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Nondormant Acorns Show Higher Seed Dispersal Effectiveness Than Dormant Ones

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Abstract: Seed dormancy has been thought to be an important survival strategy to tune the seed dispersal timing. Although a theoretical trade-off between seed dormancy and dispersal is often proposed, empirical field evidence of the trade-off between seed dormancy, spatial dispersal, and seedling recruitment is still lacking. Here, we tracked seed dispersal of several Fagaceae species exhibiting different levels of dormancy both in artificial enclosures and in the field. We presented evidence that oak species with nondormant acorns rather than those bearing dormant species exhibit reduced spatial dispersal. Despite the empirical evidence that seed germination is negatively correlated with spatial dispersal, nondormancy rather than dormancy showed higher seed dispersal effectiveness, demonstrating a negative correlation between seed dormancy and dispersal fitness. Our study, using the oak-rodent system, may provide solid evidence of a dispersal–germination trade-off between spatial and temporal correlation, highlighting the ecological role of seed germination schedule in seed dispersal and life-history evolution.

Keywords: seed germination; dormancy; trade-off; seed dispersal; seedling establishment

1. Introduction

Seed dispersal is one of the most conspicuous mutualist interactions between plants and seed-eating animals [1–4]. Seed dispersal by animals is a key factor in the assembly, maintenance, and distribution of plant populations and communities in diverse natural ecosystems [5–8]. In the seed dispersal processes, seeds provide food resources as rewards to food-hoarding animals [9,10]. In turn, scatter-hoarding animals provide seed dispersal services to plants by transporting seeds far from parent trees, increasing seed survival, and promoting seedling establishment [11–15].

Despite its crucial role in plant community dynamics, seed dispersal mediated by food-hoarding animals can be differed in space or in time [6]. As key seed dispersers, scatter-hoarding animals transport seeds away from parental plants, up to several meters or even kilometers [3,16–18], playing an important role in 'spatial dispersal'. While seed germination schedules (e.g., delayed seed germination and/or seed dormancy) usually cause seed dispersal differed in time, i.e., temporal dispersal [19,20]. Acorns of most white oak species and some intermediate oaks exhibit no dormancy and germinate rapidly in autumn [21–24]. In contrast, acorns of red oak species exhibit a delayed germination requiring a period of cold stratification before germination is possible [25]. Oaks (Fagaceae) differed in temporal dispersal and have a wide geographic distribution and frequency throughout the northern hemisphere. Therefore, understanding how oaks differ in their ability to disperse in space or in time is needed for the management of plant populations and communities, especially in response to changes in climate and natural habitats.

Although studies have expected that natural selection should favor a trade-off between dormancy and seed dispersal [26–29], we are still lacking experimental evidence of a negative correlation between optimal dispersal and optimal dormancy [30], though several

studies have demonstrated such a correlation for heteromorphic species [31–33]. Till now, the theoretical prediction of how seed dormancy affects seed dispersal effectiveness has never been tested using seed and food-hoarding animal systems, although food-hoarding animals selectively prefer acorns based on seed germination schedules [34]. In this study, we compared seed dispersal and seedling establishment of *Quercus variabilis* Blume and *Q. serrata* Thunb-producing non-dormant acorns to those of *Q. accutissima* Carruth and *Cyclobalanopsis glauca* Thunb whose acorns exhibit autumn dormancy. Although previous studies have shown that seed germination is negatively correlated with spatial dispersal, our study provided evidence that rapid germination rather than dormancy increased seedling establishment, indicating two primary combinations of trade-offs in spatial dispersal and dormancy, i.e., high dispersal effectiveness coupled with low or no dormancy in the recalcitrant species and low dispersal effectiveness affiliated with high dormancy in the orthodox species.

2. Materials and Methods

2.1. Study Site

This study was conducted in the Banruosi Experimental Forest Farm (700–1000 m, 30°45′–31°22′ N, 107°25′–103°47′ E) in Dujiangyan City of Sichuan Province, southwest China. Climatically, the site lies in the middle subtropical zone, with a mean annual temperature of 15.2 °C, and an annual precipitation of 1200–1800 mm. The weather is often cloudy and foggy, with only 800–1000 mean annual sunny hours and a mean annual relative humidity ≥80%. Vegetation in the study site is subtropical evergreen broad-leaf forest, and common tree species include *Castanopsis fargesii* Franch, *Quercus variabilis*, *Q. serrata*, *Lithocarpus harlandii* Hance ex Walp., *Cyclobalanopsis glauca*, *Pinus massoniana* Lamb., *Acer catalpifolium* Rehd., *Phoebe zhennan* S. Lee et FN Wei, and *Camellia oleifera* Abel. [35].

