

# Small gaps are preferred for the scatter hoarding of acorns by rodents

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## 9Abstract

10In general, it is accepted that gap formation significantly affects the placement of scatter-hoarded seeds  
11by small rodents, but the effects of different forest gap sizes on the seed-eating and scatter-hoarding  
12behaviors of small rodents remain unclear. Thus, we examined the effects of a closed canopy forest, forest  
13edge, and gaps with different sizes on the spatial dispersal of *Quercus variabilis* acorns and cache  
14placement by small rodents using coded plastic tags in the Taihang Mountains, China. The seeds were  
15removed rapidly and there were significant differences in the seed-eating and caching strategies between  
16the stand types. We found that *Q. variabilis* acorns were usually eaten after being removed from the  
17closed canopy forest and forest edges. By contrast, the *Q. variabilis* acorns in the forest gap stands were  
18more likely to be scatter hoarded. The dispersal distances of *Q. variabilis* acorns were significantly longer  
19in the forest gap plots compared with the closed canopy and forest edge plots. However, the proportions  
20of scatter-hoarded seeds did not increase significantly as the gap size increased. In small-scale oak  
21reforestation projects or research, creating small gaps to promote rodent-mediated seed dispersal may  
22effectively accelerate forest recovery and successional processes.

23**KEY WORDS:** gap size, rodent, scatter hoarding, seed dispersal, Taihang Mountains

## 241 INTRODUCTION

25Seeds or diaspores rely on agents such as wind and animals for their dispersal to suitable sites away from  
26the parent plant, which is a key life-history stage in plants. Various studies have demonstrated that  
27animals, especially small rodents, play vital roles in seed dispersal and they affect the seed-to-seedling  
28period of plant regeneration (Abe et al., 2006; Williams-Linera et al., 2011; Yu et al., 2017, 2018; Zhang  
29et al., 2019, 2020). Indeed, the scatter hoarding of seeds in suitable sites by rodents enhances the  
30probability of seedling settlement (Vander Wall, 2001; Steele et al., 2007; Yu et al., 2015, 2017). Many  
31factors may affect the quality and effectiveness of seed dispersal by animals, such as the microhabitat in  
32the caching site (Yu et al., 2014; Yang et al., 2016).

33 Gaps are frequent in various forest ecosystems and they have been shown to alter the microhabitat  
34heterogeneity in forest ecosystems, thereby influencing the activity and foraging behavior of rodents, as  
35well as seed germination and seedling establishment (Levey, 1988). Many studies have investigated plant  
36regeneration in forest gaps (Arevalo & Fernandez-Palacios, 2007; Albanesi et al., 2008; Burnham & Lee,  
372010; Yu et al., 2014; Zhu et al., 2014), but few have considered the interactions between seed predation  
38and seed dispersal in forest gaps and the associated closed canopy forest.

39 In some cases, small rodents can increase the likelihood of successful regeneration for gap-  
40dependent tree species by carrying the seeds of various tree species into forest gaps (Crawley, 1992; Iida,  
412006). Previous studies have indicated that forest specialists avoid gaps (Rail et al., 1997; Rodriguez et  
42al., 2001; Bakker & Van Vuren, 2004) because there is a higher perceived predation risk in open habitats  
43(Lima & Dill, 1990). The predation risk is higher for animals in relatively open habitats (e.g., forest gaps)  
44because they are easier to detected (Lima, 1998; Bélisle & Desrochers, 2002; Wilkinson et al., 2013).  
45However, a previous study found that small rodents favor open habitats when selecting cache sites (Steele

46et al., 2014). Canopy gaps are usually beneficial for seed dispersal and they are more favorable sites for  
47seed storage, thereby contributing to seedling establishment and survival (Hoshizaki, 1997; Iida, 2006).  
48Previous studies of the effects of gaps on rodent mediated seed dispersal obtained variable results. The  
49size of forest gaps is important and it affects the maintenance of species diversity and forest regeneration  
50(Wang et al., 2017). However, it is still not clear whether the sizes of gaps can affect the fate of seeds  
51removed by rodents. The contradictory results obtained in previous studies may reflect variations in the  
52stages of the coevolving plant–hoarder relationships.

53     Seed dispersal depends mainly on seed viability, the dispersal distance, and microhabitat conditions  
54which can determine the successful regeneration of tree species (Dassot & Collet, 2015; Perea et al.,  
552011, 2012). It is generally considered that heavier seeds are dispersed further compared with light seeds  
56(Jansen et al., 2004; Xiao et al., 2005a), but the dispersal distance may be affected by other factors, such  
57as the microhabitat (in both the origin and destination) or the number of dispersal movements (Perea et  
58al., 2011). The gap size also has important effects on the seed dispersal of seeds produced by tree species  
59and the success of germination (Van Ulf, 2004; Zhang et al., 2017). Recent studies have focused on the  
60effects of forest gaps on forest regeneration, but the roles of forest gaps in seed dispersal by granivorous  
61rodents are not fully understood, especially the relationship between the gap size of forest gaps and  
62rodent-mediated seed dispersal (Wang et al., 2017; Zhang et al., 2017). In particular, it is still unclear  
63whether microhabitats such as gaps can increase the dispersal distances and seed survival.

64     In this study, we analyzed the differences in the dispersal and predation of *Quercus variabilis* seeds  
65by scatter-hoarding rodents in closed canopy forest, forest edges, and gaps with different sizes. We  
66addressed the following two questions. (1) Are the decisions made by small rodents regarding scatter  
67hoarding and the distribution of caches dependent on gap size dependent? (2) Are large gaps are preferred

for to rodent-mediated seed dispersal? We hypothesized that the proportions of scatter-hoarded seeds would not increase significantly with the gap size. Thus, we aimed to obtain a better understanding of the effects of gap size on rodent-mediated seed dispersal, thereby facilitating improved forest management.

