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Consumer-mediated indirect interaction with a native plant lowers the fitness of an invasive competitor

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Abstract

1. Seed dispersal is a primary driver, via propagule pressure, of biological invasions. In animal-dispersed plants, theory predicts that indirect ecological interactions at the neighbourhood scale may determine landscape-scale patterns of seed dispersal and predation, and thus invasion.

2. Indirect interactions in seed dispersal may arise between two plant species if shared seed dispersal agents adjust their foraging decisions to the relative frequencies of co-occurring seeds. We used seed-tracking experiments and empirically parameterized simulations to test the hypothesis that an indirect interaction between two plant species, mediated by scatterhoarding rodents that both consume and disperse seeds, affects recruitment of an invasive tree. We predicted that acorns of *Quercus rubra* (invasive in Central Europe) would experience higher caching (and therefore survival) rates when they co-occurred with native *Quercus petraea* than when they occurred in isolation, that *Q. petraea* acorns would survive at lower rates with *Q. rubra* relative to isolation, and that this interaction would facilitate *Q. rubra* seedling recruitment in *Q. petraea* forests.

3. Contrary to expectations, the presence of *Q. petraea* reduced caching of *Q. rubra* acorns, and co-occurrence with *Q. rubra* increased caching of *Q. petraea*. Thus, a rodent-mediated indirect interaction may be slowing rather than facilitating the *Q. rubra* invasion. However, our simulations indicate that the magnitude of this indirect interaction will change nonlinearly as *Q. rubra* becomes more dominant on the landscape, and that the pace of invasion will accelerate as the alien species is released from the rodent-mediated effect of *Q. petraea*.

4. *Synthesis*. The presence of native *Quercus petraea* decreases recruitment rates of *Quercus rubra*, and consequently, slows down the invasion process. The strong dependence of pairwise interactions on the presence of a third-party species emphasizes the role of indirect interactions in the invasion processes.

KEYWORDS
apparent predation, dispersal, indirect interactions, invasion ecology, northern red oak, plant–plant interactions, sessile oak

1 | INTRODUCTION

Invasions are one of the main dimensions of ongoing anthropogenic global changes (Vitousek, Mooney, Lubchenco, & Melillo, 1997), and propagule pressure is a crucial factor at all stages of alien plant invasions (Rouget & Richardson, 2003; Theoharides & Dukes, 2007; Von Holle & Simberloff, 2005). Seed predation can stop an invasion (biotic resistance) or can facilitate it when native plants are preferred for consumption (enemy release) (Pearson, Callaway, & Maron, 2011; Pearson, Potter, & Maron, 2012). Analogously, a reliance of alien seeds on dispersal by animals may enhance an invasion or could prevent it if the alien plant does not have a mutualistic animal partner in its novel range (Richardson, Allsopp, D'Antonio, Milton, & Rejmanek, 2000).

Numerous plants, including major forest tree genera, are dispersed by scatterhoarding seed predators such as rodents or corvids that both consume seeds and bury them in shallow caches for future consumption (Neuschulz, Mueller, Bollmann, Gugerli, & Böhning-Gaese, 2015; Pesendorfer, Sillett, Koenig, & Morrison, 2016; Vander Wall, 2010). Because the two processes are linked, invasions by these plants may be influenced simultaneously by both seed dispersal and seed predation. In addition, because animals consider the availability of alternative resources when they make foraging decisions (Lichti, Steele, & Swihart, 2017), invasions by animal-dispersed plant species may also depend on the mixture of other plant species that are present in a community or neighbourhood.

In scatterhoarding systems, the proportion of seeds that are cached and then abandoned or that escape through germination is a key determinant of whether the plant–scatterhoarder interaction is antagonistic or mutualistic (Zwolak & Crone, 2012). The probability that seeds will be cached for an extended period rather than eaten depends strongly not only on the functional traits of the seeds (e.g., mass, chemical composition, extended dormancy) but also on the indirect effects of other seed species in the community (Lichti et al., 2017). However, the role of native scatterhoarders in plant invasions is poorly known, even in simple pairwise interactions (Richardson et al., 2000; but see Lenda, Knops, Skórka, Moroń, & Woyciechowski, 2017).

Indirect interactions among shared prey species arise when the presence of one species alters the behaviour of a common predator or mutualist towards a second species. Such interactions are ubiquitous in nature (Strauss, 1991; Werner & Peacor, 2003) and play pivotal roles in the organization of plant and animal communities (Holt & Bonsall, 2017; Holt & Lawton, 1994). However, while their influence on seed predation and herbivory is widely acknowledged (Caccia, Chaneton, & Kitzberger, 2006; Emerson, Brown, Whelan, & Schmidt, 2012; Garzon-Lopez et al., 2015; Holt & Bonsall, 2017; Werner & Peacor, 2003), their effects on seed dispersal have been largely ignored (Lichti, Steele, Zhang, & Swihart, 2014; Pesendorfer & Koenig, 2017; Shimada, 2001; Xiao & Zhang, 2016). In theory, indirect interactions could slow an invasion when dispersal of the alien species is reduced in the presence of native species. Alternatively, spread may be enhanced if the presence of a native species improves dispersal success in the alien species.