2.2. Seed Dormancy

The acorns of *Q. variabilis*, *Q. serrata*, *Q. accutissima*, and *C. glauca* mature in October in the study area. Recalcitrant acorns of *Q. variabilis* and *Q. serrata* germinate quickly and produce robust taproots (i.e., radicles) after falling on the ground in autumn (Figure S1), whereas fallen acorns of *Q. accutissima* and *C. glauca* remain dormant until April next year. Nondormant acorns gradually transfer their cotyledonary reserves into a robust inedible taproot exhibiting the potential to regenerate a normal seedling (Yi et al., 2013). In autumn 2018, we randomly selected 150 sound acorns for each species, *Q. variabilis*, *Q. serrata*, *Q. accutissima*, and *C. glauca*. For each species, we sowed 10 acorns evenly in each of the 15 containers (diameter = 12 cm, height = 20 cm). In total, 600 acorns were sowed. All containers were placed in natural conditions allowing germination. After sowing, 10 acorns of each species were randomly dug out every week for 10 weeks to measure the taproot lengths and the dry masses of the attached cotyledons, to see the differences in seed dormancy of the four Fagaceae species.

2.3. Spatial Dispersal and Seedling Establishment in the Field

To test if oak species with dormant acorns exhibit reduced spatial dispersal and seedling establishment in the field, we first tracked seed dispersal of *Q. variabilis*, *Q. serrata*, *Q. accutissima* and *C. glauca* in two separate stands in the study area in a non-masting year that experienced small seed crop. In each stand, we established 20 seed stations (1 m by 1 m) 30 m apart along two transacts. In one stand, we released 30 paired acorns of *Q. variabilis* and *Q. accutissima* in each of the 20 seed stations (a total of 600 seeds for each seed species). In another stand, 30 paired acorns of *Q. serrata* and *C. glauca* were released in the same way. Each acorn was attached by a numbered plastic tag (3 cm × 2.5 cm) with a 10 cm thin steel wire. This seed-tagging method allowed us to follow the final fate until the seeds germinated and emerged as seedlings [4,12]. We checked the seed stations every day for 10 days and then every 3–4 days until all the acorns were removed by animals. Seed fates (the destiny of each acorn manipulated by rodents) were categorized into eaten in situ

(EIS) and eaten after removal (EAR). Acorns not consumed by animals were continuously checked for the following seedling establishment. We released another bout of acorns in the same way after all the seed stations were empty, to increase sample size and the possibility of seedling establishment. In the following masting year with large seed crops, we also released two bouts of acorns in the same stations, allowing seed dispersal by seed-eating animals. In total, 9600 acorns were released in two consecutive years. In the next spring, we searched the area around each seed station (up to 30 m in radius) to determine seedling establishment (SE) from the tagged acorns, respectively.

2.4. Seedling Establishment from Artificial Caches

To test if seed dormancy affected seedling establishment pending dispersal by scatter-hoarding animals, we established 20 plots (2 m by 2 m) 20 m apart along one transact each in two stands. In stand I, we buried 50 acorns of *Q. variabilis* evenly in each of the plots with odd numbers but 50 *Q. accutissima* acorns in plots with even numbers in October 2018. Simulating the cache depth of scatter-hoarding animals, we buried the sound acorns 1 cm deep in the soil to establish artificial caches. In stand II, we established 20 plots and buried the acorns of *Q. serrata* and *C. glauca* in the same procedure. This deployment of artificial caches presumed that there was no difference in acorn caching by scatter-hoarding animals. Acorns buried in those caches were not intentionally protected and therefore accessible to potential seed predators. In total, 4000 acorns were buried for seedling establishment. In April 2019, we searched each seed plot to determine seedling establishment from the buried acorns.

2.5. Effects of Seed Dormancy on Acorn Selection by Rodents in Artificial Enclosures

To better understand how seed-eating animals respond to the acorn germination schedule of the four Fagaceae species during seed dispersal, we conducted behavioral experiments in the artificial enclosures (Figure S2). To trap animals for enclosure experiments, SJL601 steel-framed live traps baited with peanuts and carrots were placed in forests at 5 m intervals along four transects at 8:00 a.m. following the previous procedures (Yi et al., 2016). All traps were pre-baited for 1 day and protected from predators by wrapping with steel mesh. The captured animals *Leopoldamys edwardsi* Thomas, *Apodemus draco* Barett-Hamilton, *Apodemus chevrieri* Milne-Edwards, *Niviventer confucianus* Milne-Edwards, and *Niviventer fulvescens* Gray, representing the most abundant rodent species that handle and eat acorns of *Q. variabilis*, *Q. serrata*, *Q. accutissima*, and *C. glauca* in the study areas, were transported by vehicle to the animal housing room in 1 h. Animals were individually housed in the steel frame cages (H × W × L = 20 cm × 40 cm × 50 cm) and maintained at a temperature of 20 ± 3 °C. The photoperiod in the animal room was set at 14:10 h light:dark. Bedding materials, tap water, and peanuts were provided ad libitum.