## MATERIALS AND METHODS

### 2.1 Study Site

We conducted the experiment in the Huanglianshu Forest in the Taihang Mountains (112°25' E, 35°15'N), Jiyuan City, Henan Province, China. The study region is situated in the warm-temperate zone where the annual precipitation ranges from 600 to 700 mm, most of which falls between July and September. Snow cover usually lasts five or more months (from November to March), and the mean annual temperature was 14.3 °C. The forest was harvested during the 1960s and 1970s, and much of the area is now covered by secondary forests. The forest in this area has been protected against deforestation since the Taihang Macaque Natural Reserve was established in 1982. The secondary forest is dominated by *Q. variabilis* in the tree layer, and by *Vitex negundo*, *Rosa xanthina*, and *Vitex negundo*, *Rosa xanthina*, *Rhamnus bungeana* and *Cotinus coggygia* in the understory vegetation. *Apodemus peninsulae*, *Niviventer confucianus* and Père David's rock squirrel (*Sciurotamias davidianus*) are common seed predators in the study region.

### 2.2 Seed Marking

We collected mature and fresh of *Q. variabilis* seeds (acorns) from the ground outside our experimental stands for field release. Water flotation and visual inspection were employed to distinguish sound and insect-damaged or empty acorns. In total, 1500 *Q. variabilis* acorns ( $1.97 \times 1.68$  cm,  $3.58 \pm 0.21$  g,  $n = 50$ ) were randomly selected and labeled according to the tin-tagging methods reported by Zhang and Wang (2001) and Li and Zhang (2003) with slight modifications. A hole with a diameter of 0.3 mm was

drilled through the husk near the germinal disk of each seed, but without damaging the cotyledon and embryo. Flexible plastic tags ( $3.0 \times 1.0$  cm,  $< 0.1$  g) was tied to the seeds by passing thin steel thread with a length of 10 cm through the hole. Each seed was marked with a unique numbered tag in order to ensure that seeds could be readily relocated and identified. The tags were frequently still visible on the surface of the ground after their burial in the soil or leaf litter by rodents, which made them easy to find. It has been shown that the effects of tagging on the seed removal and hoarding behaviors of rodents are negligible (Zhang & Wang, 2001; Xiao et al., 2006).

### 2.3 Seed Release and Seed Removal

To examine the effects of different forest stand types, i.e., closed canopy forest (CCF), forest edge (FE), and gaps with different sizes, on the spatial dispersal of *Q. variabilis* acorns and cache placement by small rodents 10 approximately elliptical gaps with various sizes were selected in secondary forests at the end of 2015 (winter) with an area of about 10.0 ha, i.e., two large gaps measuring  $>500$  m<sup>2</sup> (LG), three medium gaps measuring 500–150 m<sup>2</sup> (MG), and five small gaps measuring  $<150$  m<sup>2</sup> (SG).

We set 6 seed stations in CCF and FE, respectively, and set 5 seed stations in LG, MG and SG, respectively. In total, 27 seed stations were set 50 m apart at the study site. We placed 30 tagged seeds at each separate seed station. The total number of seeds released was: 27 (stations)  $\times$  30 (seeds) = 810 seeds. We checked the removal of seeds from each station on a daily basis from the day after seed placement until all of the seeds were removed or consumed. We randomly searched the area around each seed station with equal amounts of effort in order to retrieve the removed seeds and record their fate following each visit. During each visit, we inspected each seed station as well as the caches found in previous visits. The post-dispersal seed fates were classified using six categories (Yi & Zhang 2008): 1) intact in situ (IIS); 2) eaten in situ (EIS); 3) moved and eaten leaving only plastic tags and seed fragments (EAR); 4)

intact but not buried after removal (IAR); 5) scatter hoarding after removal (SH); and 6) missing where their true fates were unknown (M). When a cache was found, we recorded the seed tag numbers and measured the distances of the tagged seeds from their original seed stations. A chopstick was used to mark each cache location, which was coded with the same number as the tag and placed 25 cm away from the seed cache sites. During the next visit, we also surveyed the caches located in previous visits until the caches were removed or eaten by rodents. The areas around the caches (radius <50 m) were searched in a haphazard manner with equal amounts of effort when marked cache were re-cached.

### 2.3.1 Abundance and Species Composition of Small Rodents

At the experimental site, we used 50 steel-wire live traps (30 cm × 25 cm × 20 cm) baited with peanuts to capture and identify the rodent species that potentially removed the released seeds. Traps were placed along each of two transects at 5-m intervals on September 23–26, 2017 (immediately before the seed release experiment). Traps inspections were performed twice each day at sunrise and sunset. The captured animals were weighed and released. The total trapping effort = 50 traps × 3 days = 150.

### 2.4 Data Analysis

SPSS for Windows (Version 18.0) was used to conduct the statistical analyses. We compared the numbers of remaining, eaten, and cached seeds, where each was divided by the total number of seeds released. The proportions of remaining, eaten, and cached seeds were arcsine square-root transformed before the statistical analyses. Cox regression analysis was used to test for differences in the seed removal rates among the five types. A univariate generalized linear model was employed to identify the effects of stand types on the seed dispersal distance and the six seed fates. Tukey's honest significant difference post hoc tests were performed for multiple comparisons.

## 3 RESULTS

### 1343.1 Identification of Seed-removing Rodents

135 We captured 31 rodents and *Apodemus peninsulae*, *Sciurotamias davidianus*, and *Niviventer confucianus*  
 136 accounted for 64.5%, 9.7%, and 25.8% of all the captures, respectively. We failed to capture the Eurasian  
 137 jay (*Garrulus glandarius* Linnaeus), although it was previously observed and it is considered as a  
 138 probable species that disperses and forages acorns and pine seeds.

