/10.2307/2679840

Maron, J. L., & Crone, E. (2006). Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 2575–2584. https://doi.org/10.1098/rspb.2006.3587

Moore, J. E., McEuen, A. B., Swihart, R. K., Contreras, T. A., & Steele, M. A. (2007). Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology*, *88*, 2529–2540. https://doi.org/10.1890/07-0247.1

Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology*. Sunderland, Massachusetts, USA: Sinauer.

Muñoz, A., & Bonal, R. (2011). Linking seed dispersal to cache protection strategies. *Journal of Ecology*, *99*, 1016–1025. https://doi.org/10.1111/j.1365-2745.2011.01818.x

Myczko, Ł., Dylewski, Ł., Zduniak, P., Sparks, T. H., & Tryjanowski, P. (2014). Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native (Pedunculate Oak *Quercus robur*) and an introduced oak species (Northern Red Oak *Quercus rubra*) in Europe. *Forest Ecology and Management*, *331*, 35–39. https://doi.org/10.1016/j.foreco.2014.07.027

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Palmer, T. M., Doak, D. F., Stanton, M. L., Bronstein, J. L., Kiers, E. T., Young, T. P., … Pringle, R. M. (2010). Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. *Proceedings of the National Academy of Sciences*, *107*, 17234–17239. https://doi.org/10.1073/pnas.1006872107

Perea, R., San Miguel, A., & Gil, L. (2011). Acorn dispersal by rodents: The importance of re-dispersal and distance to shelter. *Basic and Applied Ecology*, *12*, 432–439. https://doi.org/10.1016/j.baae.2011.05.002

Pesendorfer, M. B., Sillett, T. S., Koenig, W. D., & Morrison, S. A. (2016). Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. *The Condor*, *118*, 215–237. https://doi.org/10.1650/CONDOR-15-125.1

Reinhart, K. O., Johnson, D., & Clay, K. (2012). Effects of trees on their recruits in the southern Appalachians, USA. *Forest Ecology and Management*, *263*, 268–274. https://doi.org/10.1016/j.foreco.2011.09.038

Sawaya, G. M., Goldberg, A. S., Steele, M. A., & Dalgleish, H. J. (2018). Environmental variation shifts the relationship between trees and scatterhoarders along the continuum from mutualism

to antagonism. *Integrative Zoology*, *13*(3), 319–330. https://doi.org/10.1111/1749-4877.12311

Schupp, E. W. (1992). The Janzen-Connell model for tropical tree diversity - population implications and the importance of spatial scale. *American Naturalist*, *140*, 526–530. https://doi.org/10.1086/285426

Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, *188*, 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Selva, N., Hobson, K. A., Cortés-Avizanda, A., Zalewski, A., & Donázar, J. A. (2012). Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. *PLoS ONE*, *7*, e51267. https://doi.org/10.1371/journal.pone.0051267

Sork, V. L., Bramble, J., & Sexton, O. (1993). Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology*, *74*, 528–541. https://doi.org/10.2307/1939313

Stapanian, M. A., & Smith, C. C. (1984). Density-dependent survival of scatterhoarded nuts: An experimental approach. *Ecology*, *65*, 1387–1396. https://doi.org/10.2307/1939119

Steele, M. A. (2008). Evolutionary interactions between tree squirrels and trees: A review and synthesis. *Current Science*, *95*, 871–876.

Steele, M. A., Contreras, T. A., Hadj-Chikh, L. Z., Agosta, S. J., Smallwood, P. D., & Tomlinson, C. N. (2013). Do scatter hoarders trade off increased predation risks for lower rates of cache pilferage? *Behavioral Ecology*, *25*, 206–215. https://doi.org/10.1093/beheco/art107

Sunyer, P., Boixadera, E., Muñoz, A., Bonal, R., & Espelta, J. M. (2015). The interplay among acorn abundance and rodent behavior drives the spatial pattern of seedling recruitment in mature mediterranean oak forests. *PLoS ONE*, *10*(6), e0129844. https://doi.org/10.1371/journal.pone.0129844

Sunyer, P., Espelta, J. M., Bonal, R., & Muñoz, A. (2014). Seeding phenology influences wood mouse seed choices: The overlooked role of timing in the foraging decisions by seed-dispersing rodents. *Behavioral Ecology and Sociobiology*, *68*, 1205–1213. https://doi.org/10.1007/s00265-014-1731-x

Theimer, T. C. (2005). Rodent scatterhoarders as conditional mutualists. Seed Fate: Predation, Dispersal, and Seedling Establishment: 283.