Following acclimation for one week in the housing room and 2 days in the enclosures, we carried out the behavioral experiments in artificial enclosures measuring 10 m × 10 m established in an area free of trees in the vicinity of the forest (Figure S2). In each enclosure, an artificial nest and a bowl of drinking water were presented at one corner. Because *L. edwardsi*, *A. draco*, *A. chevrieri*, *N. confucianus*, and *N. fulvescens* are all nocturnal rodents, paired acorns of *Q. variabilis* and *Q. accutissima* or *Q. serrata* and *C. glauca* were given to each individual at 19:00 in the evening. After 13 h of handling by rodents, seed fates in each enclosure were checked in next morning and classified into intact in situ (IIS), eaten in situ (EIS), intact after removal (EAR), eaten after removal (EAR), scatter-hoarded (SH) and larder-hoarded (LH). By doing so, we aimed to know which animal species were legitimate seed dispersers and whether animals showed any preference for the paired acorns differing in seed dormancy. In total, 50 animals were tested individually using 1000 paired acorns.

Animal capture and handling in this study adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. The authorization to capture, handle, and maintenance of animals was issued by the Qufu Normal University. No animals died in the behavioral

experiments and all individuals were released at the exact point of capture once experiments were finished following a health inspection.

2.6. Statistical Analyses

Statistical analyses were performed with the SPSS 16.0 Package. Changes in the length of taproots and cotyledon dry masses of the acorn species were determined using a general linear model. A Cox regression model was used to compare the difference in seed survival time of paired oak species in the field; however, data in the masting year were not analyzed due to extremely slow seed removal rates from seed stations. A paired *t*-test was applied to test the differences in seed fates between the dormant and non-dormant oak species (*Q. variabilis* and *Q. accutissima* or *Q. serrata* and *C. glauca*). A chi-square *t*-test was used if the sample size was small. Data from the two seed release bouts in the same year were summed up for analysis. The differences in seedling establishment from the artificial caches of the dormant and non-dormant oak species were determined using an independent samples *t*-test.

3. Results

3.1. Dormancy of Oak Acorns

Our results showed that the length of taproots of *Q. variabilis* increased gradually and reached the maximum of 19 cm 10 weeks after sowing ($F = 22.622$, df = 9, $p < 0.001$; Figure 1a). At the same time, the average cotyledon dry mass of *Q. variabilis* decreased from 2.4 g to 1.3 g 10 weeks after germination ($F = 25.875$, df = 9, $p < 0.001$; Figure 1a). However, the acorns of *Q. accutissima* remained dormant and did not protrude taproots even 10 weeks after sowing, causing no significant changes in acorn dry masses ($F = 0.461$, df = 9, $p = 0.897$; Figure 1b). Like *Q. variabilis*, the length of taproots of *Q. serrata* increased gradually and reached the maximum of 12 cm 10 weeks after sowing ($F = 27.708$, df = 9, $p < 0.001$; Figure 1c). The cotyledon dry masses of *Q. serrata* decreased from 1.1 g to 0.6 g 10 weeks after germination ($F = 17.424$, df = 9, $p < 0.001$; Figure 1c). Similar to *Q. accutissima*, the dormant acorns of *C. glauca* did not protrude taproots 10 weeks after sowing, resulting in no change in cotyledon dry masses ($F = 0.062$, df = 9, $p = 1.000$; Figure 1d).
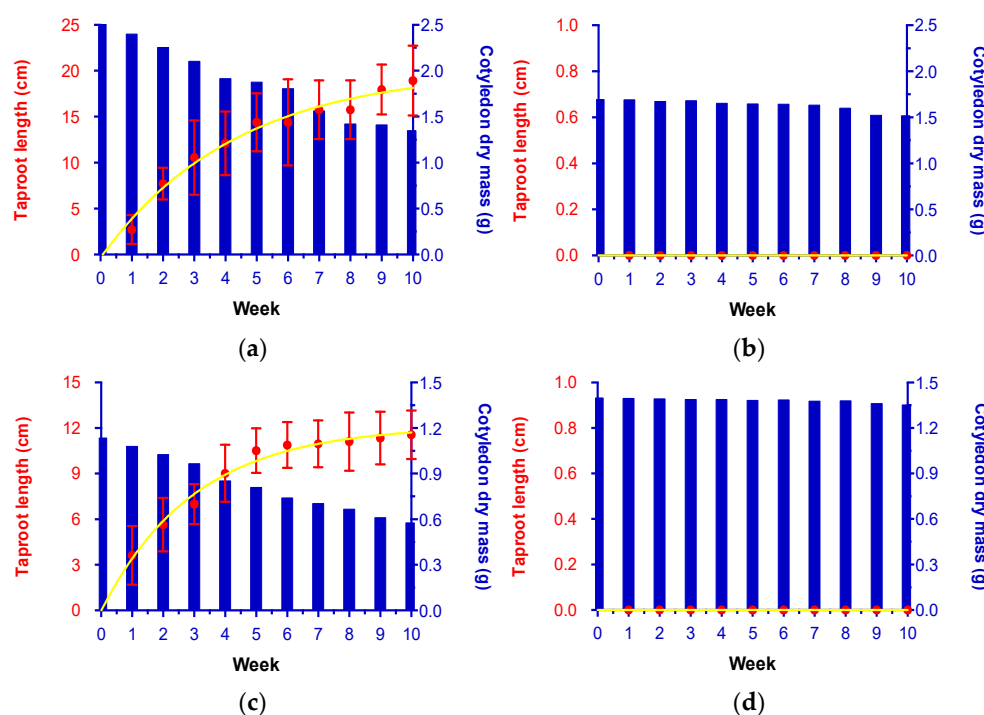

