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Scatter-hoarding rodents select different caching habitats for seeds with different traits

Bo Wang† and Richard T. Corlett

Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan Province 666303 China

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Abstract. Seed caching by scatter-hoarding rodents is an important dispersal mechanism for many plant species, and the microhabitat of the caching site influences the quality and effectiveness of this dispersal. Shrub vegetation is a major determinant of microhabitat heterogeneity in the forest understory and influences both rodent activity and foraging behavior, and seed germination and seedling establishment. However, very few studies have investigated how shrubs affect this important mutualistic plant–animal interaction and how this is influenced by seed traits. In this study, we monitored rodent choices of caching microhabitat for 3564 artificial seeds that varied in size, nutrient content, and tannin content. By analyzing 1333 primary caches and 209 secondary caches, we showed that rodents selected different caching microhabitats for seeds with different traits. Larger and more nutritious seeds were cached in shrubs more frequently than in the open, while tannin content had no effects on the probability of seeds being cached in shrubs. Furthermore, shrub cover significantly increased the distance which seeds were transported by rodents. If these caching differences apply to natural seeds and persist through seedling establishment and subsequent growth, they could play an important role in the spatial pattern of forest regeneration.

Key words: foraging behavior; habitat effect; scatter-hoarding; seed dispersal; seed predation; seed size; species interactions; tannin content.

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† **E-mail:** yangblue@xtbg.org.cn

INTRODUCTION

Seed removal by scatter-hoarding rodents is one of the most important dispersal mechanisms for many plant species (Vander Wall 1990, 2010, Lichti et al. 2017). The hoarding behavior of rodents not only transports seeds away from their mother tree, where they would suffer strong density-dependent mortality (Janzen 1970, Nathan and Muller-Landau 2000, Jansen et al. 2014), but also can increase the probability of seedling establishment by caching seeds in a suitable habitat for germination (Wenny 2001, Pearson and Theimer 2004, Roth and Vander Wall 2005, Briggs et al. 2009). Thus, the distances which seeds are moved and the microhabitats in which they are cached will have a large influence on the quality and effectiveness of seed dispersal by rodents.

When a rodent encounters a seed, seed traits can influence whether it is consumed in situ or removed and then cached, and how far it is moved (Vander Wall 2010, Wang et al. 2013). For example, larger and more nutritious seeds are more likely to be removed and are transported further (Jansen et al. 2004, Moore et al. 2007, Wang and Chen 2009, Vander Wall 2010). Defensive compounds (e.g., tannins) have also been found to influence seed caching probability and dispersal distance (Xiao et al. 2008, Wang and Chen 2009, 2011, Vander Wall 2010, Shimada et al. 2015).

Many studies have compared rodent preferences for microhabitats as caching sites, and suggested possible explanations involving the risks of predation and seed pilferage (Li and Zhang 2003, Lu and Zhang 2004, Iida 2006, Perez-Ramos et al. 2008, Muñoz and Bonal 2011, Steele et al. 2015). However, only a few studies have examined the effects of seed traits (mainly seed size) on the microhabitat of the caching sites that rodents choose. For example, Steele et al. (2014) found that squirrels preferred to cache larger acorns at greater distances from tree crowns (i.e., in open habitats), and also suggested a possible explanation that high predation risk in open habitats could reduce the pilferage of their more profitable seeds. However, Vander Wall (2003) did not find any significant differences among seeds of different sizes in chipmunk preferences for caching microhabitats.

Shrub vegetation has a large influence on microhabitat heterogeneity in the forest understory, that is, the pattern of shrub cover vs. open habitat. This is significant for both rodents and plant seeds. On the one hand, shrubs can increase rodent activity and foraging behavior by providing shelter, which decreases the predation risk and foraging cost (Kotler et al. 1991, Den Ouden et al. 2005, Perez-Ramos and Maranon 2008, Perea et al. 2011*a*). On the other hand, shrubs can influence not only seed survival, by increasing the activity of seed predators (Den Ouden et al. 2005, Perea et al. 2011*a*), but also seedling establishment, by altering light, heat, and water conditions and providing protection from herbivores (Duncan and Chapman 1999, George and Bazzaz 1999*a*, *b*, Dubois et al. 2000, Pulido and Diaz 2005, Smit et al. 2009).

