

ORIGINAL ARTICLE



Palatability and profitability of co-occurring seeds alter indirect interactions among rodent-dispersed trees

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Abstract

Beyond direct species interactions, seed dispersal is potentially affected by indirect seed–seed interactions among co-occurring nut-bearing trees which are mediated by scatter-hoarding animals as shared seed dispersers. A relevant question in such systems is to what extent different functional traits related to food palatability and profitability affect the kinds of indirect interactions that occur among co-occurring seeds, and the consequences for seed dispersal. We used field experiments to track seed dispersal with individually tagged seeds in both monospecific and mixed seed communities. We measured indirect effects based on 3 seed–seed species pairs from the family Fagaceae with contrasting seed size, tannin level, and dormancy in a subtropical forest in Southwest China. When all else was equal, the presence of adjacently placed seeds with contrasting seed traits created different indirect effects measured through a variety of dispersal-related indicators. Apparent mutualism was reciprocal due to increasing seed dispersal in mixed seed patches with mixed differences in seed tannins and dormancy. However, differences in either seed size or dormancy in co-occurring adjacently placed seeds caused apparent competition with reduced seed removal or seed dispersal (distance) in at least one species. Our study supports the hypothesis that different functional traits related to food palatability and profitability in co-occurring seeds modify foraging decisions of scatter-hoarding animals, and subsequently cause indirect effects on seed dispersal among rodent-dispersed trees. We conclude that such indirect effects mediated by shared seed dispersers may act as an important determinant of seed dispersal for co-fruiting animal-dispersed trees in many natural forests.

Key words: dispersal distance, functional trait, scatter-hoarding rodents, seed dispersal, trait-mediated indirect interactions

INTRODUCTION

Seed dispersal is a critical step in recruitment to plant populations (Wang & Smith 2002). Many nut-bearing

tree species co-occur and simultaneously fruit in temperate and (sub)tropical forests and are reliant on scatter-hoarding rodents and birds for seed dispersal (Vander Wall 2001). These nut-bearing species often overlap in their timing of fruiting and seed dispersal (Lichti *et al.* 2014). Moreover, many nut-bearing trees produce seeds with a co-varying suite of functional traits, including seed size, nutrients, and chemical and physical defenses (Vander Wall 2001; Sundaram *et al.* 2015; Wang *et al.* 2016).

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However, it is challenging to quantify the relative contribution of different co-varying functional traits to animal foraging decisions and the consequences for seed dispersal (Hadj-Chikh *et al.* 1996; Wang & Chen 2009; Chang *et al.* 2009; Xiao *et al.* 2013a; Sundaram *et al.* 2018).

In a local community when 2 or more co-fruited plants produce large amounts of mature fruits simultaneously, shared seed dispersers often become a limited resource, and these circumstances could cause either strong competition for seed dispersers or facilitation of seed dispersal by attracting seed dispersal vectors (Martínez *et al.* 2014; Albrecht *et al.* 2015). In particular, animal vectors such as scatter-hoarding rodents can act as both shared seed dispersers and seed predators, and consequently seed survival and seed dispersal are critically dependent on both direct and indirect species interactions (Vander Wall 2001; Lichti *et al.* 2014; Xiao & Zhang 2016). Although the direct species interactions have been frequently studied (Vander Wall 2010; Xiao & Krebs 2016), indirect seed-seed interactions mediated by scatter-hoarding animals, for example, apparent competition, and apparent mutualism, have also been recently recognized to have important impacts on seed survival and seed dispersal among co-occurring nut-bearing trees (Lichti *et al.* 2014; Xiao & Zhang 2016; Zhang *et al.* 2016a; Pesendorfer & Koenig 2017; Bogdziewicz *et al.* 2018; Yang *et al.* 2019a). Apparent competition occurs when neighboring seeds reduce seed dispersal but improve seed survival in situ for the focus seed species, but apparent mutualism also exists when the presence of neighboring seeds increases seed dispersal of the focus seed species (Xiao & Zhang 2016). However, we know little about whether and to what extent trait-mediated indirect interactions among co-fruited plants affect seed dispersal through shared seed vectors.

