

Contrasting patterns of short-term indirect seed–seed interactions mediated by scatter-hoarding rodents

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Summary

1. It is well known that direct effects of seed predators or dispersers can have strong effects on seedling establishment. However, we have limited knowledge about the indirect species interactions between seeds of different species that are mediated by shared seed predators and/or dispersers and their consequences for plant demography and diversity. Because scatter-hoarding rodents as seed dispersers may leave some hoarded seeds uneaten, scatter hoarding may serve to increase seed survival and dispersal. Consequently, the presence of heterospecific seeds could alter whether the indirect interactions mediated by scatter-hoarding rodents have a net positive effect, creating apparent mutualism between seed species, or a net negative effect, creating apparent competition between seed species.

2. We present a testable framework to measure short-term indirect effects between co-occurring plant species mediated by seed scatter-hoarding rodents. We tested this framework in a subtropical forest in south-west China using a replacement design and tracked the fate of individually tagged seeds in experimental patches. We manipulated the benefits to rodents by using low-tannin dormant chestnuts as palatable food and high-tannin non-dormant acorns as unpalatable food.

3. We found that seed palatability changed the amount of scatter hoarding that occurred when seeds co-occurred either among or within patches. Consistent with our predictions, scatter-hoarding rodents created apparent mutualism through increasing seed removal and seed caching, and enhancing survival, of both plant species in mixed patches compared with monospecific patches. However, if we ignore scatter hoarding and treat all seed harvest as seed predation (and not dispersal), then apparent competition between palatable chestnuts and unpalatable acorns was also observed.

4. This study is the first to demonstrate that foraging decisions by scatter-hoarding animals to scatter hoard seeds for later consumption (or loss) or consume them can influence indirect effects among co-occurring seeds, and rodent-mediated indirect effects vary depending on whether the harvested seeds are hoarded or eaten.

Key-words: apparent competition, apparent mutualism, foraging decisions, indirect effects, scatter-hoarding, seed dispersal, seed-eating rodents

Introduction

Seed-eating animals such as rodents, birds and insects are known to selectively consume a wide range of co-occurring seeds based on seed traits and subsequently have considerable impacts on plant population regeneration and vegetation dynamics (Vander Wall 1990, 2001; Crawley 1992; Hulme & Benkman 2002). One extreme example is

that of certain scatter-hoarding squirrels in North America and Asia (China). Such squirrels are highly sensitive to the germination schedule of different oak groups, as demonstrated by them removing the embryos of non-dormant acorns and leaving the embryos of dormant acorns intact (the food perishability hypothesis, Fox 1982; Steele *et al.* 2001; Xiao *et al.* 2009; Xiao & Zhang 2012). Other seed characteristics, such as tannin content and seed size, have also been shown to affect rodent hoarding decisions (e.g. Smallwood & Peters 1986; Hadj-Chikh, Steele & Smallwood 1996; Xiao *et al.* 2009; Xiao, Gao & Zhang

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2013). Both chemical and physical defences can reduce rodent predation and thus improve seed survival (Vander Wall 2001; Xiao, Wang & Zhang 2006). More frequent hoarding of seeds for later consumption has been associated with the higher handling costs of hard-hulled seeds and nuts (Xiao, Zhang & Wang 2003; Zhang *et al.* 2016), and with high secondary chemical content (e.g. *Ormosin arborea* seeds with quinolizidine alkaloids, Guimarães *et al.* 2003; and high-tannin acorns, the high-tannin hypothesis; Fleck & Woolfenden 1997; Xiao, Chang & Zhang 2008).