### 1393.2 Removal Rates From Seed Stations

140 Most of the acorns released in CCF and FE were eaten or removed by small rodents within 7 days of their  
 141 placement (Fig. 1). By contrast, only 22.0%, 40.0%, and 52.7% of the seeds released in the SG, MG, and  
 142 LG stands, respectively, were eaten or removed by small rodents. The stand type had a significant effect  
 143 on the removal rates for the seeds handled by animals ( $Wald = 36.142$ ,  $df = 4$ ,  $P < 0.001$ ).

144 Cox regression analysis showed that the seed removal speed was significantly higher in CCF than  
 145 those in SG ( $Wald = 21.491$ ,  $df = 1$ ,  $P < 0.001$ ), MG ( $Wald = 32.601$ ,  $df = 1$ ,  $P < 0.001$ ), LG ( $Wald =$   
 146  $6.483$ ,  $df = 1$ ,  $P = 0.011$ ), and FE ( $Wald = 5.499$ ,  $df = 1$ ,  $P = 0.019$ ), respectively (Fig. 1).

147 Cox regression analysis indicated that the seed removal speed in FE was significantly higher than  
 148 those in SG ( $Wald = 8.364$ ,  $df = 1$ ,  $P = 0.004$ ) and MG ( $Wald = 9.672$ ,  $df = 1$ ,  $P = 0.008$ ) but not different  
 149 to that in LG ( $Wald = 3.362$ ,  $df = 1$ ,  $P = 0.067$ ) (Fig. 1). However, Cox regression detected no significant  
 150 differences in the seed removal speed between the stands with different gap sizes ( $Wald = 4.263$ ,  $df = 2$ ,  $P$   
 151  $= 0.119$ ).

152 Fig. 1

### 1533.3 Seed Fates

154 Significant differences were found in the proportions of EAR and SH among the five stands (EAR:  $F =$   
 155  $3.239$ ,  $df = 4$ ,  $P = 0.031$ ; SH:  $F = 7.555$ ,  $df = 4$ ,  $P = 0.001$ ), but there were no significant differences in

the proportions of IIS, EIS, IAR, and M (IIS:  $F = 1.576$ ,  $df = 4$ ,  $P = 0.216$ ; EIS:  $F = 1.504$ ,  $df = 4$ ,  $P = 0.235$ ; IAR:  $F = 1.460$ ,  $df = 4$ ,  $P = 0.248$ ; M:  $F = 1.378$ ,  $df = 4$ ,  $P = 0.274$ ) (Fig. 2).

A higher proportion of seeds were SH in SG compared with CCF, FE, MG, and LG (SG vs CCF,  $P < 0.001$ ; SG vs FE,  $P < 0.001$ ; SG vs LG,  $P = 0.004$ ; SG vs MG,  $P = 0.011$ ) (Fig. 2 & 3). By contrast, slightly higher proportions of the seeds were SH in LG and MG than FE and CCF, but the differences were not significant (LG vs FE,  $P = 0.142$ ; LG vs CCF,  $P = 0.200$ ; MG vs FE,  $P = 0.057$ ; MG vs CCF,  $P = 0.084$ ) (Fig. 2).

A lower proportion of seeds were EAR in SG compared with CCF (SG vs CCF,  $P = 0.003$ ), FE (SG vs FE,  $P = 0.027$ ), and LG (SG vs LG,  $P = 0.026$ ). A slightly higher proportion of the seeds were EAR in SG than MG, but the difference was not significant (SG vs MG,  $P = 0.181$ ) (Fig. 2). Among the 1800 seeds released, only one seed survived to the seedling stage and it emerged in an SG during the following spring.

Fig. 2

Fig. 3

### 3.4 Seed Dispersal Distance

Most of the seeds were dispersed within a distance of 10 m (Fig. 3). The average dispersal distance was significantly affected by the stand types ( $F = 22.444$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 3). The dispersal distances were significantly greater in SG, MG, and LG than CCF (SG vs CCF,  $P < 0.001$ ; MG vs CCF,  $P = 0.027$ ; LG vs CCF,  $P = 0.031$ ) and FE (SG vs FE,  $P < 0.001$ ; MG vs FE,  $P = 0.008$ ; LG vs FE,  $P = 0.010$ ). The dispersal distances were significantly greater in SG than MG ( $P < 0.001$ ) and LG ( $P < 0.001$ ). By contrast, there was no significant difference in the dispersal distances between MG and LG ( $P = 0.979$ ).

Fig. 4

## DISCUSSION

Our results showed that the seed removal speed was significantly higher in CCF than the other four stand types. These differences may have been due to the simpler vegetation structure in the gaps leading to decreased seed dispersal services from scatter-hoarding rodents compared with CCF. In addition, the seed production rate was higher within the closed canopy than the gaps due to the lack of advanced regeneration. Most of the released acorns were harvested rapidly after their placement by small rodents in the CCF and FE stands, thereby demonstrating small rodents are important for the effective dispersal of this type of seed. We found that the seeds dropped from their parents were carried rapidly by rodents, as shown in previous studies (Vander Wall, 1990; Jansen & Forget, 2001; Xiao et al., 2005b; Caccia et al., 2006; Chang et al., 2012a). There were no significant differences in the seed removal rates among the stands with different gap sizes. Our results differ from those obtained in other studies where the gap size had a positive effect on the seed removal rate (Van Uft 2004; Wang et al., 2017). This difference may be explained by the similar shrub coverage and plant resources in the gaps.