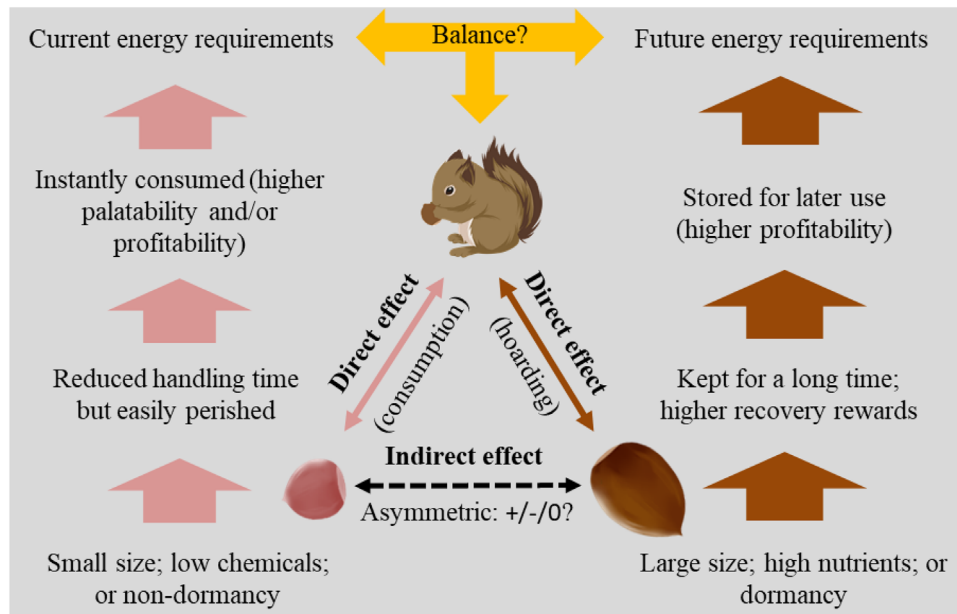
Figure 1 illustrates some potential effects of the relative palatability and profitability (i.e. food value) of adjacently-placed seeds on the types and strengths of trait-mediated indirect seed-seed interactions among rodent-dispersed trees. Functional traits in seeds often present different palatability and profitability (i.e. “utility” in Sundaram *et al.* 2018) for hoarding animals, and similarity and dissimilarity among functional traits in co-occurring seeds can affect foraging decisions of scatter-hoarding animals (Vander Wall 2001, 2010; Zhang *et al.* 2016b). Seed palatability and profitability also vary greatly over time and space as a function of seed characteristics and animal size, age, and nutrient and energy requirements (Vander Wall 2010; Sundaram *et al.* 2018). Unlike pure seed predators, scatter-hoarding rodents need to balance current energy requirements

through immediate seed consumption and future energy requirements through use after seed storage, which may help overcome seasonal and annual variation in the availability of seed resources (Gerber *et al.* 2004). A common pattern is that animals meet current energy requirements by consuming seeds with either high palatability (e.g. low secondary defense chemicals) or perishability (seeds lacking dormancy), while rejecting those with low profitability (small seeds with lower nutrients) (Hadj-Chikh *et al.* 1996; Xiao *et al.* 2008; Chang *et al.* 2009; Lichti *et al.* 2014; Sundaram *et al.* 2018). Conversely, animals hoard and store seeds with high-profitability (e.g. large size, high nutrients or dormancy) to meet future energy requirements (Hadj-Chikh *et al.* 1996; Chang *et al.* 2009; Vander Wall 2010; Sundaram *et al.* 2018). Instant consumption of highly palatable or perishable seeds may reduce handling time and predation risk during foraging (Vander Wall 2010; Sundaram *et al.* 2018). Whereas, later-use storage of highly profitable seeds can increase the certainty of food availability for weeks or months in the future, and these stored seeds can have high recovery rewards (Fig. 1a).

In this study, our major question is to what extent different functional traits among co-occurring seeds related to food palatability and profitability affect the kinds of indirect interactions that occur, and how these indirect interactions affect seed dispersal among rodent-dispersed trees. In theory, predator-mediated indirect effects can be reciprocal or non-reciprocal among co-occurring prey species (Holt & Lawton 1994; Chanton & Bonsall 2000; Veech 2000; Martínez *et al.* 2014). Moreover, we also expected that indirect effects among rodent-dispersed trees can be positive, negative, or neutral (Chanton & Bonsall 2000; Veech 2000; Xiao & Zhang 2016). When all else is equal, the theory of limiting similarity (MacArthur & Levins 1967) and the above seed palatability/profitability framework yield 2 key hypotheses, which we test with empirical experiments (Fig. 1b):

1. Co-occurring seeds with contrasting but mixed traits may experience apparent mutualism or apparent predation, manifesting via enhanced seed survival or dispersal in both species (apparent mutualism), or contrasting effects (increase vs reduction) in the co-occurring seeds (apparent predation) (Lichti *et al.* 2014; Xiao & Zhang 2016).
2. Co-occurring seeds with contrasting specific trait may experience apparent competition, manifested via reduced seed survival or dispersal in at least one species if foraging animals show strong preference (eaten or hoarded) to the specific seed trait. According to our previous studies with the same seed species

a A conceptual framework for indirect interactions among rodent-dispersed trees



b Question: To what extent do different functional traits related to seed palatability and profitability among co-occurring seeds affect the kinds of indirect interactions and how do these indirect interactions affect seed survival or dispersal among rodent-dispersed trees?