Several studies have compared the ratio of seeds cached in shrubs and open habitats within a species (Li and Zhang 2003, Lu and Zhang 2004, Perea et al. 2011*b*), without considering the potential for differences in the effects of shrubs on different seed species (but see Vander Wall 2003). Rodents usually treat different species of seeds differently during the scatter-hoarding process, because of their varied seed traits (Vander Wall 2010), so different species of seeds may be cached in different habitats. Any differences among seed species in the effects of shrub cover on seed predation and dispersal could, in turn, influence seed survival and forest regeneration.

In this study, we explore differences among seeds with different traits in the effects of shrubs on seed caching by rodents. Rodents' caching preference among different species of seeds mainly depends on seed traits (Vander Wall 2010). However, it is hard to separate the relative effects of multiple traits by using different species of natural seeds. Artificial seeds provide the opportunity to vary single traits experimentally, while keeping other traits constant (Wang and Chen 2009, 2011, 2012). We therefore used several series of artificial seeds with different traits (i.e., seed size, nutrient and tannin contents) to mimic different species of seeds. We attempt to answer the following questions: (1) "Does shrub cover affect the probability of seed caching, the dispersal distance, and the fate of cached seeds?" (2) "Do the effects of shrub cover differ among seeds with different seed traits?"

MATERIALS AND METHODS

Study area

The field data analyzed here were collected in 2007 in a natural forest at the Shangri-La Alpine Botanical Garden (27°54′ N, 99°38′ E, altitude 3456 m), Yunnan Province, southwestern China. The tree layer at 15–25 m consists largely of *Pinus densata*. Underneath, there is a single, discontinuous, shrub layer, 30–100 cm in height, dominated by an evergreen oak, *Quercus monimotricha*, and some *Rhododendron* spp., over a sparse cover of herbs and mosses. The Sichuan field mouse (*Apodemus latronum*) and Chevrier's field mouse (*Apodemus chevrieri*) are the two most abundant seed predators/dispersers in the forest (Wang and Chen 2009, 2011, 2012). Both rodent species have similar body masses (~30 g) and foraging behaviors (Wang and Chen 2011).

Shrub cover survey

Twenty-six plots (10 × 10 m) at least 20 m apart were haphazardly selected in the forest. We made a shrub map and then calculated the area of shrub cover for each plot. The mean ratio of shrub cover to open habitat was 46.2% ± 20.3% vs. 53.8% ± 20.3% (mean ± SD). This ratio was then used as the expected availability of shrub and open habitat against which to compare caching patterns of rodents.

Experimental design

We used three univariate series of artificial seeds made from clay, peanut powder, and tannin: (1) seed size—10 values: 0.2, 0.4, 0.6, 0.9, 1.2, 1.5, 2.0, 2.5, 3.0, and 4.0 cm in diameter (a total of 108 × 10 = 1080 seeds), with each seed consisting of 50% peanut powder and 50% clay, (2) nutrient content—eight values, with the percentage of peanut powder: 0, 10, 20, 30, 40, 50, 60, and 70 (totaling 108 × 8 = 864 seeds), with each seed the same size (1.5 cm in diameter), and (3) tannin—seven values of percentage of tannin: 0.1, 0.5, 1, 5, 10, 15, and 25, with each seed the same size (1.5 cm in diameter) and consisting of 50% peanut powder. Different series were created for hydrolyzable and condensed tannins, with one control containing no tannin, giving a total of 108 × 15 = 1620 seeds. These two tannin series were combined into a single treatment during our analysis, because no differences were found in the effects of the two types of tannin on rodent foraging behavior (Wang and Chen 2009). A 15 cm thin steel thread with a small red plastic tagged was connected to each artificial seed so they were easy to relocate (Xiao et al. 2006). In this study, we used seed diameter as a measure of the size of the artificial seeds, because diameter is much easier to artificially control, although most recent studies have used seed mass (Jansen et al. 2004, Moore et al. 2007, Steele et al. 2014). Both the masses and volumes of seeds tend to correlate with their energy content (Vander Wall 2003, Wang et al. 2012, Gong et al. 2015), and rodent foraging behavior responds similar to seed mass and seed volume indicators (Holl and Lulow 1997, Wang et al. 2012). The one recent exception to this showed that an *Apodemus* species, similar in size to our commonest rodents, used seed "size" (meaning length and diameter) rather than mass to assess profitability (Yi and Wang 2015).