In the present study, we found that compared with CCF and FE, more seeds were cached and less seeds were eaten after being removed from the LG, as also found in previous studies (Yang et al., 2016; Wang et al., 2017). The results clearly support the hypothesis tested in this study because the proportion of scatter-hoarded seeds did not increased significantly as the gap size increased, possibly because rodents must trade-off the risks of predation and pilferage by other animals (Yang et al., 2016). The seed fates might have varied between shrubs and open habitats because of differences in the activities and foraging behavior of rodents (Den Ouden et al., 2005, Perez-Ramos & Maranon, 2008, Perea et al., 2011). The foraging behavior of mammals is associated with assessments of foraging costs and benefits, including time, energy, and the predation risk (Schmidt & Ostfeld, 2003). The low ground coverage in large gaps may have affected the encounter rates with seeds, thereby affecting the seed predation and

201hoarding behaviors of rodent by increasing the predation risk estimated by rodents (Cintra, 1997). In  
202addition, our previous research and a study by Wang et al. (2017) concluded that the proportion of seeds  
203cached in canopy gaps was significantly lower than that in the understory (Yu et al., 2014). No seeds  
204were actually provided in the gaps so the results may have been influenced by the fact that the seeds were  
205offered only in the understory habitat. However, both of these studies found that the survival rates were  
206higher in the gaps than CCF because of the more suitable environmental conditions (especially sufficient  
207light) and lower risk of pilferage.

208     We found that the dispersal distances were significantly greater in the gaps than CCF and FE, and, a  
209previous study obtained similar results. It was also shown that an open microhabitat has positive effects  
210on the dispersal distance and seed survival (Perea et al., 2011). In addition, Steele et al. (2014) found that  
211squirrels tend to hide larger acorns further from the tree crowns i.e., in open habitats. Previous  
212quantitative studies demonstrated that heavier acorns were dispersed further compared with light acorns  
213(Jansen et al., 2004; Xiao et al., 2005a) and this does not support the energy saving hypothesis. In fact,  
214both the origin and destination microhabitats were more suitable for confirming dispersal distances.

215     All of the primary caches were recovered in CCF, FE, and SG, and subsequently predated by  
216rodents. Two seeds in the primary caches were cached in both MG and LG according to the last survey.  
217Only one seed survived until the seedling stage and it emerged in SG during the following spring. Our  
218observations agree with previous studies where only 0.02–10% of the removed seeds established  
219seedlings (Hulme 2002; Jansen et al., 2002). Thus, the foraging behavior and visitation frequencies of  
220rodents may have been higher in SG compared with LG. Our results demonstrate that small gaps had a  
221positive effect on the hoarding of *Q. variabilis* seeds. However, the effect of the gap size on seed dispersal  
222may vary according to the plant species and this requires further study.

Seed removal remains high and relatively constant over time, but partial seed damage (nonlethal) by rodents, as well as their caching and scatter-hoarding behavior, and the satiation effect could result in more seeds transitioning to the seedling stage (Martínez-Ramos et al., 2016). Our observations demonstrate that it is more important to consider both the origin and destination habitats when determining the seed dispersal distances and survival. Due to the low number of scatter-hoarded seeds, increasing openness will reduce the probability of seed survival, thereby resulting in a higher probability of either partially or totally eaten seeds.

## CONCLUSIONS

Our results clearly demonstrate that the gap size is an important factor that determines whether seeds are removed rapidly by predators or potential dispersers. Variations in the gap size can lead to different seed fates, which may eventually influence tree regeneration. We found that *Q. variabilis* acorns were usually eaten after their removal in CCF and FE. By contrast, the *Q. variabilis* acorns were more likely to be scatter-hoarded in forest gap stands. Moreover, the proportions of scatter-hoarded seeds did not increase significantly as the gap size increased. The *Q. variabilis* acorns in forest gap stands were dispersed significantly greater distances compared with those in CCF and FE. These results show that forest gaps can influence scatter-hoarding decisions and the distribution of caches by small rodents. Thus, in small-scale *Q. variabilis* reforestation projects or research, creating some small gaps to promote rodent-mediated seed dispersal may be an effective method for accelerating forest recovery and successional processes. However, the effect of the habitat type might be complex so the general applicability of our findings requires further study. Thus, we plan to extend our study to explore the possible trade-offs between dispersal capacities and other important ecological factors over diverse scales in terms of space and time.

## 245 ABBREVIATIONS

246 IIS: intact in situ; EIS: eaten in situ; EAR: moved and eaten leaving only plastic tags and seed fragments;

247 IAR: intact but not buried after removal; SH: scatter hoarding after removal; M: missing where their true

248 fates were unknown; CCF: closed canopy forest; FE: forest edge; LG: large gaps; MG: medium gaps; SG:

249 small gaps.

## 250 DECLARATIONS

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## 257 AUTHOR'S CONTRIBUTIONS

258 Conceived and designed the experiments: FY and XFY. Analyzed the data: SSW, YW and QWL. Wrote

259 the paper: FY and SSW. Performed the experiments, fieldwork FY, SSW, YW, YCL, LXZ and JMM. All

260 authors read and approved the final manuscript.