- (1) **Hypothesis:** Co-occurring seeds with contrasting but mixed traits may experience apparent mutualism or apparent predation, manifesting via enhanced seed survival or dispersal in both species (apparent mutualism), or contrasting effects (increase vs. reduction) in the co-occurring seeds (apparent predation).
- (2) **Hypothesis:** Co-occurring seeds with contrasting specific trait may experience apparent competition, manifested via reduced seed survival or dispersal in at least one species if foraging animals show strong preference to the specific seed trait.

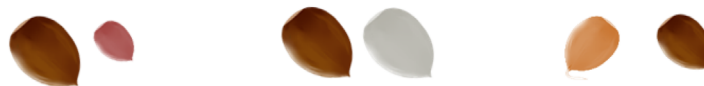


Figure 1 A conceptual framework (a) for trait-mediated direct (solid arrow) and indirect interactions (+/-/0, dashed-line arrow) among rodent-dispersed trees and one major question with two related hypotheses (b): To what extent do different functional traits related to food palatability and profitability among co-occurring seeds affects the kinds of indirect interactions and how do these indirect interactions affect seed dispersal among rodent-dispersed trees? Here the “profitability” for a given seed is considered as food value for hoarding animals. Unlike pure seed predators, scatter-hoarding rodents need to balance current energy requirement through instant consumption and future energy requirement through later-use storage. Current energy requirements through instant consumption indicate that animals prefer to firstly consume seeds with either high palatability (e.g. low secondary defense chemicals) or perishability (non-dormancy), but may reject those with low profitability (small seeds with low nutrients). Conversely, future energy requirements through later-use storage indicate that animals prefer to hoard highly profitable seeds (e.g. large size, high nutrients, or dormancy). This is because the instant consumption of high-palatable or perishable seeds may reduce both handling time and potential predation risk during foraging, while later-use storage of highly-profitable seeds can reduce uncertainty in food supply days to several months in the future.

Table 1 The properties of the seed–seed pairs used to test the trait-mediated indirect effects

Seed pairs	Seed mass (<i>n</i> = 450, mean \pm SE g)	Protein (%)	Fat (%)	Starch (%)	Crude fiber (%)	Tannin (%)	Germination schedule	Hull hardness
(1) Seed–seed pair with contrasting tannins and dormancy								
<i>Castanea henryi</i>	2.84 \pm 0.61	7.05	1.11	58.71	2.31	0.57	Dormant	Soft
<i>Quercus variabilis</i>	2.92 \pm 0.56	5.92	3.94	54.17	2.87	11.68	Nondormant	Soft
(2) Seed–seed pair with contrasting seed size								
<i>Lithocarpus harlandii</i>	2.95 \pm 0.56	5.80	0.91	66.33	1.80	1.34	Dormant	Hard
<i>Lithocarpus hancei</i>	0.84 \pm 0.38	7.87	0.89	65.03	1.45	1.37	Dormant	Hard
(3) Seed–seed pair with contrasting seed dormancy								
<i>Quercus serrata</i>	1.41 \pm 0.17	6.07	3.02	54.01	3.41	10.62	Dormant	Soft
<i>Cyclobalanopsis myrsinifolia</i>	1.56 \pm 0.39	4.80	1.88	55.42	2.24	11.05	Nondormant	Soft

The data from Xiao *et al.* (2005), Xiao *et al.* (2008), and this study (*Cy. myrsinifolia*, *L. harlandii*, and *L. hancei*). The difference in each key trait was shown for each seed pair in bold.

(Jansen *et al.* 2004) or different seed species (Xiao *et al.* 2003, 2005; Chang *et al.* 2009), for example, scatter-hoarding rodents prefer to hoard larger seeds but instantly consume smaller seeds (Vander Wall 2010; Sundaram *et al.* 2018).

We tested the above hypotheses by using field experiments to track the detailed fates (in situ survival, harvested, and then eaten elsewhere, or dispersed with or without intact embryos) of individually tagged seeds in both monospecific and mixed seed communities (Xiao & Zhang 2016). We measured the indirect effects among rodent-dispersed trees based on 3 seed–seed species pairs from family Fagaceae with contrasting seed size, tannin levels, and dormancy in a subtropical evergreen forest in Southwest China.