Six plots (2 × 2 m) >50 m apart were haphazardly set up in the forest to conduct the three univariate-trait experiments one by one. We assumed this separation was sufficient to assure independence, given the small sizes of our two dominant rodent species, although their home range sizes are not known. Other *Apodemus* species have widely varying home range sizes (hundreds of square meters to several hectares), differing among species, sexes, and individuals (Attuquayefio et al. 1986, Oka 1992, Vukicevic-Radic et al. 2006); some *Apodemus* species are territorial, especially the females (Attuquayefio et al. 1986, Wolff 1993). However, we have conducted seed dispersal experiments in this study area for more than 10 yr, and the overwhelming majority of seeds were dispersed less than 20 m (Wang and Chen 2009, 2011, 2012, Wang et al. 2012, 2014, Wang and Yang 2014, Wang and Ives 2017).

At each plot, nine subplots were established in 3 × 3 grids, with about 1 m between subplots (Appendix S1: Fig. S1). Two seeds of each value of size (or nutrient or tannin contents) were placed in each subplot. In total, 108 seeds of each kind were spread evenly over the six plots (2 seeds × 9 subplots × 6 plots). We checked the plots and recorded seed harvest (i.e., seeds eaten in situ or removed away from their releasing point) 11 times, that is, days 1, 2, 3, 4, 6, 8, 12, 16, 20, 28, and 36 after seed placement. We conducted a complete search within 20 m of each plot in all directions to relocate the removed seeds. We also conducted an extra search in a larger area in order to relocate as many seeds as possible. When we found a seed, we recorded whether it was intact or eaten, and the exact location with a directional angle and the distance to their original seed sources. For the microhabitat of the caches, we initially used similar categories to Vander Wall (2003), open, within 10 cm of the edge of a shrub, and under a shrub, but we combined the latter two categories during analysis because very few seeds were cached within 10 cm of the edge of a shrub. At subsequent visits, we checked all caches identified in the previous visit, until they were removed or eaten by rodents. If a marked cache was removed, then the area around the cache (radius of at least 20 m) was searched for re-cached seeds.

Full descriptions of the experiment design and the effects of seed traits on seed fates were reported by Wang and Chen (2009) and Wang et al. (2014).

Data analysis

A generalized linear mixed model (package "lme4") was used to analyze fates of cached seeds (i.e., eaten in situ or removed again) with a binomial error distribution and logit-link function. A linear mixed-effects model (package "nlme") was used to analyze the effects on seed dispersal distance. We fitted the response variable (i.e., dispersal distance) to a normal distribution after log transformation. In both models, fixed effects were habitat and seed traits (i.e., seed size, nutrient or tannin contents), while random effects were considered in a nested structure (subplot nested in plot). A generalized linear mixed model was also used to analyze the probability of seeds being cached in shrubs vs. open habitat, and seed traits were treated as fixed effects with the same nested structure random effects. A chi-squared test was used to test the accordance of the proportion of seeds cached in shrubs vs. open habitat with the expected ratio, that is, the availability of shrub cover and open habitat in the forest. All the analyses were performed in R (v. 3.1.2; R Core Team 2015).

RESULTS

Proportion of seed caching in shrubs vs. open

In total, 355, 340, and 638 primary cached seeds were found from our seed size, nutrient, and tannin experiments, respectively. The proportion of seeds cached in shrubs vs. open habitat was in accordance with the ratio of these two habitats (46.2% vs. 53.8%) in the forest: 46.2% cached in shrubs vs. 53.8% cached in open habitat in the seed size experiment (chi-squared test, $\chi^2 = 0.000$, df = 1, $P = 0.999$), 50.6% vs. 49.4% in the nutrient experiment ($\chi^2 = 2.634$, df = 1, $P = 0.105$), and 46.4% vs. 53.6% in the tannin experiment ($\chi^2 = 0.010$, df = 1, $P = 0.921$; Fig. 1A). The probability of seeds being cached in shrubs vs. open habitat varied greatly among seeds with different sizes or nutrient contents (Table 1). Large or higher nutrient seeds were cached in shrubs more frequently than in the open habitat (Fig. 1B, C). However, tannin content had no effects on the probability of seeds being cached in shrubs vs. open habitat (Table 1, Fig. 1D).