In seed communities, indirect effects typically arise due to differences in the palatability of co-occurring seed species (Emerson et al., 2012; Hulme & Hunt, 1999; Ostoja, Schupp, & Klinger, 2013), or due to differences in perishability (Lichti et al., 2014). A favoured seed may attract a predator to a patch, increasing predation upon less palatable species (apparent competition). Alternatively, less palatable seeds may repel the consumer from the patch, increasing survival of both seed species (apparent mutualism). Finally, when scatterhoarders perceive one species to be more useful for storage, its presence may lead the hoarders to alter their handling of other species that are less valued for storage. Specifically, hoarders may cache the less valued species at lower rates and consume them more quickly than they would in the absence of a more valued species. At the same time, because the hoarders' immediate nutritional needs are satisfied by consuming the less valued species, they may cache the preferred species at higher rates when both species are present. Thus, the two co-occurring seed species experience opposite effects. This phenomenon has been termed apparent predation because its demographic effects resemble those of a direct, pairwise predatory interaction (Lichti et al., 2014). Although it has not been empirically tested, apparent predation is likely to have strong effects on the outcomes of plant–scatterhoarder interactions if it does occur (Lichti et al., 2014). It may also be important in biotic invasions, which create novel interactions among previously isolated partners.

As long as seeds are not too large to be transported efficiently (Muñoz & Bonal, 2008a; Yi & Wang, 2015), those that require more handling time to eat due to greater size or thicker shells, contain high concentrations of tannins or other defensive phytochemicals, or are less perishable, have higher probabilities of being dispersed and buried rather than being eaten on the spot (Jansen, Bongers, & Hemerik, 2004; Lichti et al., 2017; Vander Wall, 2010; Wróbel & Zwolak, 2017; Zhang, Steele, & Yi, 2013). In particular, seeds that are less perishable than their neighbours have been found to experience enhanced dispersal success, whereas those that are more perishable than a neighbour experienced increased consumption (Lichti et al., 2014).

In this study, we tested the hypotheses that scatterhoarding rodents mediate indirect interactions between two co-occurring oak species—sessile oak *Quercus petraea* (native in Europe) and northern red oak *Quercus rubra* (native to North America). Both species are scatterhoarded by rodents (Bogdziewicz, Crone, Steele, & Zwolak, 2017; Jensen & Nielsen, 1986; Smallwood, Steele, & Faeth, 2001). In comparison with *Q. petraea*, *Q. rubra* acorns weigh twice as much, have shells that are twice as thick, and have higher lipid concentrations (Bogdziewicz, Bonal, et al., 2018). Although tannin concentrations in *Q. rubra* acorns from their native range are higher than those in *Q. petraea*, *Q. rubra* acorns in Europe show unusually low tannin concentrations for the species, and are similar to *Q. petraea* (Bogdziewicz, Bonal, et al., 2018). Finally, *Q. petraea* acorns germinate in autumn while *Q. rubra* acorns overwinter and germinate in the spring (Steele, 2008). This makes *Q. rubra* a less perishable food resource (Smallwood et al., 2001). We therefore predicted that *Q.*

rubra should be favoured for long-term storage, while *Q. petraea* should be favoured for short-term consumption, creating appropriate conditions for apparent predation to arise. Specifically, we predicted that *Q. petraea* acorns would suffer lower removal rates, greater predation, and lower caching when they co-occurred with *Q. rubra* than when they occurred in isolation. In contrast, we expected the presence of *Q. petraea* to enhance seed removal, caching, and survival in the larger, tougher, and less perishable *Q. rubra*. In consequence, we hypothesized that a rodent-mediated indirect interaction between *Q. rubra* and *Q. petraea* would increase propagule pressure from *Q. rubra* and contribute to the invasion's success. We tested these predictions by tracking the fates of acorns from both oak species in single- and mixed-species treatments. In addition, we built and parameterized a simulation model to determine how changes in the landscape scale abundance of *Q. rubra* might interact with frequency-dependent seed dispersal to affect recruitment rates of both species over the course of an invasion.

2 | MATERIALS AND METHODS

2.1 | Field experiments

We established four study sites in *Q. petraea*−*Q. rubra* mixed forests in Drawieńska Forest, western Poland (spaced 1–15 km from each other). Small mammal communities at the study sites were dominated by rodents of genus *Apodemus* sp. (most likely *A. flavicollis*), as recorded with camera traps (Bogdziewicz, Crone, & Zwolak, 2018). At each site, we selected six trees of each species. Under each tree, we placed two seed stations (treatments) consisting of eight acorns (768 acorns in total). In the "single" treatment we placed eight seeds of the tree species under which the station was placed, while in the "mixed" treatment we placed four seeds from each focal species.

We tracked acorns using a modified tin tag method (Xiao, Jansen, & Zhang, 2006). Acorns were locally collected and visually examined for oviposition holes to determine weevil infestation; only noninfested acorns were used in experiments. We drilled a 1-mm-diameter hole through the basal end of each acorn, inserted and tied a steel wire (120 mm length, 0.2 mm diameter), and attached a blue, uniquely numbered plastic tag (30 × 40 mm) to the terminal end of the wire. We placed acorns in small enclosures (eight per enclosure) with openings on each side to allow rodent access but exclude other seed-eating vertebrates such as jays (*Garrulus glandarius*).