MATERIALS AND METHODS

Study site and study species

Field experiments were conducted within a 200-km² area in the Qingcheng Mts. (900–1200 m elevation, 31°03'N, 103°43'E) in Dujiangyan City of Sichuan Province, Southwest China during the autumn (September–December) of 2014. Qingcheng Mts. is a national forest park, and its vegetation is subtropical evergreen broadleaved forest. At the study site, nut-bearing species of Fagaceae are the most common canopy trees, including *Castanea henryi*, *Castanea mollissima*, *Castanopsis fargesii*, *Castanopsis carlesii*, *Quercus serrata*, *Quercus variabilis*, *Cyclobalanopsis myrsinifolia*, *Lithocarpus harlandii*, and *Lithocarpus hancei*. Six

species are most common: *C. henryi*, *Ca. fargesii*, *Ca. carlesii*, *Cy. myrsinifolia*, *L. harlandii*, and *L. hancei*, while other Fagaceae species have limited populations with only several or dozens of individual adult trees. These Fagaceae species have high fruiting period overlap during the autumn and display several convergent and divergent traits in seeds and fruits.

In this study, we identified 3 pairs of tree species with contrasting seed size, tannin level, or dormancy (Table 1): CH–QV tannin pairs with contrasting tannin level and dormancy (CH, low-tannin but dormant *C. henryi*, and QV, high-tannin but non-dormant *Q. variabilis*), LLH–SLH size pairs with contrasting seed size (LLH, large-seeded *L. harlandii*, and SLH, small-seeded *L. hancei*), and CM–QS dormant pairs with contrasting seed dormancy (CM, dormant *Cy. myrsinifolia*, and QS, non-dormant *Q. serrata*). The properties of the 3 seed–seed pairs are given in Table 1 and the nutrient and tannin properties were based on the mixture of seeds from more than 3–5 fruiting trees for each seed species (Table 1). Seed production of these species varies greatly and their seeds are consumed and/or hoarded by several sympatric rodent species such as *Callosciurus erythraeus*, *Leopoldamys edwardsi*, *Apodemus* spp., and *Niviventer* spp. Both *Cl. erythraeus* and *Le. edwardsi* are important scatter-hoarding seed dispersers at the study site (Xiao *et al.* 2009; Xiao & Zhang 2016). Based on our long-term studies over the past 20 years in the Dujiangyan region, these rodents show similar food preferences to eat and hoard seeds mostly based on seed size, tannins, and dormancy (Xiao *et al.* 2005, 2008; Chang *et al.* 2009). In addition, our field observation with embryo-removed *Q. variabilis*

seeds indicates that *Cl. erythraeus* (Pallas squirrel) was the primary scatter hoarder species because no other rodent species cut the embryo of non-dormant seeds at the study site (Xiao *et al.* 2009; Xiao & Zhang 2016).

Experimental design

During the fruiting season, we collected seeds for the 3 seed–seed pairs in the study. *C. henryi*, *Q. serrata*, *Cy. myrsinifolia*, *L. harlandi*, and *L. hancei* were collected from Qingcheng Mt. and *Q. variabilis* seeds were collected from the nearby Banruosi Experimental Forest (31°4'N, 103°43'E) because *Q. variabilis* seeds were not available at the study site. Seeds were randomly selected for the seed–seed pair experiments to give a total of 2700 seeds and each tree species from at least 5 fruiting individual trees was randomly selected. For each of the 3 seed–seed pairs, we identified 1 or 2 key traits with distinct difference between the paired seeds, but carefully selected seeds that were as similar as possible in other traits such as morphology, phenology, and nutrients (Table 1). All seeds were individually labeled with a numbered plastic tag attached by a 10-cm-long thin stainless-steel wire (see detailed procedures in Xiao *et al.* 2006).

During the autumn (September–December 2014), we used the same sites and seed tracking procedures established by Xiao and Zhang (2016) to study the direct and indirect interactions between scatter-hoarding rodents and nut-bearing trees with the 3 seed pairs. Three survey sites with 27 foraging stations in total (9 stations at each site, and separated by at least 50 m) were established at different altitudes (QZG, 950 m; CYDX, 1000 m; CYDX, 1050 m). Each foraging station included 3 seed patches with 100 tagged seeds on the ground: 2 as monospecific patches (25 seeds of either seedA or seedB) and 1 as a mixed patch (25 seeds of each seed species) with seeds of the 2 species, and separated 10 m from other patches within each foraging station.

Understory vegetation at each foraging station was cleared. After 4 weeks, we checked each foraging patch and searched 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. at the food station), or “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 the removed seeds that were hoarded or eaten.

Data analysis

After 4 weeks, all seed patches had been visited by seed-eating animals and nearly all seeds had been either consumed or removed from each seed patch. In this study, only dispersal-related indicators were used to quantify the indirect effects of seed dispersal between adjacently-placed seeds (Xiao & Zhang 2016). We included 3 dispersal-related indicators: the proportion of seeds removed from each seed patch, the proportion of seeds dispersed with intact embryos from each patch, and dispersal distance of the dispersed seeds from the seed source.