Though direct effects of seed predators and/or dispersers can have strong effects on seedling establishment (Crawley 1992; Hulme & Benkman 2002), we have only limited knowledge about the indirect seed–seed interactions by shared seed predators and dispersers and their consequences for plant demography and diversity (Chaneton & Bonsall 2000). Short-term apparent competition and apparent mutualism between neighbouring prey (here seeds) are two major predator-mediated indirect interactions (Holt & Kotler 1987; Holt & Lawton 1994; Chaneton & Bonsall 2000; Barbosa *et al.* 2009; Underwood, Inouye & Hambäck 2014). Apparent competition occurs between two prey species when one prey species experiences higher predation (abundance declines) because of the presence of a second prey species, whereas apparent mutualism arises when the survival (or abundance) of both prey species is enhanced by the presence of the second prey species (Holt & Lawton 1994; Chaneton & Bonsall 2000). Both theoretical and empirical studies have shown that indirect effects are often scale dependent due to high heterogeneity in spatial availability of alternative food resources (Holt & Kotler 1987; Hjältén, Danell & Lundberg 1993; Holt & Lawton 1994; Brown & Morgan 1995; Chaneton & Bonsall 2000; Bergvall *et al.* 2006; Kitzberger, Chaneton & Caccia 2007; Emerson *et al.* 2012). In addition, predator-mediated indirect effects can be reciprocal or not reciprocal among co-occurring prey species (Chaneton & Bonsall 2000; Veech 2000; Martínez, García & Herrera 2014). They may also be influenced by the presence of natural enemies of the predators (Root 1973; Stiling, Rossi & Cattell 2003), and foraging microhabitats within a habitat (Brown & Morgan 1995; Caccia, Chaneton & Kitzberger 2006; Kitzberger, Chaneton & Caccia 2007).

Growing evidence indicates that both the quality and density of the focal seed species and the characteristics and density of co-occurring seeds can result in short-term indirect effects between seed species, which are mediated by rodent seed predators (Veech 2000, 2001; Caccia, Chaneton & Kitzberger 2006; Pearson, Callaway & Maron 2011; Emerson *et al.* 2012; Schnurr, Ostfeld & Canham 2012; Ostoja *et al.* 2013; Garzon-Lopez *et al.* 2015). If scatter-hoarding rodent seed dispersers hide some seed caches and they are not retrieved, scatter hoarding can increase seed survival and dispersal relative to when seeds are immediately consumed upon harvest

(Vander Wall, Kuhn & Beck 2005; Xiao, Zhang & Krebs 2013). Through altering seed survival, scatter hoarding foraging decisions could change whether the presence of heterospecific seeds leads to rodents creating apparent mutualism or competition. However, all previous studies on this topic (that we are aware of) have measured only seed harvest by animals and not considered the effects of scatter hoarding. Consequently, the findings are applicable only to pure seed predators. Therefore, if seed-fate data are also measured after harvest, contrasting patterns of indirect seed–seed effects mediated by scatter-hoarding animals might be observed (Fig. 1).

A FRAMEWORK FOR MEASURING INDIRECT SEED–SEED INTERACTIONS VIA SCATTER-HOARDING RODENTS

In most conditions, we know that there are more than two seed species co-occurring in a given forest, and each seed species may have some isolated fruiting trees forming monospecific patches and also have overlapping canopies with other seed species as mixed patches (e.g. seed A and B in Fig. 1). Thus, we expect that indirect interactions among these co-occurring seed species would be most common when these seed species have shared seed predators and/or seed dispersers.

When co-occurring seeds are distributed in isolated or mixed patches of a forest, patch use or habitat selection is the first decision made by foraging animals to determine where to find food, and it can be affected by both quality and quantity of co-occurring seeds (see Brown & Morgan 1995). When two or more seed species co-occur within patches; however, the fate of each seed handled by scatter-hoarding rodents is more complicated and can be shown in a dichotomous way according to a sequence of foraging decisions (Fig. 1): harvested vs. not harvested (avoid); removed vs. eaten *in situ* after harvest; cached vs. eaten elsewhere after removal; and dispersed (cached with intact embryos) vs. dead (cached with removed embryos). Previous studies have measured seed harvest or removal within patches by rodent seed predators (Fig. 1 solid line box P). However, scatter-hoarding rodents as seed dispersers (dashed line box D) include additional behavioural decisions such as the caching of seeds with intact embryos (benefit to seed dispersal) once harvested or encountered (Fig. 1). In most cases, scatter-hoarding rodents do not cut out the embryos of cached seeds, and the final step could be deleted. Therefore, indirect seed–seed interactions may be viewed quite differently depending on whether the harvested seeds are hoarded (dispersed) or not by the animals. Considering scatter-hoarding rodents as seed dispersers, we can make the following predictions with unpalatable and palatable seeds co-occurring in a habitat: (i) apparent competition occurs when neighbouring unpalatable seeds reduce the removal and subsequent dispersal of palatable seeds because of reduced foraging in mixed patches; whereas (ii) apparent mutualism arises