We deployed acorns in October 2016 and recorded acorn fates every day for the first 10 days and then on the 15th and 30th days. Final fates were determined in April 2017. At each check, we recorded acorns that were eaten at the seed station or that were removed. If removed, we searched in a ~20 m radius around the seed station, with haphazard searches conducted at longer distances. For all acorns, we measured the distance from the depot (if relocated) and categorized the fate of the acorn as: (i) consumed, (ii) cached in the in the topsoil, or (iii) missing. Cached acorns were marked with a stick and their fate was further monitored at each check. To minimize

the risk that sticks might be used as foraging cues, they were placed at least 50 cm from caches.

2.2 | Data analysis: Field experiments

Seed fate was analysed using a series of four conditional, logit-link, binomial generalized linear mixed models (GLMMs): (1) first, seeds either remained in situ and were apparently untouched or were harvested by rodents, (2) given harvest, seeds were either eaten in situ or removed from the stations, (3) removed seeds were either missing or found, and (4) acorns that were both removed and found either remained cached or were eaten ex situ. Seeds that were not found were assumed to be missing at random given no apparent differences in the probability of disappearance among species or treatments. We used the proportion of seeds harvested, removed, found, or cached as the response variable at the four respective branch points, and at stages 2–4, data were restricted to those seeds that had "succeeded" in the previous stage. All four models included a fixed effect of treatment (single vs. mixed) and random effects of tree nested within study site. We built separate models for each species. In addition, we tested for treatment effects on acorn dispersal distance with a Gaussian, linear mixed model, using log-transformed dispersal distance as the response; this model had the same fixed and random effects as the binomial models. Analyses were implemented via the lme4 package in R (Bates, Maechler, Bolker, & Walker, 2015; R Core Team, 2017). The data were deposited in Open Science Framework repository (Bogdziewicz, 2018).

The framework described above involves several consecutive statistical tests on the same data. Even one significant result would be sufficient to reject the global null hypothesis that indirect interactions do not occur between the studied species. Thus, we used conservative, Bonferroni corrected alpha-values to maintain the correct experiment-wise error rate (Forstmeier, Wagenmakers, & Parker, 2017). We ran four tests for each species (eight in total), thus the level of significance for each test was adjusted to alpha = 0.05/8 = 0.00625.

Finally, we estimated the probability of seedling recruitment. We first assessed the probability of acorn survival in situ (1 − probability of harvesting) and the probability of survival after harvest (probability of caching/probability of harvesting). Because the acorn survival probabilities combine results from several of the GLMMs, we used parametric bootstrapping from the parameter distributions for fitted GLMMs to obtain confidence intervals on survival. The probability of seedling emergence given seed survival was obtained from previous experiments in which we sowed *Q. petraea* and *Q. rubra* acorns either on the litter layer, mimicking acorns that fell from trees and survived in situ, or in topsoil, mimicking acorns cached by rodents (Bogdziewicz, Crone, et al., 2018). From these field tests, the conditional probability of seedling emergence for intact acorns that remained in situ was 0.18 in *Q. petraea* and 0.25 in *Q. rubra*; for cached acorns, it was 0.39 in *Q. petrea* and 0.71 in *Q. rubra*.

2.3 | Simulation model

Invasion is a landscape-scale phenomenon. Depending on their location within a partially invaded landscape, individual mice may be exposed to no *Q. rubra* acorns, a mixture of acorn species, or no *Q. petraea* acorns. As a result, we expected seed handling behaviour to vary across the landscape and to change over time as *Q. rubra* coverage increased. To understand how hoarder behaviour might affect invasion dynamics, we built a model that integrates the local-scale inferences from our field results across simulated landscapes. Details of the scaling model and simulations are provided in Supplement S1, and R code is given in S2. Briefly, we simulated fractal landscape maps at 11 levels of invasion. At the landscape scale, *Q. rubra* canopy coverage in these maps ranged continuously from near 0% to near 100%. Although the exact arrangements varied randomly, the degree of *Q. rubra* aggregation was selected to mimic patterns that have been reported in invaded Polish forests (Woziwoda, Kopeć, & Witkowski, 2014). In maps representing the beginning of the invasion process, *Q. rubra* was limited to a few clusters of small patches that were randomly distributed across the landscape. At moderately advanced stages of invasion, *Q. rubra* occurred mainly in large, contiguous patches, with occasional "satellite" patches outside the main invasion front, and at the final stages, *Q. rubra* dominated the landscape, while *Q. petraea* was limited to clusters of small refugia.

To integrate the effects of foragers' local-scale decision-making over the landscape, we overlaid each map of tree species coverage with a simulated map of *A. flavicollis* home ranges. Population densities and home range sizes were based on data from the PanTHERIA database (Jones et al., 2009). Next, seeds at 20,000 randomly selected points on each map were allocated among the mice whose home ranges overlapped the points, and each mouse independently determined the fates of the seeds allocated to it according to one of two alternative behavioural models based on our field data (see below). Landscape-level seed fates were taken as the average proportion of seeds in each fate category, and these were combined with the estimated seedling emergence rates from Bogdziewicz, Crone *et al.* (2018) to yield landscape-level per-seed and absolute recruitment rates.