We fitted generalized linear mixed models (GLMMs) in R 3.5.1 (R Core Team 2018) using the Package lme4 (Bates *et al.* 2013). For each seed–seed pair, the seed removal or dispersal data were analyzed in GLMMs with a binomial distribution and logit link function. The GLMMs tested the effects of neighborhood treatment (monospecific vs mixed seeds) as a fixed factor and seed patch as a random factor. We also used GLMMs with a Gaussian error distribution to test the effects of neighborhood treatment on dispersal distance (log transformed) of the hoarded seeds with seed patch as a random factor. We found that our GLMM models fit the data and that the data met the assumptions of the model when we checked the variation of fitted residuals with a Bayesian simulation-based way by using simulateResiduals function in the DHARMa package (Hartig 2016). No overdispersion was detected with the “overdisp_fun”_function coded by Ben Bolker (2020, <https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html>). Moreover, we also used a likelihood ratio test to measure the significance of the fixed effects via the Anova function of the car package (Fox & Weisberg 2011). In addition, the Bayesian method was used with blmer function in “blme” package (Dorie 2015) to test the effects of neighborhood treatment on seed dispersal distance because of singularity in the GLMM analysis of *C. henryi* seed dispersal distance.

RESULTS

Adjacently placed seeds with contrasting seed tannins and dormancy

The removed proportion (94%) of bitter high-tannin dormancy-capable *Q. variabilis* seeds was only a little higher with the presence of sweet low-tannin *C. henryi* seeds compared to when *Q. variabilis* was the only type of seed available (91%) (Table 2 and Fig. 2a). The proportion of *Q. variabilis* dispersed was not significantly influenced