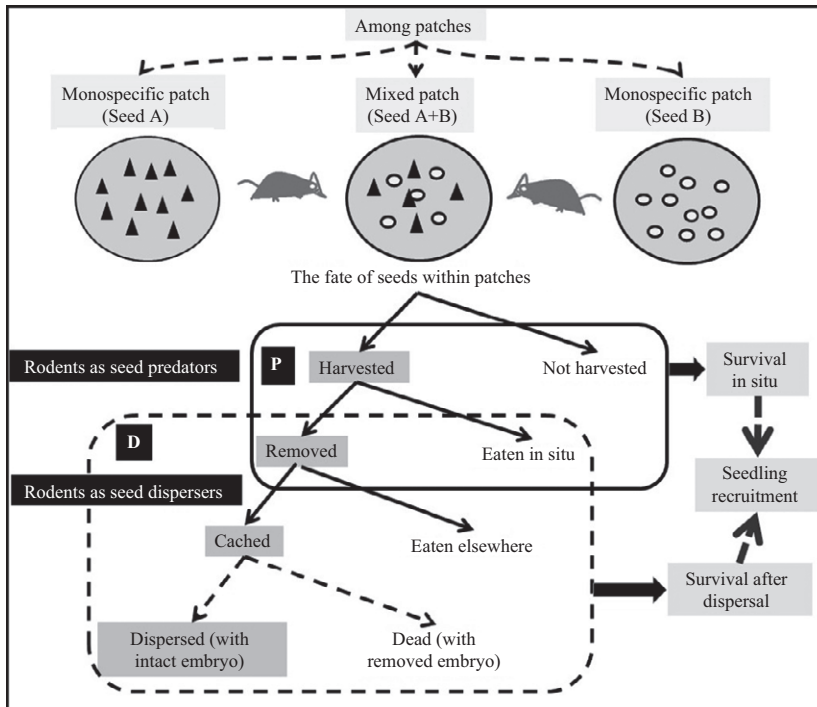


Fig. 1. A framework for indirect seed–seed interactions via foraging decisions by scatter-hoarding rodents. Here, we assume that two rodent-dispersed seed species A and B co-occur within a given forest, and each species has some isolated fruiting trees forming monospecific patches (only seed A or B) and also has overlapping canopies with each other as mixed patches (seed A+B). The fate of seeds handled by scatter-hoarding rodents can be shown in a dichotomous way according to a sequence of foraging decisions. Previous studies have measured seed harvest or removal within a food patch by rodent seed predators (solid line box P), but scatter-hoarding rodents as seed dispersers (dashed line box D) also include additional behavioural decisions such as caching of seeds with intact embryos (a benefit to seed dispersal) or with removed embryos (no benefit to seed dispersal).

when neighbouring palatable seeds increase the removal and subsequent dispersal of unpalatable seeds because of increased foraging time in mixed patches.

A CASE STUDY

We present here a case study to test the above framework in a subtropical forest in south-west China using a replacement design and tracked the fate of individually tagged seeds in experimental patches. We manipulated the benefits to rodents using low-tannin dormant chestnuts (*Castanea henryi*) as palatable food and high-tannin non-dormant acorns (*Quercus variabilis*) as unpalatable food. The replacement design was used to compare focal seeds with other co-occurring seeds with constant total density in a given patch foraged by shared seed predators and/or dispersers (see recent review in Underwood, Inouye & Hambäck 2014). In the study site, Pallas's squirrel (*Callosciurus erythraeus*) is the primary scatter hoarder of large seeds from Fagaceae species (Xiao *et al.* 2009; Z. Xiao, unpublished data), although several other rodent species, such as *Apodemus* spp. and *Niviventer* spp., are also found to eat and occasionally hoard these seeds (Xiao, Chang & Zhang 2008). We found that these rodent species preferred to harvest (consume or hoard) palatable chestnuts over unpalatable acorns (Xiao, Chang & Zhang 2008; Xiao *et al.* 2009). In addition, Pallas's squirrel is the only rodent species to remove the embryos from several Fagaceae species (e.g. *Castanea* spp., *Quercus* spp. and *Cyclobalanopsis* spp.) prior to hoarding, and other rodent species do not show such embryo-removal

behaviour (Xiao, Chang & Zhang 2008; Xiao *et al.* 2009). The behavioural parameters from these seed-eating rodents measured in this study included seed encounter per patch (i.e. the probability of at least one seed being harvested from a food patch), seed harvest, seed hoarding and dispersal within patches. We aimed to test the following four key predictions to assess how patterns of indirect effects changed with related behavioural parameters:

- (1) Animals will harvest (eat or hoard) palatable chestnuts first and harvest fewer unpalatable acorns (as predicted by the high-tannin hypothesis); additionally, non-dormant acorns will have a higher embryo-removal probability if they are hoarded compared with dormant chestnuts (as predicted by the food perishability hypothesis).
- (2) Seed encounter will be reduced by the presence of unpalatable acorns in a patch, but increase with the presence of palatable chestnuts in a patch, causing seed encounter to be higher in mixed patches than monospecific patches.
- (3) When rodents act as pure seed predators, unpalatable acorns will be subject to higher predation when in the presence of palatable chestnuts (apparent competition), whereas seed predation of unpalatable acorns will be reduced if animals prefer to consume palatable chestnuts (apparent mutualism).
- (4) When rodents act as seed dispersers by scatter hoarding of seeds, unpalatable acorns will reduce the removal and subsequent dispersal of palatable chestnuts (apparent competition), whereas palatable

chestnuts will increase the removal and subsequent dispersal of unpalatable acorns (apparent mutualism).

Materials and methods

STUDY SITE AND STUDY SPECIES

Field experiments were performed in the Qingcheng Mts. (900–1200 m elevation, 31°03'N, 103°43'E) in Dujiangyan City of Sichuan Province, south-west China, during the autumn of 2008. The habitat is subtropical evergreen broadleaved forest, where nut-bearing species such as Fagaceae species are the most common canopy trees, including *Castanea henryi*, *Castanea mollissima*, *Castanopsis fargesii*, *Castanopsis carlesii*, *Quercus serrata*, *Q. variabilis*, *Cyclobalanopsis myrsinarfolia*, *Lithocarpus harlandi* and *L. hancei*. The ground flora is poorly developed, consisting of small patches of *Dicranopteris pedata* or grasses. The understorey layer is mainly composed of *Camellia* spp., *Symplocos stellaris* and *Pittosporum daphniphyloides*. Seed production of these Fagaceae species varies greatly during the past 10 years and their seeds are consumed and/or hoarded by several rodent species (Z. Xiao, unpublished data).

Two Fagaceae species, *C. henryi* and *Q. variabilis*, were selected as experimental food items because their seeds vary greatly in tannin levels: *Q. variabilis* represented unpalatable seeds (11.7% tannin) and *C. henryi* represented palatable seeds (0.6% tannin) (Xiao, Zhang & Wang 2003; Xiao, Chang & Zhang 2008; Xiao *et al.* 2009). In the study site, *C. henryi* had a relatively large population (over 20 fruiting trees per ha.), but fewer *Q. variabilis* trees were found (Z. Xiao, unpublished data). Therefore, *C. henryi* chestnuts were much more abundant than *Q. variabilis* acorns in the study area. The fruit-ripening period of *Q. variabilis* occurred from late September to November, a little earlier than that of *C. henryi* (October to December).

EXPERIMENTAL DESIGN

We collected *C. henryi* chestnuts from Qingcheng Mt. and *Q. variabilis* acorns from the nearby Banruosi Experimental Forest because only few *Q. variabilis* individuals occurred in the study site. Seeds from each seed species were randomly selected for foraging experiments (total, 1620 seeds, from at least five fruiting individuals randomly selected for each species). Due to some variation in seed mass between the two species, we used only seeds with fresh seed mass of 2.5–3.5 g. The sampled seeds showed no sign of germination (i.e. no radicle protruding from the pericarp) at the start of the experiment. Each seed was labelled with a numbered plastic tag attached by a thin stainless steel wire of 10 cm long (see detailed procedures in Xiao, Jansen & Zhang 2006).

Most areas in Qingcheng Mt. are steep, so we chose three relatively gentle-sloped sites at different altitudes (QZG, 950 m; CYDX, 1000 m; CYDX, 1050 m). These three sites were separated from each other by at least 500–1000 m to ensure visitation by different individual squirrels at each site. In late October 2008, we established three foraging stations for each site, each ca. 50 m apart (see similar design for fox and grey squirrels in Emerson *et al.* 2012). Each foraging station included three foraging patches, two as monospecific patches and one as a mixed patch with seeds of the two species, and separated 10 m from other

patches within each foraging station. Based on Xiao *et al.* (2009) and the species-specific signs of embryo removal from the hoarded seeds, Pallas's squirrels were the primary visitors to these foraging patches.