Figure 1. Exploitation of cotyledons and taproot elongation of *Q. variabilis* (**a**), *Q. accutissima* (**b**), *Q. serrata* (**c**), and *C. glauca* (**d**) along with exploitation of acorns.

3.2. Spatial Dispersal in Response to Seed Dormancy in the Filed

In the non-masting year, seed-eating animals preferred to disperse acorns of *Q. accutissima* over *Q. variabilis* in the first seed release bout (*Wald* = 23.121, df = 1, *p* < 0.001) but not in the second bout (*Wald* = 1.334, df = 1, *p* = 0.248; Figure 2a,b). Acorns of *C. glauca* were removed quickly than those of *Q. serrata* regardless of seed release bouts (*Wald* = 20.218, df = 1, *p* < 0.001; *Wald* = 6.866, df = 1, *p* = 0.001; Figure 2c,d). We detected no difference in the proportion of acorns eaten in situ and eaten after removal between *Q. variabilis* and *Q. accutissima* (*t* = 1.097, df = 19, *p* = 0.286; *t* = 0.798, df = 19, *p* = 0.453; Figure 3a). Despite this, seedling establishment from acorns of *Q. variabilis* was significantly higher than that from *Q. accutissima* (*t* = 3.317, df = 19, *p* = 0.004; Figure 3a). Similarly, seed-eating animals showed no preference for either acorns of *Q. serrata* or *C. glauca* to eat in situ in the field (*t* = −1.526, df = 19, *p* = 0.143; Figure 3b). The proportion of acorns of eaten after removal was marginally higher in *Q. serrata* than in *C. glauca* (*t* = −1.885, df = 19, *p* = 0.075). More seedlings of *Q. serrata* were established than *C. glauca* in the field (*t* = 2.258, df = 19, *p* = 0.036; Figure 3b). Although dormant acorns were dispersed faster, seedlings are more likely to establish from nondormant species than dormant species even in non-masting years.