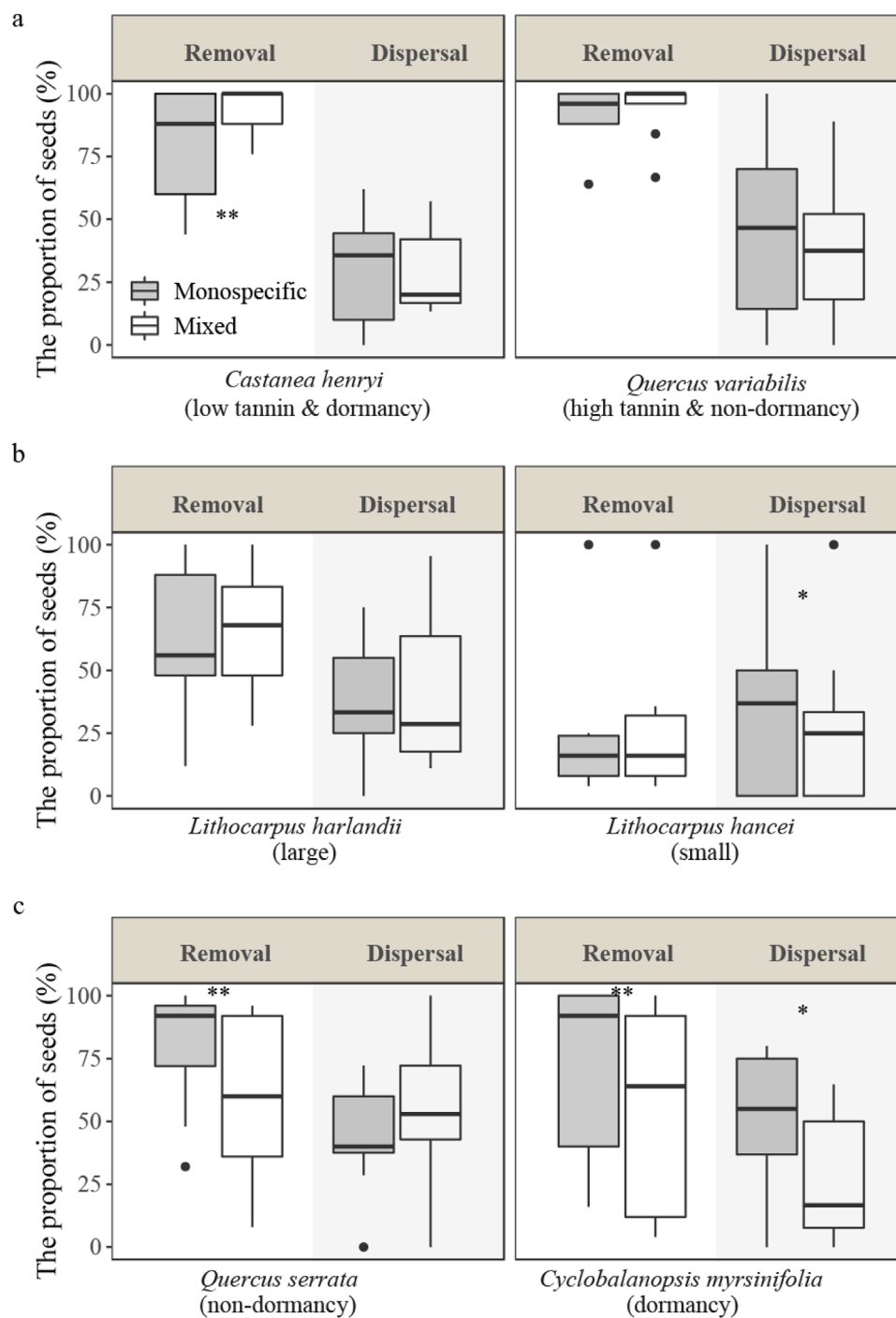


Figure 2 Proportions of seeds removed and then dispersed with intact embryos in monospecific and mixed patches for the 3 seed–seed pairs with contrasting seed tannins (*Castanea henryi* vs *Quercus variabilis*), seed size (*Lithocarpus harlandii* vs *L. hancei*), and seed dormancy (*Q. serrata* vs *Cyclobalanopsis myrsinifolia*). * and ** above pairs of bars for $P < 0.05$, $P < 0.01$, and refer to Table 2 for the statistical tests in the legend.

Table 2 Summary of the indirect effects (positive, negative, or neutral) of the presence of adjacently placed seeds on seed removal, seed dispersal, and dispersal distance of focus seeds for the 3 seed–seed pairs with contrasting seed tannins (*Castanea henryi*, CH vs *Quercus variabilis*, QV), seed size (*Lithocarpus harlandii*, LHL vs *L. hancei*, LHS), and seed dormancy (*Q. serrata*, QS vs *Cyclobalanopsis myrsinifolia*, CM) based on generalized linear mixed models

Seed pair	Adjacently placed seeds	Focus seeds	Indicator	χ^2	df	P	Sign of indirect effect
Tannin/dormancy	CH	QV	Removed	0.935	1	0.334	Neutral
			Dispersed	0.147	1	0.702	Neutral
			Dispersal distance	8.719	1	0.003	Positive
	QV	CH	Removed	19.058	1	<0.001	Positive
			Dispersed	0.055	1	0.815	Neutral
			Dispersal distance	4.93	1	0.026	Positive
Seed size	LHS	LHL	Removed	2.788	1	0.130	Neutral
			Dispersed	0.820	1	0.365	Neutral
			Dispersal distance	1.122	1	0.290	Neutral
	LHL	LHS	Removed	0.867	1	0.352	Neutral
			Dispersed	5.302	1	0.021	Negative
			Dispersal distance	0.260	1	0.210	Neutral
Dormancy	CM	QS	Removed	29.855	1	<0.001	Negative
			Dispersed	2.902	1	0.088	Neutral
			Dispersal distance	7.257	1	0.007	Negative
	QS	CM	Removed	21.471	1	<0.001	Negative
			Dispersed	4.039	1	0.044	Negative
			Dispersal distance	0.234	1	0.628	Neutral

The statistic significances were used likelihood ratio tests to estimate. Indicators in bold had significant effects (* $P < 0.05$ and ** $P < 0.01$).

by the presence of *C. henryi* (Table 2 and Fig. 2a), but the average dispersal distance was greater in mixed patches compared to *Q. variabilis* in monospecific patches (Table 2 and Fig. 3). For low-tannin non-dormant *C. henryi*, the presence of high-tannin dormancy-capable *Q. variabilis* seeds in mixed patches led to a higher proportion of seeds being removed (Fig. 2a) and a greater dispersal distance than those in monospecific patches (Table 2 and Fig. 3), but the proportion of seeds dispersed was not significantly changed (Table 2 and Fig. 2a).

Adjacently placed seeds with contrasting size

The presence of the larger seeds did not significantly change the proportion of small *L. hancei* seeds removed but significantly reduced the proportion dispersed (Table 2 and Fig. 2b). The presence of large *L. harlandii* seeds did not increase the average dispersal distance of

small *L. hancei* seeds (Table 2 and Fig. 3). In addition, we did not find significant indirect effects of small-seeded *L. hancei* on large-seeded *L. harlandii* based on the 3 dispersal-related indicators.