We conducted all field work from late October to early December 2008. We placed 180 tagged seeds on the ground at each foraging station (area: 1 m²): two patches with either 60 *C. henryi* or *Q. variabilis* seeds and another mixed patch with 30 seeds of each seed species. Understorey vegetation for each foraging station was removed, and thus, all foraging stations were done with the same procedure. After one week, we checked each foraging patch and monitored the area around each foraging patch (diameter: 30 m) to retrieve tagged seeds and record their fates. Seeds at each foraging patch were categorized as 'remaining' (untouched), 'eaten *in situ*' (i.e. in the food station) and 'removed' from the food station, while those removed from foraging patches were categorized as hoarded (i.e. buried in the surface soil or covered with leaf litter), eaten (marks and seed fragments found) or missing (not retrieved). In addition, hoarded seeds were carefully excavated to identify whether their embryos were removed by animals. Distances to each foraging patch were also measured for hoarded or eaten seeds.

DATA ANALYSIS

To evaluate indirect effects, we considered two major types of foraging decisions by scatter-hoarding squirrels: seed encounter indicated patch use, and seed fate once encountered (i.e. selection within patches), which was divided into four successive dispersal measurements (Xiao 2016): harvested (including removed and eaten *in situ*) vs. not harvested; removed vs. eaten *in situ*; cached (including all hoarded seeds with intact or removed embryos) vs. eaten elsewhere; and dispersed (i.e. hoarded seeds with intact embryos) vs. dead (i.e. those with removed embryos, Fig. 1). The seed encounter data and the above seed-fate data represent binary outcomes, so we analysed each of them with generalized linear mixed models (GLMMs) with a binomial distribution (Package LME4, Bates *et al.* 2013; R 3.2.0, R Development Core Team 2015). The model for seed encounter included neighbourhood treatment (monospecific vs. mixed) and seed species as fixed factors and foraging station nested in site as a random factor. The analyses for seed-fate data for each seed species included neighbourhood treatment as a fixed factor and foraging station nested in site as a random factor. In addition, we also considered the indirect effects on dispersal distance of hoarded seeds. We used GLMMs with Gaussian error distribution to test the effects of neighbourhood treatment on dispersal distance (log₁₀-transformed) of the hoarded seeds with site as a random factor.

Results

During the experiments, we retrieved 75.7% of palatable chestnuts (181 seeds were missing) and 97.8% of the tagged unpalatable acorns (18 seeds missing). For unpalatable acorns, the rate of seed encounter was much higher in mixed patches (56%) than in monospecific patches (22%; $z = 28.27$, $P < 0.001$), which is consistent with Prediction (2). Conversely, nearly all of the monospecific or mixed patches containing palatable chestnuts were encountered by foraging animals. The

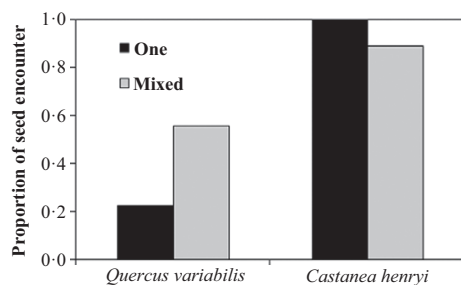


Fig. 2. Percentage of seed encounter of patches with *Quercus variabilis* (high-tannin non-dormant acorns as unpalatable food) and/or *Castanea henryi* (low-tannin dormant chestnuts as palatable food) for neighbourhood treatments (one vs. mixed patches).

interaction between neighbourhood treatment and seed species also had a strong effect on seed encounter ($z = -28.71$, $P < 0.001$; Fig. 2).

Squirrels harvested nearly all palatable chestnuts compared to <40% of unpalatable acorns, indicating a preference for the former over the latter (Prediction 1). The presence of palatable chestnuts in mixed patches significantly increased the harvest of unpalatable acorns 9%, compared to 2% in monospecific patches; $Z = -8.30$, $P < 0.001$, and the presence of unpalatable acorns in mixed patches marginally reduced the harvest of palatable chestnuts (Fig. 3a; Tables 1 and 2). In contrast, the removal rate of each seed species was increased in the presence of the other seed species, indicating apparent mutualism as in Prediction 3 if seeds were cached or apparent competition as in Prediction 4 if seeds were consumed (Fig. 3b; Table 1).