For indirect seed–seed interactions to occur, foragers must handle seeds in a context-dependent manner that depends on the presence or frequency of other seed species. To understand how the indirect interactions observed in our field studies affect seedling recruitment at the landscape scale, we built two multinomial-response regression models for each acorn species, representing the probabilities of different seed fates (intact in situ, eaten in situ, eaten ex situ, cached ex situ, or missing) under two alternative behavioural hypotheses. The null model included only intercept terms; scatter-hoarders in this model respond differently to each acorn species, but do not respond to their relative frequencies, so indirect interactions cannot occur. By contrast, seed fate probabilities in the alternative model depended on the relative frequency of *Q. rubra* (from 0 to 1). The difference between scenarios run using the null and the frequency-dependent models therefore represents the effect of indirect interactions on seed fate.

We parameterized the multinomial models by fitting them to our field data in the R package MCMCglmm (Hadfield, 2010; details of the modelling procedures, fits, and posterior predictive checks appear in Supplement S1). Separate fits were obtained for *Q. petraea* and *Q. rubra*, and all four models included tree nested within site as random effects. The null models were fit only to data from the single-species treatments.

In the simulations, we assumed that each mouse's decision-making process was independent of other mice, and in the frequency-dependent scenarios, we assumed that behaviour depended on the proportion of *Q. rubra* acorns within each mouse's home range. Rather than assuming that all mice behave similarly, we also parameterized each mouse's behaviour with a separate sample from the posterior parameter distribution for the relevant multinomial regression model. Thus, our simulations integrated over behavioural variation as well as landscape composition. Finally, we repeated the simulations at five different ratios of local *Q. petraea* to *Q. rubra* seed production, to account for masting behaviour of the species (cf. Kelly, 1994): 10:1, 2:1, 1:1, 1:2, and 1:10. In total, we ran 100 replicate simulations at each combination of 11 invasion levels, 5 seed production ratios, and 2 behaviour scenarios, yielding a total of 11,000 simulations.

To visualize the effects of indirect interactions on propagule pressure, we graphed the mean landscape-scale recruitment rates from simulations under the null versus the frequency-dependent scenarios as a function of the seed production ratio and landscape-scale relative abundance of *Q. rubra*. Although we treat relative frequency as a continuous variable, we emphasize that this is a prospective analysis based on data taken at only two seed frequencies.

3 | RESULTS

3.1 | Field experiments

We established fates for 77% of the acorns of both study species. Almost all experimental acorns were harvested (Figure 1). However, the presence of alien *Q. rubra* decreased harvest rates of native *Q. petraea* and increased their in situ seed survival; this effect was marginally nonsignificant after the Bonferroni correction (Table 1, Figure 1). Conversely, the presence of *Q. petraea* did not affect harvest rates of *Q. rubra* (Table 2, Figure 1). Removal of acorns from seed stations did not differ among treatments (Table 1 and 2), and equalled roughly 60% in both species (Figure 1).

Acorn caching was strongly affected by the treatments, but the direction of the effects was opposite to our prediction that *Q. petraea* would enhance the survival of *Q. rubra* acorns. Caching probabilities for *Q. petraea* were significantly greater in the presence of *Q. rubra* (Table 1). After removal, the probability that a *Q. petraea* acorn would remain cached equalled 10% in the single treatment, but when paired with *Q. rubra*, the probability increased over five-fold to 50% (Figure 1). In contrast, the probability of *Q.*
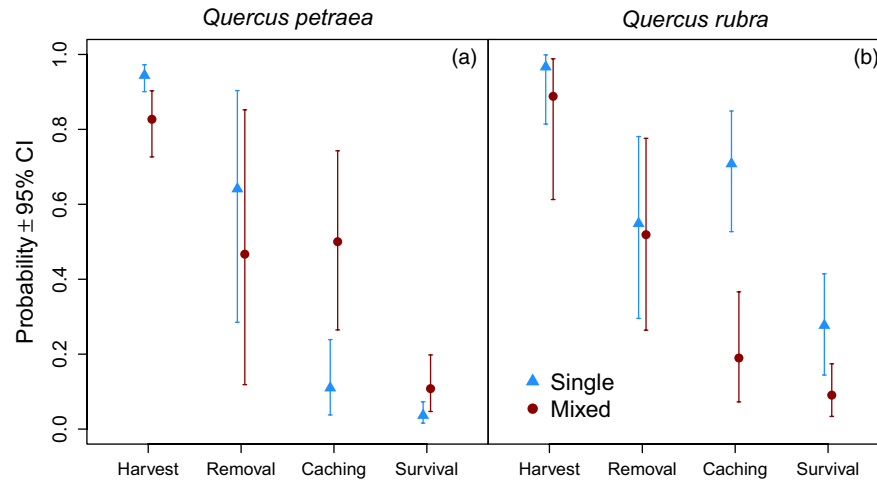
FIGURE 1 Estimated fate probabilities for acorns dispersed by rodents (±95% bootstrap confidence intervals) in (a) *Quercus petraea* and (b) *Quercus rubra*. Blue triangles indicate single-species patches where only the focal species was presented, and red circles indicate mixed patches where acorns of both species were present. Harvested acorns were removed from the station or consumed in situ. The estimated removal probability is conditioned on harvest, and the caching probability is conditioned on removal. The probability of survival is calculated as $(1 - P(\text{harvest})) \times P(\text{survival in situ}) + P(\text{harvest}) \times P(\text{removal}) \times P(\text{caching}) \times P(\text{survival in cache})$. Germination probabilities for *Q. petraea* were fixed at 0.18 for in situ acorns and 0.39 for cached acorns, versus 0.25 and 0.71 for *Q. rubra* (Bogdziewicz, Crone, et al., 2018) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Summary of the indirect effects of the presence of alien *Quercus rubra* on the fate of native *Quercus petrea*. Effects significant at the α = 0.00625 level are given in bold (significance level was changed using the Bonferroni correction, see Data analysis for rationale)