Adjacently placed seeds with contrasting seed dormancy

Compared to monospecific patches, seed dormancy reduced the proportion of seeds removed of both non-dormant *Q. serrata* (mixed, 59% vs monospecific, 79%) and dormant *Cy. myrsinifolia* (mixed, 55% vs monospecific, 71%) in mixed patches (Table 2 and Fig. 2c). Moreover, the presence of non-dormant *Q. serrata* also significantly reduced the dispersal proportion (mixed, 27% vs monospecific, 48%) of dormant *Cy. myrsinifolia* seeds compared to that in monospecific patches (Table 2 and Fig. 2c). However, average dispersal distance

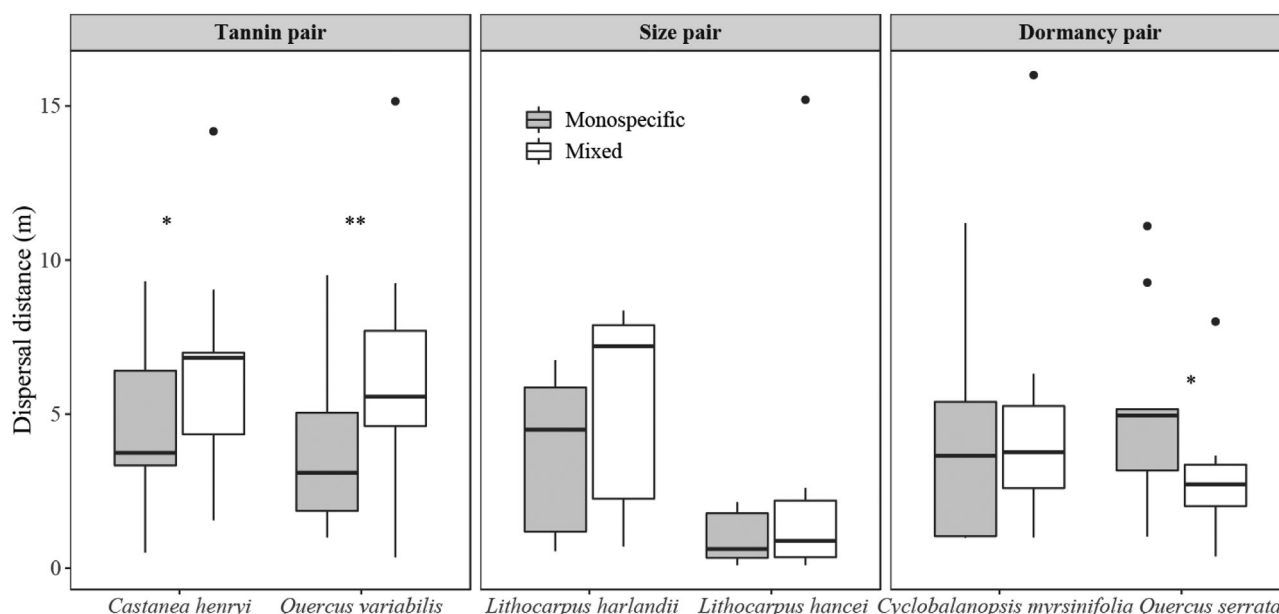


Figure 3 Dispersal distance (m) of the dispersed seeds from both monospecific and mixed patches for the three seed–seed pairs with contrasting seed tannins (*Castanea henryi*, CH vs *Quercus variabilis*, QV), seed size (*Lithocarpus harlandii*, LHL vs *L. hancei*, LHS), and seed dormancy (*Q. serrata*, QS vs *Cyclobalanopsis myrsinifolia*, CM). * and ** above pairs of bars for $P < 0.05$, $P < 0.01$, and refer to Table 2 for the statistical tests in the legend.

of non-dormant *Q. serrata* seeds was reduced when dormant *Cy. myrsinifolia* seeds were present in mixed patches (Table 2 and Fig. 3).

DISCUSSION

Based on the 3 seed pairs with contrasting seed tannins, size, or dormancy, our study showed that the presence of adjacently placed (neighboring) seeds with contrasting seed traits created different indirect effects, as revealed by 3 dispersal-related indicators. We found that compared to seeds in monospecific patches, contrasting seed tannins and dormancy in neighboring seeds (based on *C. henryi* vs *Q. variabilis* seed pairs) increased *C. henryi* seed removal and both species' seed dispersal distance in mixed seed patches (supporting apparent mutualism in **Hypothesis 1**). However, our results also supported the **Hypothesis 2** that neighboring seeds with contrasting seed size or dormancy caused negative indirect effects leading to decreased dispersal in at least one seed species. Therefore, our results support our idea that neighboring seeds with contrasting profitability and palatability can modify foraging decisions of scatter-hoarding rodents, and thus cause different indirect effects that affect seed dispersal among co-occurring animal-dispersed trees.