Shrub effects on dispersal distance

Seeds cached in shrubs were transported further (10.6 ± 0.7 m, mean ± SE) than seeds cached in open habitats (3.7 ± 0.4 m) in the seed size experiment (Table 2, Fig. 2A). A similar pattern was found in the nutrient experiment, with the mean dispersal distances being 12.1 ± 0.7 m in shrubs and 8.5 ± 0.6 m in open habitats (Table 2, Fig. 2A). Furthermore, a significant interaction was found between habitat and both seed size and nutrient content, meaning that shrub cover decreased the positive effects of these seed traits on dispersal distance (Table 2, Fig. 2B, C). In the tannin experiment, however, no differences in dispersal distance were found between seeds cached in shrubs and open habitats (8.8 ± 0.5 m vs. 8.2 ± 0.5 m; Table 2, Fig. 2A), and there was no interaction between tannin and habitat (Table 2, Fig. 2D). Furthermore, a much smaller random effect was found in the nutrient experiment, which suggested a more consistent pattern of dispersal distance among plots in the nutrient experiment than in either the size or tannin experiments.

Shrub effects on seed fates at primary caches

Among the 1333 seeds in primary caches, only seven, from the nutrient experiment, were left intact in situ at the end, while the others were either eaten in situ or removed for a second time. Habitat (i.e., shrub vs. open) had neither a main effect nor an interactive effect with seed size (nutrient or tannin contents) on whether a cached seed would be eaten in situ or removed by rodents (Table 3).

Shrub effects on the secondary caching process

In total, 209 secondary cached seeds were found in the three experiments, and the proportion cached in shrubs vs. open habitat was also accordant with the ratio of shrub cover to open habitat in the forest (chi-squared test, $\chi^2 = 1.869$, df = 1, $P = 0.172$ in seed size experiment, $\chi^2 = 0.571$, df = 1, $P = 0.450$ in nutrient experiment, and $\chi^2 = 1.088$, df = 1, $P = 0.297$ in tannin experiment; Appendix S1: Fig. S2A). The proportion of caches in shrubs vs. open habitat varied significantly among seeds with different sizes (generalized linear mixed model, $Z = 2.669$, $P = 0.008$) but not for either nutrient ($Z = -0.746$, $P = 0.456$) or tannin contents ($Z = -1.654$, $P = 0.098$). Larger seeds were cached in the shrubs more often than in the open habitats (Appendix S1: Fig. S2B). Shrub cover also significantly influenced the secondary dispersal distance of seeds (Appendix S1: Table S1). Seeds in shrub cover were further from their original release plots than seeds in open habitat both in the seed size (14.5 ± 1.7 m vs. 12.5 ± 2.9 m, mean ± SE) and in the nutrient experiments (26.5 ± 2.9 m vs. 14.6 ± 1.4 m), but