Dispersal stage	Estimate	SE	z	p
Harvest				
Intercept	2.87	0.39	7.28	**<0.001**
Mixed treatment	−1.26	0.47	−2.70	0.007
Removal				
Intercept	0.59	0.54	1.08	0.28
Mixed treatment	−0.28	0.35	−0.78	0.43
Caching				
Intercept	−2.20	0.53	−4.17	**<0.001**
Mixed treatment	2.19	0.75	2.92	**0.003**
Distance				
Intercept	4.51	0.41	14.42	**<0.001**
Mixed treatment	0.51	1.21	0.81	0.62

TABLE 2 Summary of the indirect effects of the presence of native *Quercus petrea* on the fate of alien *Quercus rubra*. Effects significant at a Bonferroni-corrected α = 0.00625 are shown in bold (significance level was changed using the Bonferroni correction, see Data analysis for rationale)

Dispersal stage	Estimate	SE	z	p
Harvest				
Intercept	3.60	0.64	5.66	**<0.001**
Mixed treatment	−0.46	0.50	−0.91	0.36
Removal				
Intercept	0.20	0.28	0.70	0.48
Mixed treatment	0.23	0.28	0.84	0.40
Caching				
Intercept	1.04	0.35	2.94	**0.003**
Mixed treatment	−2.62	0.61	−4.25	**<0.001**
Distance				
Intercept	4.73	0.31	15.42	**<0.001**
Mixed treatment	0.63	1.00	0.63	0.53

rubra acorns remaining cached after removal was fourfold lower when paired with *Q. petraea* (17%) than in the single treatment (73%, Table 2, Figure 1). As a result of these differences, net seed survival in the mixed treatment was significantly greater for *Q. petraea* and lower for *Q. rubra*, relative to the single treatment, confirming that strong indirect apparent predation does occur in this system (Figure 1).

Dispersal distances of acorns were not affected by the treatment (Table 1 and 2). The mean dispersal distance of *Q. petraea* equalled 268 cm (±377 cm, *SD*, *N* = 166), while *Q. rubra* was dispersed a mean

of 196.38 cm (±184 cm, *N* = 123). Seed fate diagrams are presented in the Online Supplement S3.

3.2 | Simulation model

Our empirically parametrized simulations indicate that, in contrast to the null model, frequency-dependent foraging decisions by scatterhoarders result in nonlinear changes to seed predation and caching rates that reduce the invasiveness of *Q. rubra* (Figures 2 and 3). In the model, when *Q. rubra* is scarce on the landscape or

FIGURE 2 Effects of landscape-scale relative abundance and relative seed production on expected landscape-level seed fate probabilities in *Quercus petraea* (a–d) and *Quercus rubra* (e–h) with frequency-dependent (light, blue lines) versus frequency-independent (dark, red lines) rodent seed handling behaviour. Each line represents the mean response over 1,100 replicate simulations that were distributed randomly along the *x*-axis. Line styles represent different ratios of interspecific seed productivity, and differences between the red and blue lines for a given style reflect the effects of indirect interactions. Scenarios in which *Q. rubra* was rare but dominated productivity (solid blue lines) had seed fate probabilities equivalent to those where *Q. rubra* was abundant, but *Q. petraea* dominated production (dotted blue lines). Iis (a, e) means "intact in situ", eis (b, f) means "eaten in situ", ear (c, g) means "eaten after removal", and car (d, h) denotes "cached after removal" [Colour figure can be viewed at wileyonlinelibrary.com]
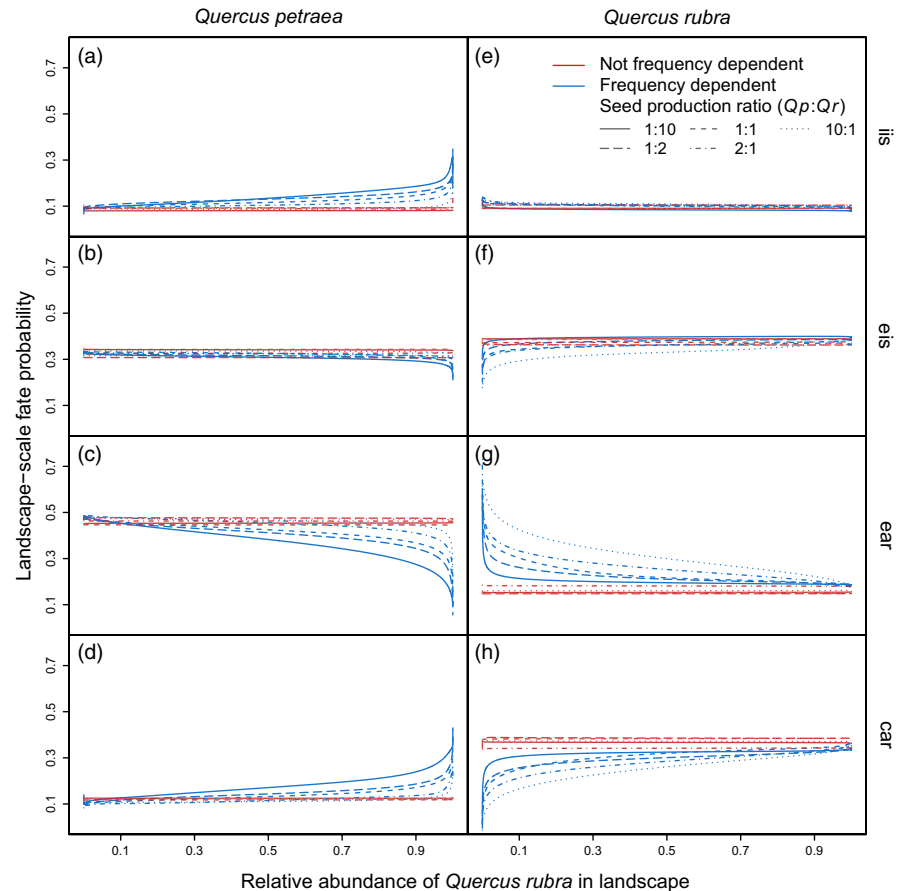
produces relatively few acorns per unit area, most mice encounter it infrequently and only in combination with *Q. petraea*. As a result, mice in the frequency-dependent scenarios cache *Q. rubra* at lower probabilities than in the null model scenarios due to the suppressing indirect effect of *Q. petraea* (Figure 2h), and consume most of the *Q. rubra* that might otherwise be cached (Figure 2g). As *Q. rubra* becomes more common, more mice encounter it at higher relative abundances (or alone) and therefore remove and cache its acorns at higher rates under the frequency-dependent versus the null model (Figure 2h). Although the proportion of *Q. rubra* seeds that are eaten in situ also increases (Figure 2f), the magnitude of this change is relatively small compared with the postremoval fate categories. In summary, our model indicates that relative to context-independent behaviour, the seed handling behaviours observed in our field results would reduce *Q. rubra* propagule pressure during all stages of an invasion and at all seed production ratios (Figure 3b,c). However, as the relative abundance of *Q. rubra* increases, responses under the frequency-dependent model decay toward the null model; thus, as the invasion progresses, the effects of scatterhoarder behaviour on *Q. rubra* propagule pressure decline.