Seed caching of unpalatable acorns increased in the presence of palatable chestnuts in mixed patches, indicating apparent mutualism as in Prediction 4 (Table 1), but the presence of unpalatable acorns had no detectable effect on seed caching of palatable chestnuts when in the presence of unpalatable acorns (Fig. 3c). Neighbourhood treatment had no significant effect on seed dispersal of either seed species (Fig. 3d; Tables 1 and 2).

Mean dispersal distance for hoarded palatable chestnuts was much longer than that for unpalatable acorns, but neighbourhood treatment did not change dispersal distances of hoarded chestnuts with the presence of unpalatable acorns (Fig. 3e, Table 1). However, mean dispersal distance of hoarded unpalatable acorns increased with the presence of chestnuts, indicating apparent mutualism, as in Prediction 4 ($P < 0.05$; Fig. 3e, Table 2).

Discussion

Our study is the first to investigate how the interpretation of apparent competition and apparent mutualism varied depending on which behavioural parameters were measured by tracking the fate of individual seeds after harvest. This is more than a question of which measurement to use because the different measurements represent

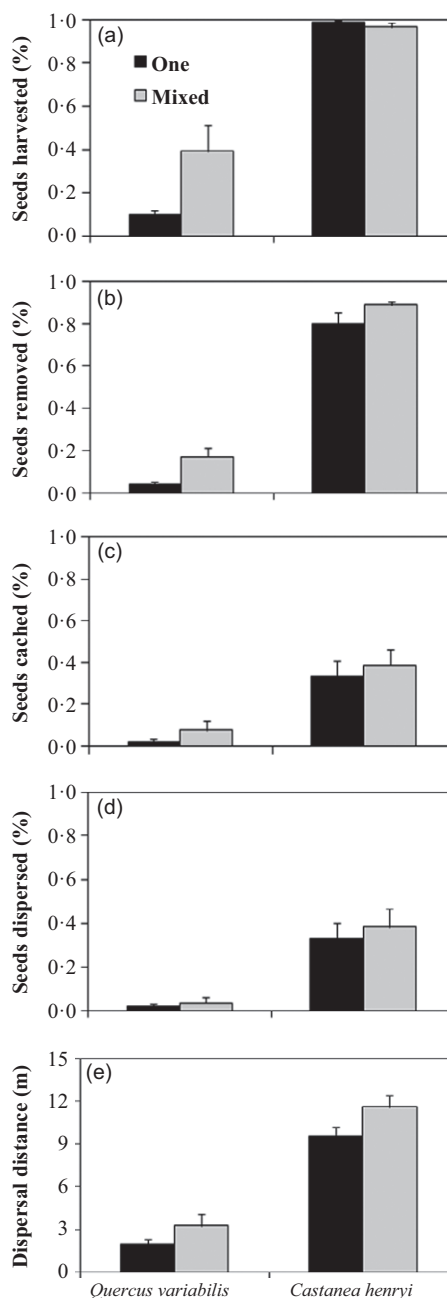


Fig. 3. Proportions of seeds (a) harvested, (b) removed, (c) cached, (d) dispersed and (e) dispersal distance (m) of hoarded seeds from *Quercus variabilis* (high-tannin non-dormant acorns as unpalatable food) and *Castanea henryi* (low-tannin dormant chestnuts as palatable food). Neighbourhood treatments: one, monospecific patches with either *Q. variabilis* acorns or *C. henryi* chestnuts; mixed, mixed patches with equal numbers of both *Q. variabilis* acorns and *C. henryi* chestnuts. Error bars show standard error (1 SE).

different stages in seed dispersal. Both among and within patches, the palatability of co-occurring seeds changed foraging decisions by scatter-hoarding animals, and these foraging decisions caused indirect effects between co-occurring seeds to vary in strength depending on whether the harvested seeds were hoarded or not.