In the masting year, paired acorns were seldomly removed by animals at the early stage of seed release, while disappeared suddenly within 2–3 days 20 days after seed release. Therefore, it was hard to tell whether seed-eating animals prefer which acorn species. Our field survey showed no difference in the proportion of acorns eaten in situ between *Q. variabilis* and *Q. accutissima* (*t* = −0.238, df = 19, *p* = 0.814; Figure 3c). However, acorns of non-dormant *Q. variabilis* were less likely to be eaten after removal than dormant *Q. accutissima* (*t* = 4.175, df = 19, *p* = 0.001). Consequently, seedling establishment from acorns of *Q. variabilis* was significantly higher than that from *Q. accutissima* (*t* = 4.805, df = 19, *p* < 0.001; Figure 3c). There was no significant difference in the proportion of acorns eaten in situ between *Q. serrata* and *C. glauca* (*t* = 2.254, df = 19, *p* = 0.036; Figure 3d). Seed-eating animals removed and consumed the same proportion of acorns of *Q. serrata* and *C. glauca* (*t* = 0.000, df = 19, *p* = 1.000). Although a small number of seedlings were established, more acorns of *Q. serrata* established seedlings than *C. glauca* (X^2 = 9.783, df = 1, *p* = 0.002; Figure 3d). Therefore, seed crop size did not change the likelihood of seedling establishment of nondormant species compared to dormant species.
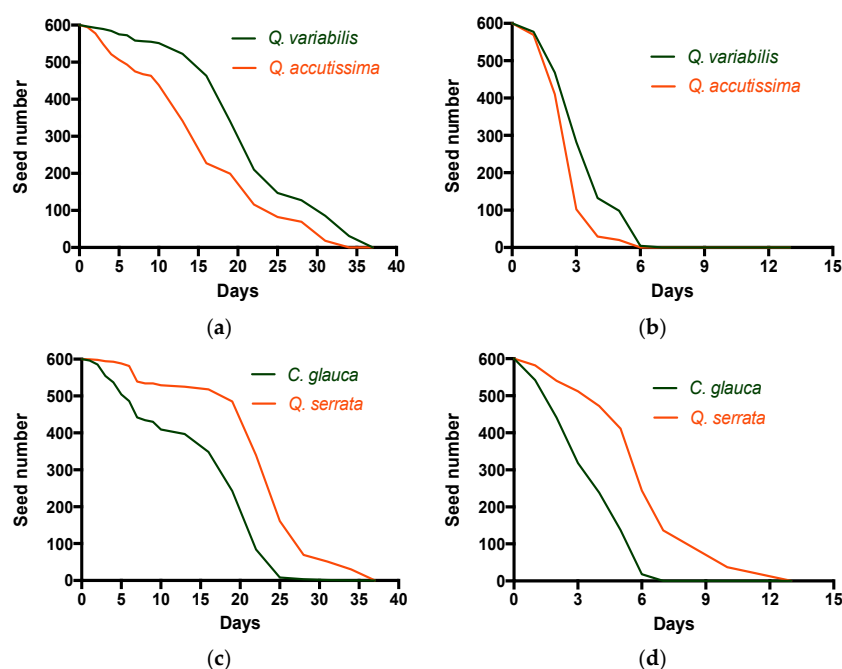

Figure 2. Field acorn removal of *Q. variabilis* and *Q. accutissima* (**a**,**b**), and *Q. serrata* and *C. glauca* (**c**,**d**) in the non-masting year.
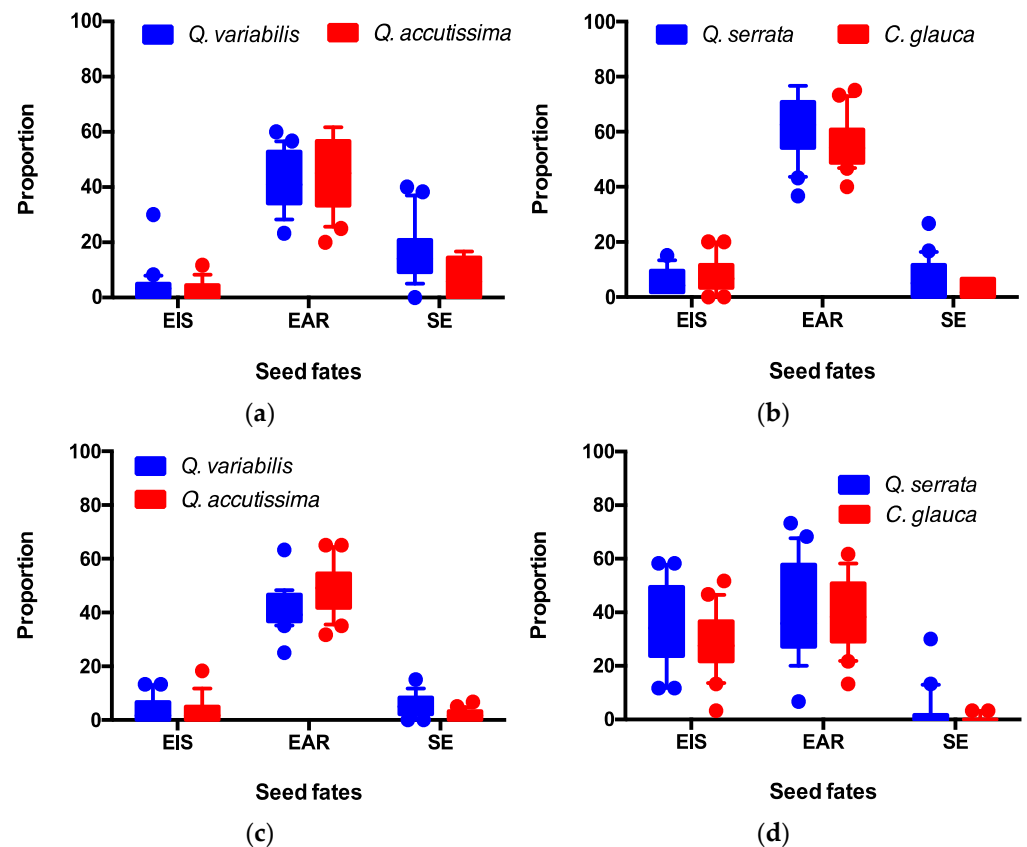
Figure 3. Seed fates of *Q. variabilis* and *Q. accutissima* (**a**), *Q. serrata* and *C. glauca* in a masting year (**b**) as well as *Q. variabilis* and *Q. accutissima* (**c**), *Q. serrata* and *C. glauca* in a non-masting year (**d**). EIS, EAR, and SE indicate acorns eaten in situ, eaten after removal, and seedling establishment from the released acorns, respectively.