In contrast to *Q. rubra*, *Q. petraea* experiences greater dispersal success in the frequency-dependent versus the null scenarios when *Q. rubra* is more prominent on the landscape or produces a larger portion of the seed crop (Figure 2a,b). In addition to being cached more frequently and eaten less frequently (Figure 2c,d),

Q. petraea acorns in simulations where *Q. rubra* dominates landscapes or seed production remain intact in situ more frequently (Figure 2a). As the relative frequency of *Q. rubra* on the landscape increases, the difference between the null and frequency-dependent responses for *Q. petraea* increases hyperbolically (Figure 2a–d and Figure 3a).

As a result of the indirect effects on individual seed fate probabilities shown in Figure 2, per capita seed survival rates in *Q. petraea* (Figure 3a) and *Q. rubra* (Figure 3b) in the frequency-dependent scenarios show opposite responses to the landscape-scale relative abundance of *Q. rubra*. In comparison to the null model, the probability that a *Q. petraea* acorn will successfully establish as a seedling is greater in the field-parameterized model, especially when *Q. petraea* is rare (Figure 3a). In contrast, survival of *Q. rubra* acorns under the frequency-dependent model is quite low (but >0) when *Q. rubra* is rare, increases rapidly at relative abundances below approximately 0.3, and then asymptotically converges towards the null model from below (Figure 3b). Differences in seed productivity between the two species alter the slopes and inflection points of these curves, but do not alter their basic shapes. As a result, although *Q. rubra* has a fitness advantage in almost all scenarios, and its advantage increases exponentially with increasing dominance of the landscape, the rodent-mediated indirect interaction with *Q. petraea* noticeably reduces the rate at which this increase occurs (Figure 3c). In addition, the net effect of frequency dependence on the relative fitness of
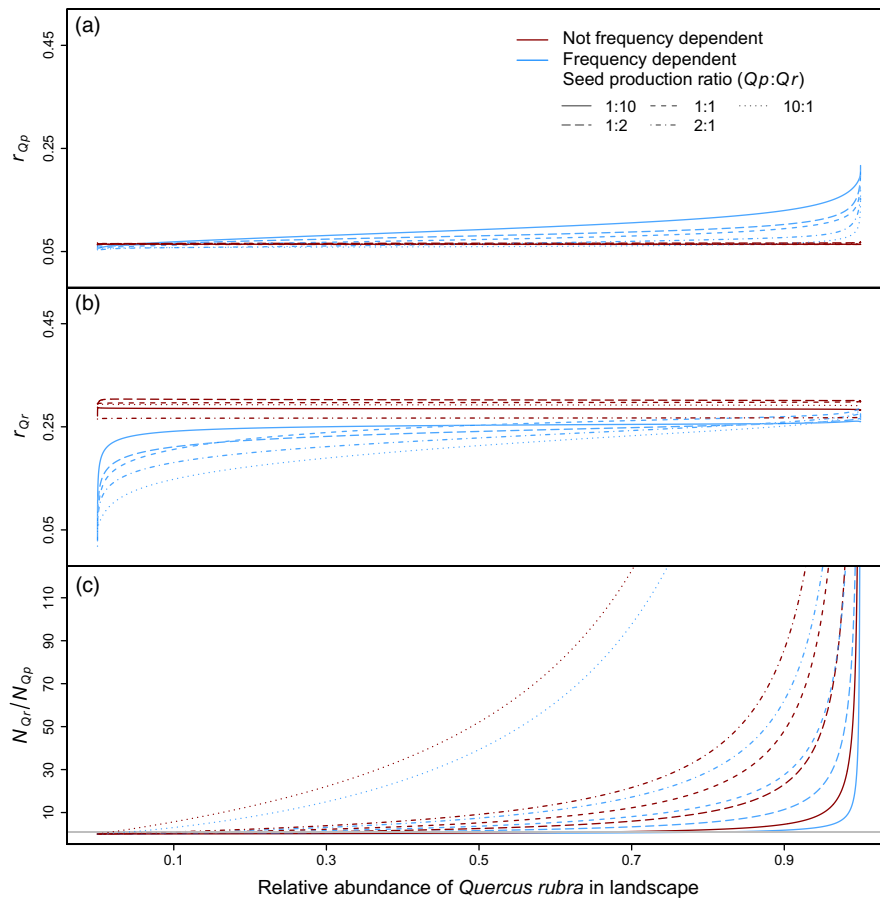
FIGURE 3 Effects of landscape-scale relative abundance and relative seed production on mean landscape-level per capita seed survival in *Quercus petraea* (a) and *Quercus rubra* (b), with frequency-dependent (light, blue lines) versus frequency-independent (dark, red lines) rodent seed handling behaviour. The ratio of total *Q. rubra* to *Q. petraea* seedling recruitment rates is shown in (c). Each line represents the mean response over 1,100 replicate simulations that were distributed randomly along the *x*-axis. Line styles represent different ratios of interspecific seed productivity, and differences between the red and blue lines for a given style reflect the effects of indirect interactions. Frequency-dependent rodent behaviour reduces but does not eliminate the fitness advantage of *Q. rubra* [Colour figure can be viewed at wileyonlinelibrary.com]