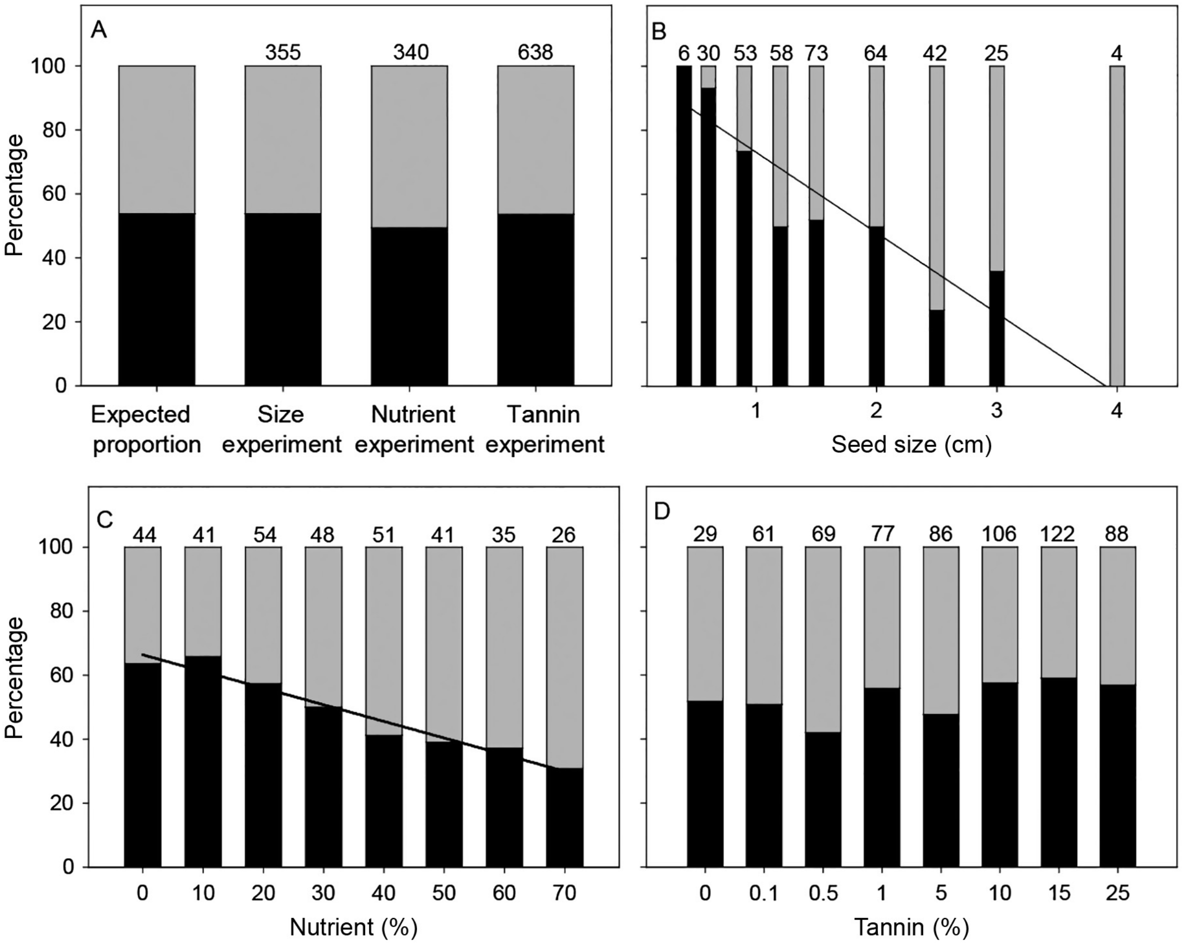

Fig. 1. Differences in proportions of seeds cached in shrubs vs. open habitats. Black bars represent seeds cached in open habitat (or proportion of open habitats available in the forest in Panel A), while gray bars seeds cached in shrubs (or proportion of shrub covers available in the forest in Panel A). (A) The ratio of shrub cover to open habitat available in the forest was accordant with the total proportion of seeds cached in shrubs vs. open habitat in each of the three experiments (chi-squared test, $P > 0.1$). (B) Proportions of seeds cached in shrubs vs. open habitats among seeds with different sizes; the line in the figure showed a significant relationship between seed size and ratio of seeds cached in shrubs to open habitat (Pearson's correlation, $r^2 = 0.883$, $P < 0.001$). (C) Proportions of seeds cached in shrubs vs. open habitat among seeds with different nutrient contents; the line in the figure showed a significant relationship between nutrient content and ratio of seeds cached in shrubs to open habitat ($r^2 = 0.952$, $P < 0.001$). (D) Proportions of seeds cached in shrubs vs. open habitat among seeds with different tannin contents. Numbers above the bars showed the sample sizes.

not in the tannin experiment (13.1 ± 1.4 m vs. 14.8 ± 1.4 m).

DISCUSSION

In our study, the rodents had no overall caching preference between shrubs and open habitats. Many previous studies have found that rodents show a significant preference for caching seeds under shrubs or tree canopies, possibly because of reduced predation risk (Li and Zhang 2003, Lu and Zhang 2004, Iida 2006, Perea et al. 2011*b*), while some others have found the opposite, and attributed this to a reduced risk of pilferage in the open (Muñoz and Bonal 2011, Steele et al. 2015). Our study did find, however, that rodents

Table 1. Summary of the generalized linear mixed model to test the effects of seed traits on the probability of seeds being cached in shrubs or open habitat after removed from the seed-releasing plots.