In this study, we found that trait dissimilarity related to relative palatability and profitability in neighboring seeds can cause different indirect effects (positive, negative, or neutral) and that such effects were seen in all 3 dispersal-related indicators for the rodent-dispersed trees (Table 2). For the *C. henryi* versus *Q. variabilis* seed pairs with contrasting seed tannins and dormancy, we found that apparent mutualism was reciprocal for each other due to increasing seed dispersal in mixed seed patches. However, when all else was equal, seed size caused asymmetric indirect effects between co-occurring seeds. We found that contrasting seed size in neighboring seeds only weakly increased seed dispersal of large-seeded *L. harlandii*, but reduced seed dispersal (but not dispersal distance) of small-seeded *L. hancei*. In addition, contrasting seed dormancy in neighboring seeds significantly reduced seed removal of both *Q. serrata* and *Cy. myrsinifolia*, reduced seed dispersal of dormant *Cy. myrsinifolia*, and reduced dispersal distance of *Q. serrata* in mixed patches. These results indicate that differences in seed size or dormancy can lead to apparent competition for seed dispersal among co-occurring seeds. Overall, our results indicate that the signs and magnitudes of the above indirect effects were related to dissimilarity of functional traits in seeds, as indicated by several dispersal metrics.

Our results provide evidence supporting the idea that each specific trait in seeds could have strong impacts on foraging decisions of scatter-hoarding animals as shared seed dispersers, and subsequently cause different direct and indirect effects on co-occurring nut-bearing plants. In our study, in situ survival (or decreased probability of seed harvest) would be beneficial for high-tannin or smaller seeds because these seeds have significant behavioral and physiological costs for hoarding rodents (Smallwood & Peters 1986; Shimada & Saitoh 2003; Vander Wall 2010). Otherwise, it would be better to be harvested than left undispersed. In general, larger seeds often indicate higher profitability (food value) for later-use storage than smaller ones (Jansen *et al.* 2004; Xiao *et al.* 2005; Vander Wall 2010; Sundaram *et al.* 2018). This indicates that smaller seeds may be more likely to be instantly consumed and thus benefit the dispersal of larger seeds (e.g. large-seeded *L. harlandii* in this study). In contrast, smaller seeds may also receive some benefits, such as increased dispersal distance or increased in situ survival after they are rejected, when larger seeds co-occur.

Interpretation is complicated by the fact that seed dormancy is not just linked to either palatability or profitability, but often indicates whether a given seed is perishable or not for storage and late use. Consistent with this pattern, some scatter-hoarding squirrels in North America and China are highly sensitive to reduced energy valued of seeds through rapid germination when they hoard non-dormant white oak seeds (Steele *et al.* 2001; Xiao *et al.* 2009). When considering storage-for-later-use, dormant seeds may be more profitable than non-dormant ones, but such profitability for non-dormant white oak seeds may also be achieved after scatter-hoarding squirrels cut seed embryos prior to hoarding (Steele *et al.* 2001; Xiao *et al.* 2009). In this study, we found that compared to zero seeds of dormant *C. henryi*, up to 10 *Q. variabilis* seeds in the entire experiment were found to be hoarded with removed embryos. Thus, embryo removal by scatter-hoarding squirrels can further reduce seed dispersal success of non-dormant *Q. variabilis* (Xiao & Zhang 2016).

In addition, tannin levels often indicate whether a given seed is more palatable or not (Smallwood & Peters 1986; Xiao *et al.* 2008; Wang & Chen 2009; Xiao & Zhang 2016; Kuprewicz & Garcia-Robledo 2019). High-tannin seeds (e.g. many *Quercus* species) often have significant behavioral and physiological costs due to their toxic effects (Smallwood & Peters 1986; Shimada & Saitoh 2003; Vander Wall 2010). However, hoarding animals can benefit from the storage of high-tannin seeds if seed chemicals can reduce microbe infestation and tannins can be degraded to a tolerable level for digestion during stor-

age (Fleck & Woolfenden 1997; Sundaram *et al.* 2018). This may be an important reason why many seeds with high levels of defensive chemicals are usually hoarded (Guimarães *et al.* 2003; Xiao *et al.* 2008).

In conclusion, our empirical evidence supports the hypothesis that dissimilarity of functional traits in co-occurring seeds related to food palatability and profitability could modify foraging decisions of scatter-hoarding rodents, and such decisions create reciprocal and asymmetric indirect effects among co-occurring plants (Fig. 1). This indicates that trait-mediated indirect effects mediated by shared seed dispersers may act as an important determinant of seed dispersal for co-fruited animal-dispersed trees in many natural forests. In this study, we found that each of the above seed traits (and likely some other co-varying traits in natural seeds) display different palatability and/or profitability, which could cause synergistic or antagonistic effects on seed dispersal among co-occurring plants. Therefore, foraging-mediated indirect effects of seed dispersal among co-occurring fruited plants may depend on a combination of multiple functional traits (or syndromes) in seeds (Sundaram *et al.* 2018) and also the availability of co-occurring seeds (Xiao *et al.* 2013b; Pesendorfer & Koenig 2017; Yang *et al.* 2019b). Since most studies about indirect seed-seed effects by shared animal vectors have lasted only a short time (few days, weeks or seasons), it is worthwhile to test the long-term consequences from short-term indirect effects among animal-dispersed trees and how the magnitude and sign of short-term indirect effects vary over time.

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