Q. rubra is stronger when *Q. rubra* dominates seed productivity (this may be seen by comparing the vertical distances between similar line styles at the same value on the *x*-axis in Figure 3c).

4 | DISCUSSION

Indirect interactions between co-occurring plant species can greatly change the quality of dispersal services provided by animals to their plant partners. In contrast to our predictions, *Q. rubra* acorns, which we expected rodents to prefer for caching over *Q. petraea* acorns, were cached in lower proportions than *Q. petraea* in mixed presentations. Furthermore, the presence of *Q. rubra* acorns increased, rather than decreased, the caching rate of *Q. petraea* relative to the single treatment. Although *Q. rubra* acorns were successfully dispersed in both field treatments, they experienced lower survival probabilities when co-occurring with *Q. petraea* than in isolation. In contrast, the fitness of *Q. petraea* acorns was increased by co-occurrence with *Q. rubra*. Thus, rodent-mediated apparent predation by *Q. petraea* on *Q. rubra* is likely to be slowing the alien oak's invasion of central Europe.

The relative abundance of *Q. rubra* in Polish forests is increasing over time (Woziwoda, Potocki, et al., 2014). Our empirically parameterized simulations predict that as *Q. rubra* becomes more dominant, its release from apparent predation will increase its

propagule pressure, likely accelerating the pace of the invasion (Dyderski & Jagodziński, 2018; Jagodziński, Dyderski, Horodecki, & Rawlik, 2018; Myczko, Dylewski, Zduniak, Sparks, & Tryjanowski, 2014; Theoharides & Dukes, 2007; Von Holle & Simberloff, 2005). However, our model also predicts that per capita survival of *Q. petraea* acorns will increase as *Q. rubra* becomes increasingly dominant because higher proportions of the native seeds will experience the positive effects of indirect interactions. Thus, rodent behaviour may function to slow the disappearance of *Q. petraea* from the landscape, even as it enables invasion by the alien species. Indirect effects due to interactions between consumer diet selection or prey handling and neighbourhood composition, similar to those observed here, are likely to influence species' rates of spread in many ecosystems, and should affect native as well as invasive species. The strength and direction of these effects will depend on the type of indirect interaction (apparent competition, mutualism, or predation), and on the functional traits of both the prey and the consumer.

While our results confirmed the existence of an indirect interaction called "apparent predation" (Lichti et al., 2014), they violated our expectations for the direction of the interaction based on the seed species' functional traits. *Q. rubra* acorns are larger than *Q. petraea* acorns, have higher lipid concentrations, and remain dormant through the winter, while *Q. petraea* acorns germinate immediately after seed fall. Of all these traits, delayed germination

has been considered to have the most decisive influence on rodent seed dispersal (Lichti et al., 2017). However, this conclusion was based on American and Asian systems where species with delayed germination have long evolutionary histories. In contrast, with the exception of *Q. rubra*, no oak species in middle Europe exhibits this trait. Thus, the rodents in this system may be unable to discriminate between seeds with different germination schedules. Experience is an important determinant of seed choice strategies in rodents (Muñoz & Bonal, 2008b). However, given the short life spans of focal rodents (up to 1.5 years in the wild), the opportunity for learning is very limited; typically, an individual wood mouse stores acorns over only one winter (Pucek, Jedrzejewski, Jedrzejewska, & Pucek, 1993). Moreover, although handling techniques are refined through experience, the basic responses to seed germination in North American scatterhoarders are genetically determined (Steele et al., 2006). Thus, we hypothesize that because they lack evolutionary experience with delayed germination, rodents in central European oak forests are insensitive to acorn germination schedules.