3.3. Seedling Establishment from Artificial Caches

We found more seedlings established from the artificial caches of *Q. variabilis* than from those of *Q. accutissima* ($t = 2.499$, df = 18, $p = 0.022$; Figure 4). The same pattern was found between *Q. serrata* and *C. glauca* ($t = 5.595$, df = 18, $p < 0.001$; Figure 4). The results suggest that oak species producing dormant acorns are less likely to establish seedlings in the field.
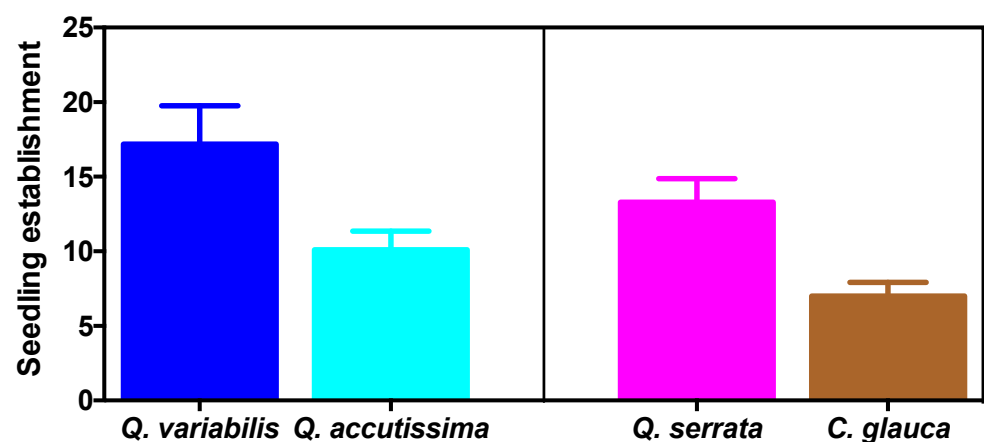
Figure 4. Seedling establishment from artificial caches of *Q. variabilis*, *Q. accutissima*, *Q. serrata*, and *C. glauca*. Bars sharing different letters indicate statistically significant at *p* < 0.05 level.