## 261 DATA ACCESSIBILITY STATEMENT

262 Seed dispersal: Dryad <https://doi.org/10.5061/dryad.g1jwstqpm>.

## 263 ETHICS APPROVAL AND CONSENT TO PARTICIPATE

264 Not applicable.

## 265 COMPETING INTERESTS

266 The author declares that he has no competing interests.

## 267 REFERENCES

- 268 Abe, H., Matsuki, R., Ueno, S., Nashimoto, M., Hasegawa, M. (2006) Dispersal of *Camellia japonica*  
 269 seeds by *Apodemus speciosus* revealed by maternity analysis of plants and behavioral observation of  
 270 animal vectors. *Ecological Research*, 21, 732-740. <https://doi.org/10.1007/s11284-006-0179-5>.
- 271 Arevalo, J.R., & Fernandez-Palacios, J.M. (2007) Treefall gaps and regeneration composition in the laurel  
 272 forest of Anaga (Tenerife): a matter of size? *Plant Ecology*, 188, 133-143.  
 273 <https://doi.org/10.1007/s11258-006-9152-1>.
- 274 Albanesi, E., Gugliotta, O.I., Mercurio, I., & Mercurio, R. (2008) Effects of gap size and within-gap  
 275 position on seedlings establishment in silver fir stands. *iForest-Biogeosciences and Forestry*, 1, 55-  
 276 59. <https://doi.org/10.3832/ifor0448-0010055>.
- 277 Bakker, V.J., & Van Vuren, D.H. (2004) Gap-crossing decisions by the red squirrel, a forest-dependent  
 278 small mammal. *Conservation Biology*, 18, 689-697. <https://doi.org/10.1111/j.1523-1739.2004.00149.x>.
- 280 Barcelos, A.R., Bobrowiec, P.E.D., Sanaiotti, T.M., & Gribel, R. (2013) Seed germination from lowland  
 281 tapir (*Tapirus terrestris*) fecal samples collected during the dry season in the northern Brazilian  
 282 Amazon. *Integrative Zoology*, 8, 63-73. <https://doi.org/10.1111/1749-4877.12003>
- 283 Bélisle, M., & Desrochers, A. (2002) Gap-crossing decisions by forest birds: an empirical basis for  
 284 parameterizing spatially-explicit, individual-based models. *Landscape Ecology*, 17, 219-231.  
 285 <https://doi.org/10.1023/A:1020260326889>.
- 286 Burnham, K.M., & Lee, T.D. (2010) Canopy gaps facilitate establishment, growth, and reproduction of  
 287 invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. *Biological Invasions*, 12, 1509-  
 288 1520. <https://doi.org/10.1007/s10530-009-9563-8>.
- 289 Caccia, F.D., Chaneton, E.J., & Kitzberger, T. (2006) Trophic and non-trophic pathways mediate  
 290 apparent competition through post-dispersal seed predation in a Patagonian mixed

- forest. *Oikos*, 113, 469-480. <https://doi.org/10.1111/j.2006.0030-1299.14390.x>.
- Chang, G., Jin, T.Z., Pei, J.F., Chen, X.N., Zhang, B., & Shi, Z.J. (2012) Seed dispersal of three sympatric oak species by forest rodents in the Qinling Mountains, Central China. *Plant Ecology*, 213, 1633-1642. <https://doi.org/10.1007/s11258-012-0118-1>.
- Cintra, R. (1997) Leaf litter effects on seed and seedling predation of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in Amazonian forest. *Journal of Tropical Ecology*, 13, 709-725. <https://doi.org/10.1017/S0266467400010889>
- Crawley, M.J. (1992) Seed predators and plant population dynamics. In M. Fenner (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. Vol. 7 (pp. 157-191). Wallingford, CABI Publishing.
- Dassot, M., & Collet, C. (2015) Manipulating seed availability, plant competition and litter accumulation by soil preparation and canopy opening to ensure regeneration success in temperate low-mountain forest stands. *European Journal of Forest Research*, 134, 247-259. <https://doi.org/10.1007/s10342-014-0847-x>.
- Den Ouden, J., Jansen, P.A., & Smit, R. (2005) Jays, mice and oaks: predation and dispersal of *Quercus robur* and *Q. petraea* in North-western Europe. In P.M. Forget, J.E. Lambert, P.E. Hulme, & S.B. Vander Wall (Eds.), *Seed Fate: Predation, Dispersal and Seedling Establishment*. (pp. 223-240). Wallingford, CABI Publishing.
- Hoshizaki, K., Suzuki, W., & Sasaki, S. (1997) Impacts of secondary seed dispersal and herbivory on seedling survival in *Aesculus turbinata*. *Journal of Vegetation Science*, 8, 735-742. <https://doi.org/10.2307/3237379>.
- Hulme, P.E. (2002) Seed eaters: seed dispersal, destruction and demography. In D.J. Levey, M.R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, Evolution and Conservation*. (pp. 257-273). Wallingford, CABI Publishing.

- 314 Iida, S. (2006) Dispersal patterns of *Quercus serrata* acorns by wood mice in and around canopy gaps in a  
 315 temperate forest. *Forest Ecology and Management*, 227, 71-78.  
 316 <https://doi.org/10.1016/j.foreco.2006.02.010>.
- 317 Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Den Ouden, J., & Van Wieren, S.E. (2002)  
 318 The role of seed size in dispersal by a scatter-hoarding rodent. In D.J. Levey, W.R. Silva, & M.  
 319 Galetti (Eds.), *Seed dispersal and frugivory: Ecology, Evolution and Conservation*. (pp. 209-225).  
 320 Wallingford, CABI Publishing.
- 321 Jansen, P.A., Bongers, F., & Hemerik, L. (2004) Seed mass and mast seeding enhance dispersal by a  
 322 neotropical scatter-hoarding rodent. *Ecological Monographs*, 74, 569-589.  
 323 <https://doi.org/10.1890/03-4042>.
- 324 Jansen, P.A., & Forget, P.M. (2001) Scatter-hoarding rodents and tree regeneration. In F. Bongers, P.  
 325 Charles-Dominique, P.M. Forget, & M. Théry (Eds.), *Dynamics and plant–animal interactions in a*  
 326 *neotropical rainforest*. (pp. 275-288). Dordrecht, Kluwer Academic Publisher.
- 327 Levey, D.J. (1988) Tropical wet forest treefall gaps and distributions of understory birds and  
 328 plants. *Ecology*, 69, 1076-1089. <https://doi.org/10.2307/1941263>.
- 329 Li, H.J., & Zhang, Z.B. (2003) Effect of rodents on acorn dispersal and survival of the Liaodong oak  
 330 (*Quercus liaotungensis* Koidz.). *Forest Ecology and Management*, 176, 387-396.  
 331 [https://doi.org/10.1016/S0378-1127\(02\)00286-4](https://doi.org/10.1016/S0378-1127(02)00286-4).
- 332 Lima, S.L., & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and  
 333 prospectus. *Canadian Journal of Zoology*, 68, 619-640. <https://doi.org/10.1139/z90-092>.
- 334 Lima, S.L. (1998) Stress and decision-making under the risk of predation: recent developments from  
 335 behavioral, reproductive and ecological perspectives. *Advances in the Study of Behavior*, 27, 215-