Parameter	Estimate ± SE	*Z*	*P*	Random effects Position : Plot	Plot
Seed size experiment (*n* = 355)				0.312	0.478
Intercept	−1.956 ± 0.382	−5.123	<0.001		
Size	1.165 ± 0.189	6.184	<0.001		
Nutrient experiment (*n* = 340)				0.787	0.298
Intercept	−0.618 ± 0.302	−2.044	0.041		
Nutrient	2.201 ± 0.611	3.605	<0.001		
Tannin experiment (*n* = 638)				0.241	0.232
Intercept	−0.011 ± 0.160	−0.070	0.944		
Tannin	−0.017 ± 0.010	−1.765	0.078		

selected different caching habitats for seeds with different traits. High-quality seeds (i.e., large size or high nutrient content) were cached more often in shrubs, while low-quality seeds were cached more often in open habitats. Perea et al. (2011*a*) found a similar pattern, with heavy seeds preferentially removed under shelter, while Vander Wall (2003) found no effects of seed size on caching microhabitat choice of chipmunks.

A preference for caching seeds under shrubs has been attributed to the shelter decreasing predation risk and foraging costs during seed caching and subsequent management (Kotler et al. 1991, Den Ouden et al. 2005, Perez-Ramos and Maranon 2008, Perea et al. 2011*a*). Rodents prefer to scatter-hoard plant seeds far away from the mother trees and at low density, which could protect their caches by reducing pilferage (Jenkins and Peters 1992, Jenkins et al. 1995). Aggregating all seed under shrubs would increase cache density, so some seeds may be cached in open habitats. Caching and subsequently managing high-quality seeds, especially large seeds, may increase handling time and thus risk, so rodents should logically prefer to cache the high-quality seeds in shrubs. However, Steele et al. (2014) found that eastern gray squirrels preferred to cache larger acorns in open habitats (i.e., outside tree canopies), apparently because pilferage rates were low in open habitats, possibly due to the high predation risk. These opposite preferences of caching habitat for larger seeds may result from

Table 2. Summary of the linear mixed-effects model to test the effects of habitat and seed traits on seed dispersal distance (random effects are presented as standard deviations).

Parameter	Estimate ± SE	df	*t*	*P*	Random effects Position : Plot	Plot
Seed size experiment (*n* = 355)					0.236	0.368
Intercept	−0.925 ± 0.217	301	−4.261	<0.001		
Size	1.172 ± 0.097	301	12.069	<0.001		
Habitat	1.865 ± 0.248	301	7.512	<0.001		
Size × Habitat	−0.543 ± 0.137	301	−3.969	<0.001		
Nutrient experiment (*n* = 340)					0.014	0.0003
Intercept	0.823 ± 0.106	284	7.744	<0.001		
Nutrient	2.950 ± 0.311	284	9.484	<0.001		
Habitat	0.688 ± 0.166	284	4.138	<0.001		
Nutrient × Habitat	−1.045 ± 0.433	284	−2.414	0.016		
Tannin experiment (*n* = 638)					0.138	0.259
Intercept	1.998 ± 0.137	583	14.581	<0.001		
Tannin	−0.046 ± 0.006	583	−7.294	<0.001		
Habitat	0.138 ± 0.115	583	1.195	0.233		
Tannin × Habitat	0.014 ± 0.010	583	1.484	0.138		