3.4. Acorn Selection by Seed-Eating Rodents in Enclosures

Our behavioral experiments in the enclosures showed that all the five rodent species consumed acorns of *Q. variabilis*, *Q. accutissima*, *Q. serrata*, and *C. glauca* (Figure 5). *L. edwardsi*, *A. draco*, and *A. chevrieri* appeared to be scatter-hoarders, while *N. confucianus* and *N. fulvescens* were larder-hoarders. *L. edwardsi* preferred to scatter-hoard acorns of *Q. accutissima* over *Q. variabilis* ($t = -6.637$, df = 5, $p = 0.001$; Figure 5a), and *C. glauca* over *Q. serrata* ($t = -2.408$, df = 11, $p = 0.035$; Figure 5f). *A. draco* and *A. chevrieri* preferred to scatter-hoard acorns of *C. glauca* over *Q. serrata* ($t = -2.485$, df = 9, $p = 0.035$; $t = -3.191$, df = 9, $p = 0.011$; Figure 5g,h), but showed no preference for acorns either of *Q. accutissima* or *Q. variabilis* ($t = -1.430$, df = 9, $p = 0.186$; $t = -1.539$, df = 9, $p = 0.158$; Figure 5b,c). As larder-hoarders, *N. confucianus* and *N. fulvescens* did not selectively hoard acorns of *Q. variabilis* and *Q. accutissima* ($t = -0.368$, df = 9, $p = 0.722$; $t = 0.780$, df = 9, $p = 0.455$; Figure 5d,e), as well as *Q. serrata* and *C. glauca* ($t = 1.935$, df = 9, $p = 0.085$; $t = -0.471$, df = 9, $p = 0.649$; Figure 5i,j). This indicated that at species level rodents preferred to disperse dormant acorns over nondormant acorns under the caged conditions.
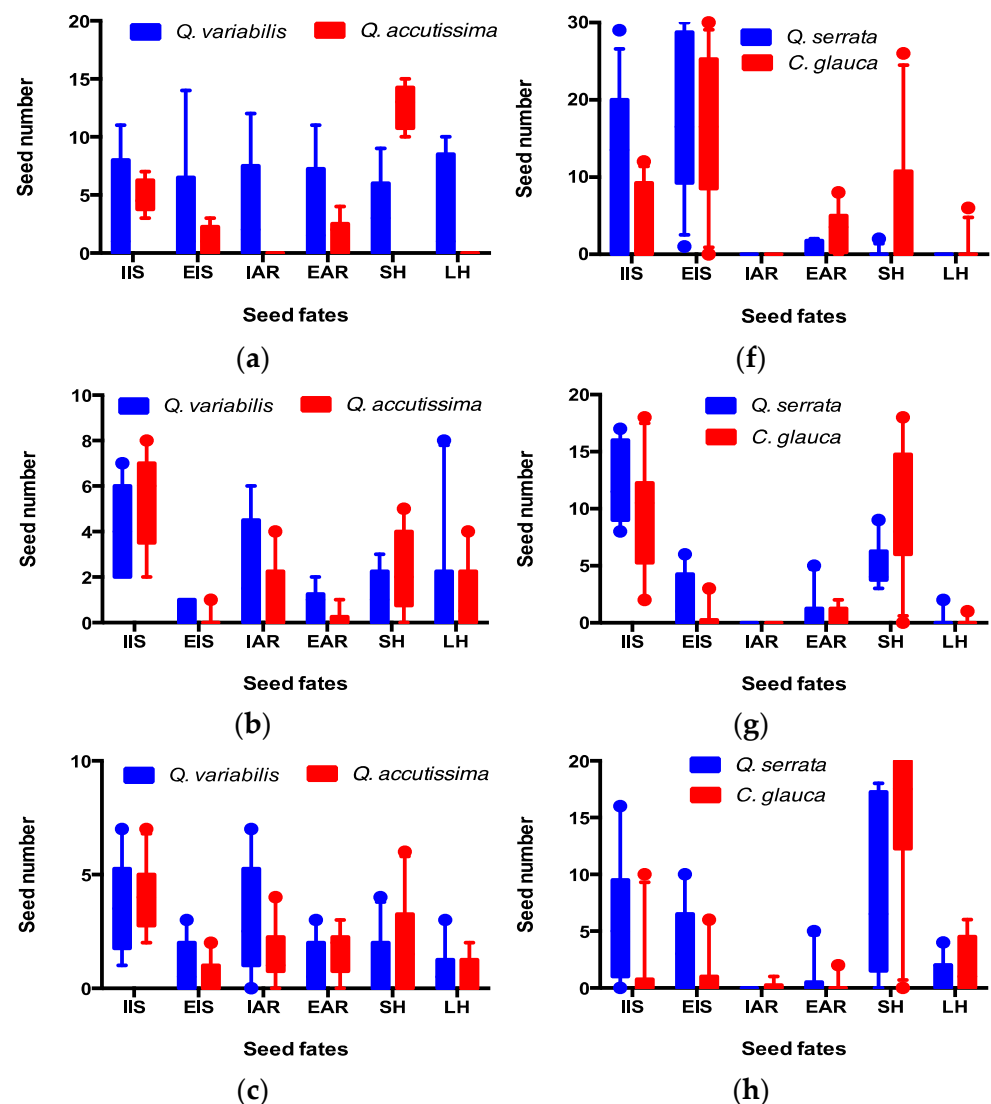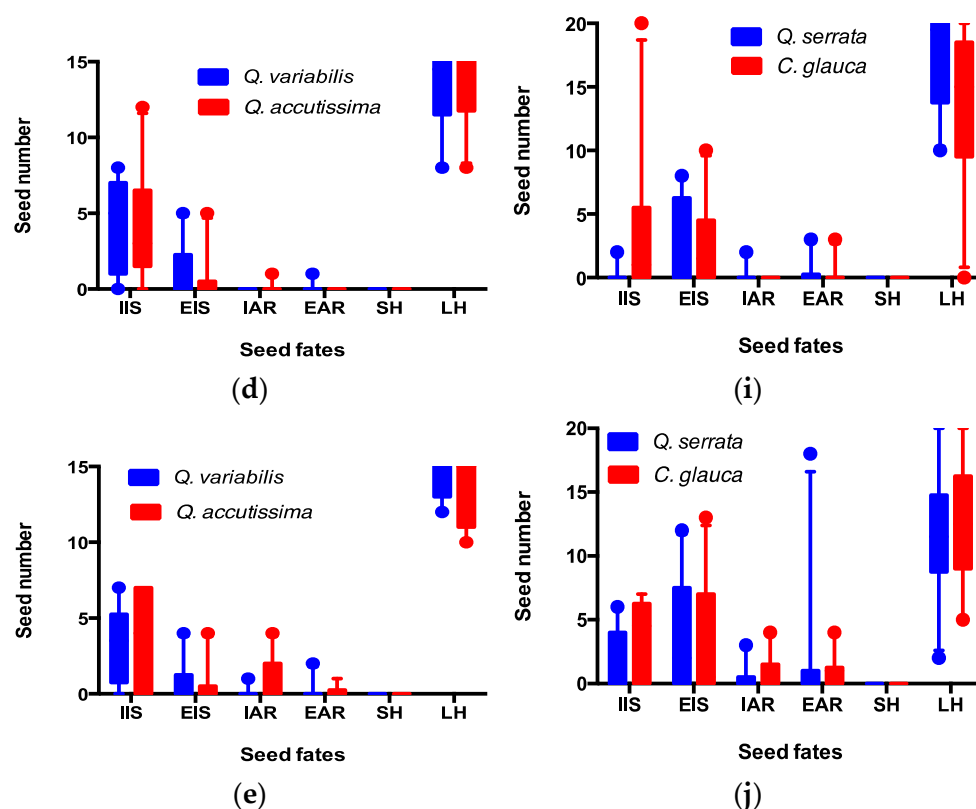