290. [https://doi.org/10.1016/S0065-3454\(08\)60366-6](https://doi.org/10.1016/S0065-3454(08)60366-6).
- Martínez-Ramos, M., Pingarrón, A., Rodríguez-Velázquez, J., Toledo-Chelala, L., Zermeño-Hernández, I., & Bongers, F. (2016) Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica*, 48, 745-757. <https://doi.org/10.1111/btp.12382>.
- Moore, J.E., McEuen, A.B., Swihart, R.K., Contreras, T.A., & Steele, M.A. (2007) Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology*, 88, 2529-2540. <https://doi.org/10.1890/07-0247.1>
- Perea, R., San Miguel, A., & Gil, L. (2011) Acorn dispersal by rodents: the importance of re-dispersal and distance to shelter. *Basic and Applied Ecology*, 12, 432-439. <https://doi.org/10.1016/j.baec.2011.05.002>.
- Perea, R., San Miguel, A., Martínez-Jauregui, M., Valbuena-Carabaña, M., & Gil, L. (2012) Effects of seed quality and seed location on the removal of acorns and beechnuts. *European Journal of Forest Research*, 131, 623-631. <https://doi.org/10.1007/s10342-011-0536-y>.
- Perez-Ramos, I.M., & Maranon, T. (2008) Factors affecting post-dispersal seed predation in two coexisting oak species: microhabitat, burial and exclusion of large herbivores. *Forest Ecology and Management*, 255, 3506-3514. <https://doi.org/10.1016/j.foreco.2008.02.032>.
- Rail, J.F., Darveau, M., Desrochers, A., & Huot, J. (1997) Territorial responses of boreal forest birds to habitat gaps. *Condor*, 99, 976-980. <https://doi.org/10.2307/1370150>.
- Rodríguez, A., Andrén, H., & Jansson, G. (2001) Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos*, 95, 383-396. <https://doi.org/10.1034/j.1600-0706.2001.950303.x>.
- Schmidt, K.A., & Ostfeld, R.S. (2003) Songbird populations in fluctuating environments: predator responses to pulsed resources. *Ecology*, 84, 406-415. [https://doi.org/10.1890/0012-9658\(2003\)084\[0406:SPIFEP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0406:SPIFEP]2.0.CO;2).

- 359 Steele, M.A., Contreras, T.A., Hadj-Chikh, L.Z., Agosta, S.J., Smallwood, P.D., & Tomlinson, C.N.  
 360 (2013) Do scatter hoarders trade off increased predation risks for lower rates of cache pilferage?  
 361 *Behavioral Ecology and Sociobiology*, 25, 206-215. <https://doi.org/10.1093/beheco/art107>.  
 362 Vander Wall, S.B. (1990) *Food hoarding in animals*. University of Chicago Press. Chicago.  
 363 Vander Wall, S.B. (2001) The evolutionary ecology of nut dispersal. *Botanical Review*, 67, 74-117.  
 364 <https://doi.org/10.1007/BF02857850>.  
 365 Van Ulf, L.H. (2004) The effect of seed mass and gap size on seed fate of tropical rain forest tree species  
 366 in Guyana. *Plant Biology*, 6, 214-221. <https://doi.org/10.1055/s-2004-815736>.  
 367 Wang, J., Yan, Q.L., Yan, T., Song, Y., Sun, Y.R., & Zhu, J.J. (2017) Rodent-mediated seed dispersal of  
 368 *Juglans mandshurica* regulated by gap size and within-gap position in larch plantations: implication  
 369 for converting pure larch plantations into larch-walnut mixed forests. *Forest Ecology and*  
 370 *Management*, 404, 205-213. <https://doi.org/10.1016/j.foreco.2017.08.033>.  
 371 Wilkinson, E.B., Branch, L.C., & Miller, D.L. (2013) Functional habitat connectivity for beach mice  
 372 depends on perceived predation risk. *Landscape Ecology*, 28, 547-558.  
 373 <https://doi.org/10.1007/s10980-013-9858-0>.  
 374 Williams-Linera, G., Alvarez-Aquino, C., Hernández-Ascención, E., & Toledo, M. (2011) Early  
 375 successional sites and the recovery of vegetation structure and tree species of the tropical dry forest  
 376 in Veracruz, Mexico. *New Forests*, 42, 131-148. <https://doi.org/10.1007/s11056-010-9242-8>.  
 377 Xiao, Z.S., Jansen, P.A., & Zhang, Z.B. (2006) Using seed-tagging methods for assessing post-dispersal  
 378 seed fate in rodent-dispersed trees. *Forest Ecology and Management*, 223, 18-23.  
 379 <https://doi.org/10.1016/j.foreco.2005.10.054>.  
 380 Xiao, Z.S., Zhang, Z.B., & Wang, Y.S. (2005a) Effects of seed size on dispersal distance in five rodent-  
 381 dispersed fagaceous species. *Acta Oncologica*, 28, 221-229.