In the absence of sensitivity to germination schedules, and without differences in tannin concentration (Bogdziewicz, Bonal, et al., 2018), mice may treat *Q. rubra* acorns like large *Q. petraea*, and this may help explain our results. *Q. rubra* was more likely than *Q. petraea* to escape predation when both species were presented in isolation (Figure 1). Due to their larger mass and greater lipid content, fewer *Q. rubra* acorns would be needed to satiate hunger in individual mice, causing them to cache larger numbers of any available species (see Supplement S1: Relative food value of acorns). When the patch is mixed, *Q. petraea* appears to "steal" the benefits of satiation from *Q. rubra*, likely because *Q. petraea* acorns are easier for the small rodents in our system to handle and transport (Muñoz & Bonal 2008a; Muñoz, Bonal, & Espelta, 2012).

Our landscape simulations condition forager behaviour in the frequency-dependent scenarios on the relative frequency of *Q. rubra* in each mouse's neighbourhood. One consequence of this relationship is that invasion dynamics should depend of the spatial distribution of invaders. Under the relatively aggregated distributions used in our simulations, we would expect the invasion's spread to be driven primarily by trees on the outer edges of *Q. rubra* patches (Williams & Levine, 2018), where *Q. petraea* is most abundant and apparent predation is expected to have the strongest effects. Although our results indicate that acorns within *Q. rubra* patches will survive at higher rates, this may not have much effect on spatial spread. However, additional modelling work will be needed to confirm this supposition.

Our landscape model also provides insights into the effects that large-scale interannual differences in fecundity (masting) might have on invasion dynamics. For example, if *Q. petraea* produces many more acorns in a given year than *Q. rubra*, then a larger proportion of mice experience high relative frequencies of *Q. petraea*, and the landscape-scale seed fate probabilities resemble a landscape with a lower relative abundance of *Q. rubra* trees than actually are present. Additional modelling work is needed to fully understand how such fluctuations might affect invasion dynamics over time, and to understand how these temporal patterns might interact with the spatial distribution of *Q. rubra* on the landscape. However, based on Figure 3c, we might reasonably expect the invasion to "surge" forward during years of low relative productivity by *Q. petraea*, producing fluctuations in invasions speed similar to those reported by Sullivan, Li, Miller, Neubert, and Shaw (2017).

Although it is instructive, our model makes several important simplifying assumptions. Among the most important, it was parameterized using data on a limited set of relative species frequencies (0%, 50%, or 100%), and assumes that the multinomial model fit to these data can be extrapolated over the full frequency range. Although our results with regard to seed survival appear to be reasonable based on posterior predictive checks (Supplement S1), future experimental work is required to verify the functional forms of the responses.

Our model also assumes that neither acorns nor rodents will undergo any relevant evolutionary changes during the period of invasion. It is difficult to know whether this assumption is reasonable. However, given the large difference in generation times between oak trees and wood mice, and the fact that rodents in multiple systems have evolved sensitivity to seed dormancy (Lichti et al., 2017), it is plausible that *A. flavicollis* in central Europe will respond similarly to the presence of *Q. rubra* and will do so quickly relative to the time-scale of the invasion. In this event, the apparent predatory interaction between *Q. rubra* and *Q. petraea* could disappear, or could even be reversed, with potential to rapidly extirpate *Q. petraea* from the system. Similarly, the spread of another invasive species, the North American tree squirrel *Sciurus carolinensis* (Bertolino, Lurz, Sanderson, & Rushton, 2008), which evolved sympatrically with *Q. rubra* and is highly sensitive to seed dormancy, could substantially alter or reverse the existing indirect interaction.

The intrinsic ability of resident communities to resist biotic invasions has generated considerable research interest in recent years (Levine, Adler, & Yelenik, 2004; Nunez-Mir et al., 2017). In particular, sudden releases from biotic resistance, for example, due to decreases in the abundance of seed predators, have been shown to enable invasions of "noninvasive" alien species (Allington, Koons, Ernest, Schutzenhofer, & Valone, 2013; Shea & Chesson, 2002). Our study indicates that such releases could result from the disappearance of negative indirect interactions (apparent predation or competition) as native plants are gradually displaced from communities. In addition, changes in consumer behaviour due to evolution, learning, or changes in the consumer community have the potential to dramatically alter the outcomes of these interactions, potentially resulting in abrupt changes to system dynamics. In addition to accentuating the strong dependence of pairwise interactions on the presence of a third-party species, our unexpected finding that dispersal success in invasive *Q. rubra* is hindered by the presence of *Q. petraea* emphasizes critical roles that the identities and functional traits of all the species involved in an interaction play in determining its outcomes. Theoretically, the strength and direction of these interactions can be predicted by models of trait-dependent consumer behaviour.

AUTHORS' CONTRIBUTIONS

M.B. conceived the study and collected the data; M.B., R.Z., and N.I.L. designed it and analysed the data. All authors wrote and contributed substantially to the revising of the paper.

DATA ACCESSIBILITY

Data used in this study are archived in the Open Science Framework: doi.org/https://doi.org/10.17605/OSF.IO/2AQXN (Bogdziewicz, 2018).

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