Vander Wall, S. B. (1992). The role of animals in dispersing a "Wind-Dispersed" pine. *Ecology*, *73*(2), 614–621. https://doi.org/10.2307/1940767

Vander Wall, S. B. (2002). Masting in animal-dispersed pines facilitates seed dispersal. *Ecology*, *83*(12), 3508–3516. https://doi.org/10.1890/0012-9658(2002)083[3508:MIADPF]2.0.CO;2

Vander Wall, S. B., & Joyner, J. W. (1998). Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): Potential effects on plant reproductive success. *Canadian Journal of Zoology*, *76*, 154–162. https://doi.org/10.1139/z97-169

Woziwoda, B., Kopec, D., & Witkowski, J. (2014). The negative impact of intentionally introduced *Quercus rubra* L. on a forest community. *Acta Societatis Botanicorum Poloniae*, *83*, 39–49. https://doi.org/10.5586/asbp.2013.035

Woziwoda, B., Potocki, M., Sagan, J., Michal, Z., Tomusiak, R., & Wilczynski, S. (2014). Commercial forestry as a vector of alien tree species - the case of *Quercus rubra* L. Introduction in Poland. *Baltic Forestry*, *20*(1), 131–141.

Wróbel, A., & Zwolak, R. (2017). Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community. *Integrative Zoology*, *12*(6), 457–467. https://doi.org/10.1111/1749-4877.12265

Xia, K., Tan, H. Y., Turkington, R., Hu, J. J., & Zhou, Z. K. (2016). Desiccation and post-dispersal infestation of acorns of *Quercus schottkyana*, a dominant evergreen oak in SW China. *Plant Ecology*, *217*, 1369–1378. https://doi.org/10.1007/s11258-016-0654-1

Xiao, Z., Zhang, Z., & Krebs, C. J. (2013). Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: Testing the predator satiation hypothesis and the predator dispersal hypothesis. *Journal of Ecology*, *101*, 1256–1264. https://doi.org/10.1111/1365-2745.12113

Xiao, Z., Zhang, Z., & Wang, Y. (2005). Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecologica*, *28*, 221–229. https://doi.org/10.1016/j.actao.2005.04.006

Yang, Y. Q., Zhang, M. M., & Yi, X. F. (2016). Small rodents trading off forest gaps for scatter-hoarding differs between seed species. *Forest Ecology and Management*, *379*, 226–231. https://doi.org/10.1016/j.foreco.2016.08.005

Yi, X. F., Liu, G. Q., Steele, M. A., Shen, Z., & Liu, C. Q. (2013). Directed seed dispersal by a scatter-hoarding rodent: The effects of soil water content. *Animal Behaviour*, *86*, 851–857. https://doi.org/10.1016/j.anbehav.2013.07.028

Zwolak, R., Bogdziewicz, M., Wróbel, A., & Crone, E. E. (2016). Advantages of masting in European beech: Timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia*, *180*, 749–758. https://doi.org/10.1007/s00442-015-3511-3

Zwolak, R., & Crone, E. E. (2012). Quantifying the outcome of plant–granivore interactions. *Oikos*, *121*, 20–27. https://doi.org/10.1111/j.1600-0706.2011.19849.x

Zwolak, R., Pearson, D. E., Ortega, Y. K., & Crone, E. E. (2010). Fire and mice: Seed predation moderates fire's influence on conifer recruitment. *Ecology*, *91*, 1124–1131. https://doi.org/10.1890/09-0332.1

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Bogdziewicz M, Crone EE, Zwolak R. Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. *J Ecol*. 2019;00:1–10. https://doi.org/10.1111/1365-2745.13307