- 382 <https://doi.org/10.1016/j.actao.2005.04.006>.
- 383 Xiao, Z.S., Zhang, Z.B., & Wang, Y.S. (2005b) The effects of seed abundance on seed predation and
- 384 dispersal by rodents in *Castanopsis fargesii* (Fagaceae). *Plant Ecology*, 177, 249-257. [https://doi.org/](https://doi.org/10.1007/s11258-005-2321-9)
- 385 [10.1007/s11258-005-2321-9](https://doi.org/10.1007/s11258-005-2321-9).
- 386 Yang, Y.Q., Zhang, M.M., & Yi, X.F. (2016) Small rodents trading off forest gaps for scatter-hoarding
- 387 differs between seed species. *Forest Ecology and Management*, 379, 226-231.
- 388 <https://doi.org/10.1016/j.foreco.2016.08.005>.
- 389 Yi, X.F., Zhang, J.X., & Wang, Z.Y. (2015) Large and small acorns contribute equally to early-stage oak
- 390 seedlings: a multiple species study. *European Journal of Forest Research*, 134, 1019-1026.
- 391 <https://doi.org/10.1007/s10342-015-0906-y>
- 392 Yi, X.F., & Zhang, Z.B. (2008) Seed predation and dispersal of glabrous filbert (*Corylus heterophylla*)
- 393 and pilose filbert (*Corylus mandshurica*) by small mammals in a temperate forest, northeast
- 394 China. *Plant Ecology*, 196, 135-142. <https://doi.org/10.1007/s11258-007-9340-7>.
- 395 Yu, F., Shi, X.X., Wang, D.X., Wang, T., Yi, X.F., & Lou, Y.G. (2014) Seed predation patterns favor the
- 396 regeneration of dominant species in forest gaps compared with the understory in an oak-pine mixed
- 397 forest. *Acta Theriologica*, 59, 495-502. <https://doi.org/10.1007/s13364-014-0192-y>.
- 398 Yu, F., Shi, X.X., Wang, D.X., Yi, X.F., Fan, D.F., Guo, T.D., & Lou, Y.G. (2015) Effects of insect
- 399 infestation on *Quercus aliena* var. *acuteserrata* acorn dispersal in the Qinling Mountains, China.
- 400 *New Forests*, 46, 51-61. <https://doi.org/10.1007/s11056-014-9446-4>.
- 401 Yu, F., Shi, X.X., Yi, X.F., & Ma, J.M. (2018) Rodent-mediated seed dispersal shapes species composition
- 402 and recruitment dynamics in ecotones. *Frontiers in Plant Science*, 9, 1911.
- 403 <https://doi.org/10.3389/fpls.2018.01911>.
- 404 Yu, F., Shi, X.X., Zhang, X., Yi, X.F., Wang, D.X., & Ma, J.M. (2017) Effects of selective logging on

- rodent-mediated seed dispersal. *Forest Ecology and Management*, 406, 147-154.  
<https://doi.org/10.1016/j.foreco.2017.10.001>.
- Zhang, B., Chen, X.N., Steele, M.A., Li, J.G., & Chang, G. (2019) Effects of insect infestation on rodent-mediated dispersal of *Quercus aliena*: results from field and enclosure experiments. *Integrative Zoology*, 14, 104-113. <https://doi.org/10.1111/1749-4877.12350>
- Zhang, H.M., Yan, C., Wu, S.Q., Si, J.J., Yi, X.F., Li, H.J., & Zhang, Z.B. (2020) Effects of masting on seedling establishment of a rodent-dispersed tree species in a warm-temperate region, northern China. *Integrative Zoology*, 0, 1-12. <https://doi.org/10.1111/1749-4877.12450>
- Zhang, M.M., Wang, Z.Y., Liu, X.L., & Yi, X.F. (2017) Seedling predation of *Quercus mongolica* by small rodents in response to forest gaps. *New Forests*, 48, 83-94. <https://doi.org/10.1007/s11056-016-9557-1>.
- Zhang, Z.B., & Wang, F.S. (2001) Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). *Acta Ecologica Sinica*, 21, 839-845. <https://doi.org/10.3321/j.issn:1000-0933.2001.05.024>.
- Zhu, Y.J., Yang, X.J., Baskin, C.C., Baskin, J.M., Dong, M., & Huang, Z.Y. (2014) Effects of amount and frequency of precipitation and sand burial on seed germination, seedling emergence and survival of the dune grass *Leymus secalinus* in semiarid China. *Plant and Soil*, 374, 399-409.  
<https://doi.org/10.1007/s11104-013-1892-9>.

423Figure legends

424Fig. 1 *Quercus variabilis* seed removal rates after deposition at the seed stations. Data represent the mean

425  $\pm$  standard error.

426Fig. 2 Fates of *Quercus variabilis* seeds after dispersal by small rodents in different stands. Data represent

427 the as mean  $\pm$  standard error.

428Fig. 3 Scatter hoarding pathways for 810 tagged *Quercus variabilis* seeds after placement at seed stations.