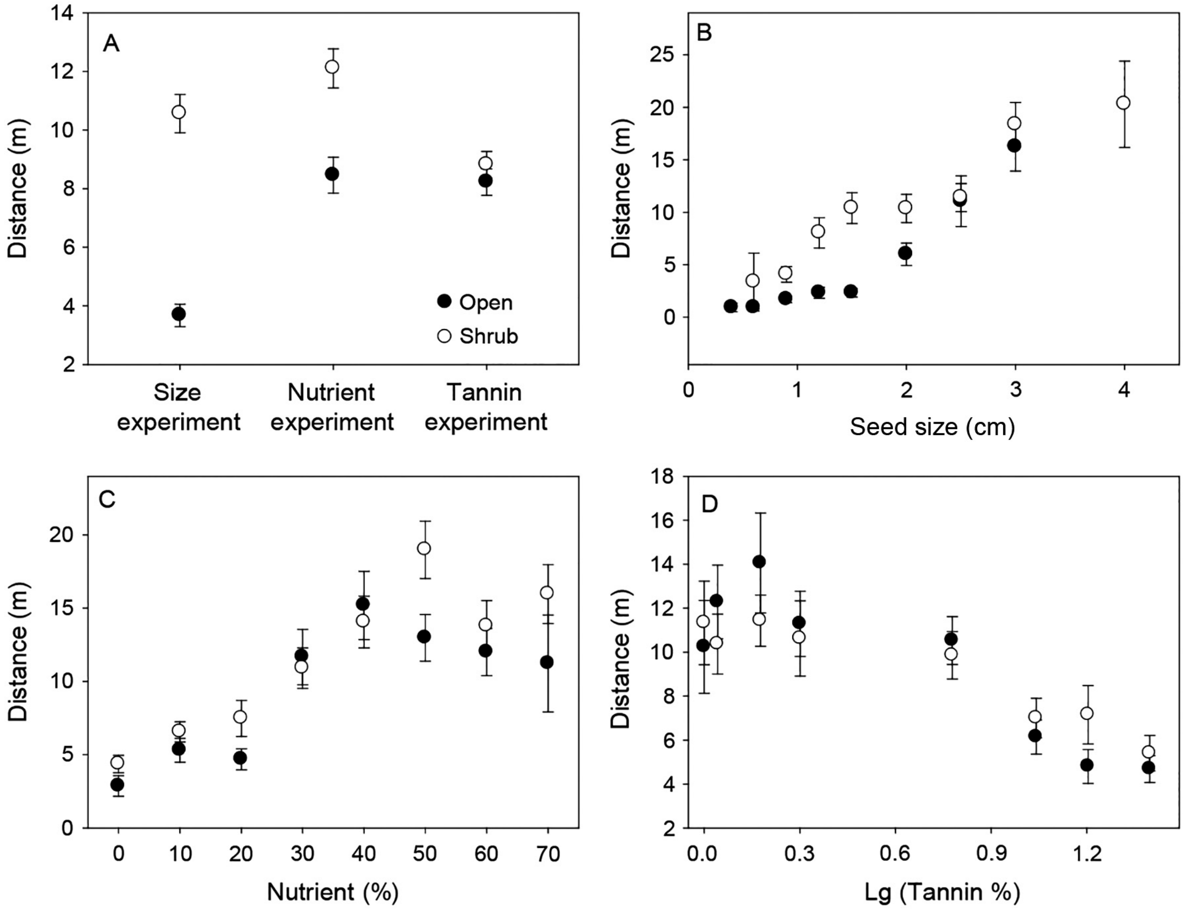

Fig. 2. Comparison of dispersal distances (mean ± SE) between seeds cached in shrubs and open habitats. (A) The whole pattern of the dispersal distance of cached seeds in shrubs vs. open habitats in each of the three experiments. (B) Comparison of dispersal distances between seeds cached in shrubs and open habitats among seeds with different sizes. (C) Comparison among seeds with different nutrient contents. (D) Comparison among seeds with different tannin contents. See Table 2 for statistical analysis.

the relative size differences between the seeds and the rodents: ~1% of squirrel body mass in Steele et al. (2014) but >50% of *Apodemus* body mass for the largest seeds in this study. In a recent review paper (Lichti et al. 2017), the authors discussed how the locations selected for caching by rodents changed with variation in habitat structure, and the perceived predation and pilferage risks. Open habitats could bring high predation risk but low pilferage rates (Steele et al. 2014, 2015, Lichti et al. 2017), and predation risk may be more crucial for small rodents than large ones during their foraging decisions. Thus, the small *Apodemus* species in our study may trade off higher pilferage rates of shrub caches for lower risks of predation, while the large squirrels in Steele et al. (2014) may benefit more from reduced pilferage in the open at a relatively small cost in increased predation risk. However, this study was conducted in only one year with small *Apodemus* species; some of the patterns might change under different ambient conditions, for example, different intensity of competition for seeds and possibly differences in memory capacity among different rodent species. Furthermore, reciprocal pilferage might play a larger role in our wood mouse system than in the squirrel system (Vander Wall and Jenkins 2003, Steele et al. 2011).