Table 1. Summary of the indirect effects of the presence of palatable *Castanea henryi* chestnuts (neighbouring seeds) on squirrels' foraging decisions to unpalatable *Quercus variabilis* acorns based on generalized linear mixed models. Fixed factors in bold had significant effects ($P < 0.05$)

Behavioural parameters and fixed factors	Estimate	SD	z/t^*	P
Harvested				
(Intercept)	-0.51	0.31	-1.64	0.1
Neighbourhood treatment	-2.12	0.26	-8.30	<0.001
Removed				
(Intercept)	-2.48	0.47	-5.25	<0.001
Neighbourhood treatment	-1.42	0.32	-4.47	<0.001
Cached, including those with removed and intact embryos				
(Intercept)	-3.79	0.71	-5.35	<0.001
Neighbourhood treatment	-0.87	0.41	-2.15	0.032
Dispersed (cached with intact embryos)				
(Intercept)	-4.17	0.68	-6.13	<0.001
Neighbourhood treatment	-0.27	0.48	-0.56	0.578
Dispersal distance (m) of all cached seeds				
(Intercept)	0.71	0.18	3.93	<0.05
Neighbourhood treatment	-0.12	0.29	-0.42	> 0.1

* t^* is from significant effects of GLMMs with binomial distribution, and ' z ' from that of GLMMs with Gaussian error distribution.

Table 2. Summary of the indirect effects of the presence of unpalatable *Quercus variabilis* acorns (neighbouring seeds) on squirrels' foraging decisions to palatable *Castanea henryi* chestnuts based on generalized linear mixed models. Fixed factors in bold had significant effects ($P < 0.05$)

Behavioural parameters and fixed factors	Estimate	SD	z/t^*	P
Harvested				
(Intercept)	4.36	1.46	2.99	0.003
Neighbourhood treatment	3.05	1.59	1.92	0.055
Removed				
(Intercept)	2.37	0.38	6.26	<0.001
Neighbourhood treatment	-0.60	0.26	-2.30	0.022
Cached, including those with removed and intact embryos				
(Intercept)	-0.81	0.31	-2.63	0.009
Neighbourhood treatment	-0.08	0.19	-0.44	0.662
Dispersed (cached with intact embryos)				
(Intercept)	-0.37	0.35	-1.06	0.289
Neighbourhood treatment	0.002	0.22	0.01	0.994
Dispersal distance (m) of all cached seeds				
(Intercept)	2.18	0.08	26.89	<0.001
Neighbourhood treatment	-0.37	0.10	-3.66	<0.05

* t^* is from significant effects of GLMMs with binomial distribution, and ' z ' from that of GLMMs with Gaussian error distribution.

In this study, all else being equal, squirrels would have had an equal encounter probability with the two focal seed species either among or within experimental patches since seed size was similar between them. Thus, rodent foraging decisions are more likely to have been affected by seed palatability (e.g. tannin content and germination

schedule in this study). Our results confirmed the first prediction and our previous observations that in both monospecific and mixed patches, the animals harvested (ate or hoarded) palatable chestnuts first compared to unpalatable acorns (as predicted by the high-tannin hypothesis), and non-dormant acorns had a higher embryo-removal probability than dormant chestnuts (as predicted by the food perishability hypothesis, Steele *et al.* 2001; Xiao *et al.* 2009). The remaining three predictions also received some support from our analyses. Both among and within patches, short-term apparent mutualism was seen through reduced seed consumption rates (increased dispersal), produced by increased seed encounter, seed removal and seed caching of both species in mixed patches compared to those in monospecific patches (Prediction 2 and 4, Figs 2 and 3). In particular, the presence of palatable chestnuts resulted in higher seed removal of unpalatable acorns (Prediction 4). Though the presence of unpalatable acorns had no strong effect on seed dispersal of the preferred chestnuts, the weak indirect effect on seed dispersal of unpalatable acorns likely resulted from frequent embryo removal (52%) of cached acorns in mixed patches compared to only 8% embryo removal of cached acorns in monospecific patches. Apparent competition occurred when the presence of non-dormant acorns reduced survival or dispersal of dormant acorns. However, squirrels may treat non-dormant acorns as dormant acorns (reducing embryo removal) because the former may be mimicking the latter in some way (e.g. both show no visible signs of germination; Fox 1982). Thus, apparent mutualism could occur when the presence of dormant acorns reduces embryo removal of non-dormant acorns that are also hoarded. This did not occur, and instead, we found that apparent competition occurred because the embryo-removal probability of non-dormant acorns increased in mixed patches, which resulted in reduced seed dispersal (Prediction 3).