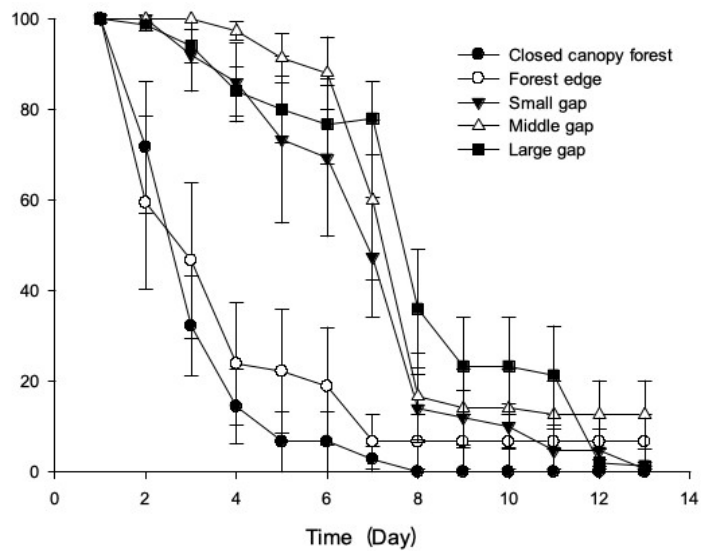
429 I, II, III, IVand V represent closed canopy forest, forest edge, large gap, medium gap and small

430 gap, respectively.

431Fig. 4 Dispersal distances of *Quercus variabilis* seeds after primary dispersal from the seed release

432 stations in different stands. Data represent the as mean  $\pm$  standard error.

433Fig. 1

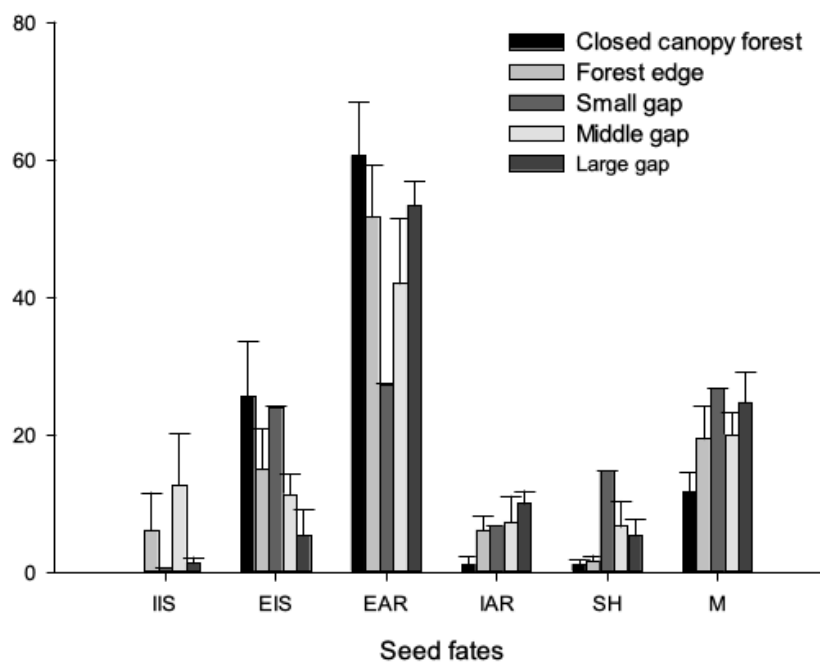


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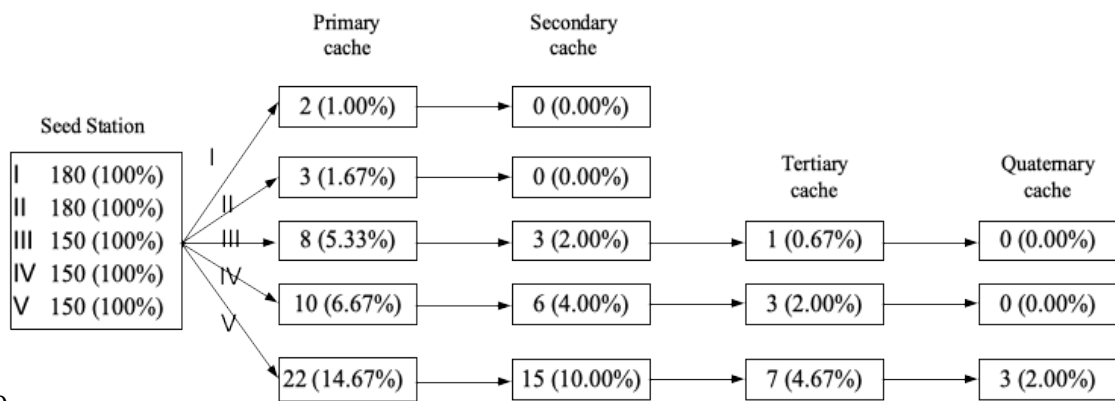
436 Fig. 2

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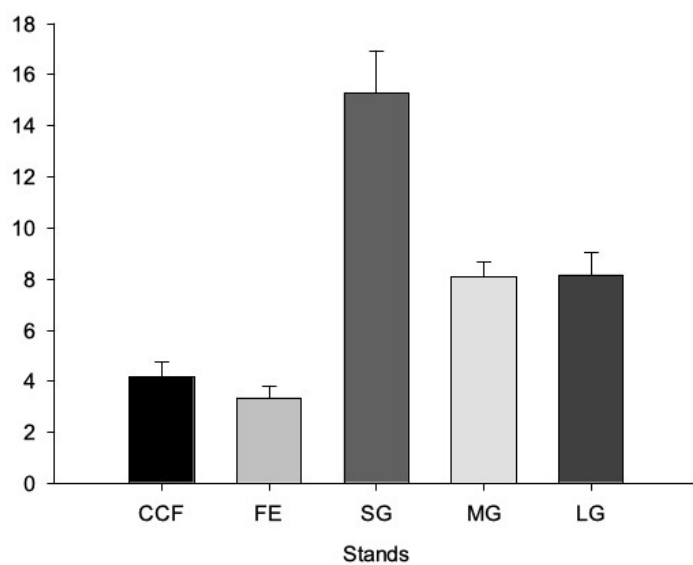
439 Fig. 3



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441

442Fig. 4



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