This study also found that shrub cover significantly increased the distances seeds were

Table 3. Summary of the generalized linear mixed model to test the effects of habitat and seed traits on seed fate at primary caches (i.e., whether a cached seed would be eaten in situ or removed by a rodent).

Parameter	Estimate ± SE	Z	P	Random effects: Position : Plot	Random effects: Plot
Seed size experiment (n = 355)				<0.0001	0.392
Intercept	−2.447 ± 0.535	−4.571	<0.001		
Size	2.279 ± 0.397	5.739	<0.001		
Habitat	0.040 ± 0.809	0.049	0.961		
Size × Habitat	−0.458 ± 0.551	−0.831	0.406		
Nutrient experiment (n = 340)				<0.0001	0.843
Intercept	3.537 ± 0.690	5.125	<0.001		
Nutrient	−2.356 ± 1.285	−1.834	0.067		
Habitat	0.018 ± 0.823	0.022	0.983		
Nutrient × Habitat	−0.133 ± 1.835	−0.073	0.942		
Tannin experiment (n = 638)				<0.0001	0.931
Intercept	0.986 ± 0.439	2.249	0.025		
Tannin	0.012 ± 0.018	0.694	0.487		
Habitat	−0.032 ± 0.304	−0.106	0.916		
Tannin × Habitat	−0.014 ± 0.025	−0.570	0.569		

transported by rodents. Some studies showed similar positive effects of shrub cover on seed dispersal distance, because animals would transport seeds for longer distances in order to find secure sites with shelters (e.g., shrubs) to cache them (Vander Wall 1990, Lu and Zhang 2004, but see Perea et al. 2011*b*).

Our results showed that rodents selected different caching habitats for seeds with different sizes or nutrient contents, but not for different tannin contents. Tannins in seeds have both costs and benefits to scatter-hoarding animals; that is, they have directly negative effects on animals' physiology and survival (Downs et al. 2003, Wang and Chen 2011), but may reduce losses of cached seeds to insects (Smallwood et al. 2001). These opposed effects may prevent rodents from choosing different habitats to cache seeds with different tannin contents. Furthermore, rodents' preferences for tannin are not always consistent (Wang and Chen 2009, 2011), which may also be a possible explanation.

Seed fates might be different between shrubs and open habitats because of the differences in rodent activity and foraging behavior (Den Ouden et al. 2005, Perez-Ramos and Maranon 2008, Perea et al. 2011*a*). Many studies have shown that seeds in shrubs were removed more quickly than seeds in open habitats (Bartholomew 1970, Herrera 1984, Kollmann and Schill 1996, but see Russell and Schupp 1998). Perea et al. (2011*b*) found that seeds further from shelters had a higher probability of being removed and a lower one of being eaten in situ. In our study, however, most of the seeds were retrieved by rodents in a very few days after being cached, with the fate being either eaten in situ or removed for a second time, and habitat had no effects on this. This may reflect a low predator density in our study site, which would reduce the benefits of the shelter offered by shrubs.

In our study, shrub cover appeared to enhance dispersal quality for high-quality seeds, by increasing the seed dispersal distance and possibly also by providing an improved microclimate in the harsh environment of our high-altitude site. High-quality seeds (i.e., larger size or more nutrients) usually have more opportunity to overcome environmental stresses and establish seedlings (Gross 1984, Jakobsson and Eriksson 2000). Artificial seeds were used in this study, so we could not assess shrub effects on seed germination and seedling survival. However, these subsequent recruitment processes depend on the initial seed dispersal process studied here. We have demonstrated that rodents select different caching microhabitats for seeds with different traits. Seed traits vary widely among plant species (Blate et al. 1998, Gong et al. 2015), so differences in caching microhabitat among different species of seeds could play an important role in the spatial pattern of regeneration in plant communities where scatter-hoarding is a major dispersal mechanism.

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