Failure to consider scatter hoarding behaviour strongly changed our impression of the indirect effects between seeds of different species. Compared with this study, other studies about the indirect effects from rodent-seed interactions found that apparent competition was common because the removal of less preferred seed species increased with the presence of more palatable seed species (Veech 2000, 2001; Caccia, Chaneton & Kitzberger 2006; Pearson, Callaway & Maron 2011; Emerson *et al.* 2012; Ostoja *et al.* 2013). In this study, we found a similar result when we treated all harvested seeds as consumed (not dispersed) (Prediction 3). However, if part of the seeds removed by scatter-hoarding animals were hoarded intact, leading to successful seed dispersal and germination, apparent mutualism would be seen between heterospecific seeds (Prediction 4).

Various studies have reported that the mutualism between scatter-hoarding animals and seed plants is context dependent (Theimer 2005; Klinger & Rejmánek 2010; Zhang *et al.* 2016). However, little is known about

how the indirect effects among co-occurring rodent-dispersed plants can be changed in a community with temporally variable seed availability (but see Kitzberger, Chaneton & Caccia 2007). Besides seed palatability characteristics shown in this study, availability of each seed species co-occurring in a given forest often varies considerably over time and space. Such variation can affect foraging decisions of scatter-hoarding rodents, leading to large changes in seed predation and dispersal, such as poor seed dispersal but high seed survival in seed-rich years or sites, and higher seed dispersal in seed-poor years or sites (Xiao, Zhang & Krebs 2013). In general, shared predators (here scatter-hoarding rodents) can also switch from focal seeds to other co-occurring seeds based on the changes in the availability of focal seeds (Kitzberger, Chaneton & Caccia 2007). Therefore, higher or reduced seed availability of one species can either reduce or increase seed dispersal or predation of co-occurring species (Kitzberger, Chaneton & Caccia 2007; Lichti *et al.* 2014; Z. Xiao, unpublished data). It is worthwhile testing whether such indirect seed–seed interactions are reciprocal or not due to spatiotemporal variation in seed availability (Caccia, Chaneton & Kitzberger 2006; Martínez, García & Herrera 2014). In addition, shared seed dispersers are often a limited resource for co-occurring animal-dispersed plants because their densities are low. Such rare seed dispersers may be more likely to produce apparent competition, especially when one seed species is highly dependent on limited seed dispersers compared to a plant species with more seed dispersers.

In conclusion, our study presents a testable framework to measure and understand indirect effects between co-occurring seeds mediated by scatter-hoarding rodents as seed predators and dispersers. The framework established in this study can be applied to rodent seed systems or other similar systems. Our study has shown that foraging decisions by scatter-hoarding animals can result in short-term indirect interactions between heterospecific seeds, and the indirect effects may vary depending on whether the harvested seeds are hoarded or eaten. In most forest ecosystems, scatter-hoarding animals act as shared seed dispersers and predators for many co-occurring seed species (Vander Wall 1990, 2001; Schnurr, Ostfeld & Canham 2012; Lai, Guo & Xiao 2014; Garzon-Lopez *et al.* 2015; Zhang *et al.* 2016). We highlight that considering context-dependent behavioural patterns of seed use by seed-eating rodents may give different measures of rodent-mediated indirect interactions and their effect on seed survival, seed dispersal and early recruitment among co-occurring plants. Further testing is required to determine to what extent animal-mediated indirect effects among co-occurring seeds are context or scale dependent, because many other important factors can potentially affect patterns of seed predation/dispersal and selectivity. These include spatial and seed availability of co-occurring seeds in a given forest, rodent density of the focal and other species, the

abundance of rodent predators, and microsite types and conditions in the understorey (Brown & Morgan 1995; Chaneton & Bonsall 2000; Schnurr *et al.* 2004; Caccia, Chaneton & Kitzberger 2006). In addition, future work should investigate the long-term consequences of short-term indirect effects for late-stage seed fates if the magnitude and sign of indirect effects vary over time (Kitzberger, Chaneton & Caccia 2007).

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Data accessibility

Data available from figshare: <https://dx.doi.org/10.6084/m9.figshare.3189775.v1> (Xiao 2016).

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