Figure 5. *Cont.*

Figure 5. Seed fates of *Q. variabilis* and *Q. accutissima* (**a–e**), as well as *Q. serrata* and *C. glauca* (**f–j**) manipulated by *Leopoldamys edwardsi*, *Apodemus draco*, *A. chevrieri*, *Niviventer confucianus*, and *N. fulvescens*, respectively. IIS, EIS, IAR, EAR, SH, and LH indicate acorns intact in situ, eaten in situ, intact after removal, eaten after removal, scatter-hoarded, and larder-hoarded, respectively.

4. Discussion

Our results clearly showed that non-dormant acorns of *Q. variabilis* and *Q. serrata* produced robust taproots after seed fall. Consequently, 40–50% of the cotyledon dry mass was lost 10 weeks after germination. These results coincide with the previous studies on a variety of white oak species [22–24,36,37]. Compared to *Q. variabilis*- and *Q. serrata*-producing nondormant acorns, acorns of *Q. accutissima* and *C. glauca* remained dormant and failed to protrude the robust taproots throughout the autumn and winter.

In agreement with previous findings [30,38,39], seed dormancy appeared to increase seed spatial dispersal in our study. Although seed-eating animals showed a significant preference to disperse and cache acorns of *Q. accutissima* and *C. glauca* both in the enclosures and field, more seedlings of *Q. variabilis* and *Q. serrata* were established than those of *Q. accutissima* and *C. glauca* after spatial dispersal by seed-eating animals. One possible reason for this discrepancy could be that scatter-hoarding animals are less likely to revisit and recover their caches containing germinating acorns [40]. In addition, acorns of *Q. variabilis* and *Q. serrata* in the artificial caches were more likely to establish seedlings than *Q. accutissima* and *C. glauca*. Fox [36] suggested that acorns of nondormant oaks become less attractive to seed predators if they germinate because the cotyledon reserves are rapidly transferred into the robust taproots that are inedible to seed predators. In this scenario, acorns of *Q. variabilis* and *Q. serrata* cached by seed-eating animals are expected to have a higher opportunity than *Q. accutissima* and *C. glauca* to escape post-dispersal predation and then establish seedlings from those caches. This speculation is well supported by the fact that acorns of *Q. variabilis* were less likely to be eaten after removal than *Q. accutissima*. In contrast to the traditional tradeoff between dormancy and dispersal [39], the nondormant cotyledons help acorns of *Q. variabilis* and *Q. serrata* achieve higher dispersal fitness than those of *Q. accutissima* and *C. glauca*, indicating that the trade-off between temporal disper-

sal (dormancy) and spatial dispersal determines the ultimate seed dispersal effectiveness. Our results were somewhat inconsistent with the 'perishability hypothesis' stating that animals tend to eat more perishable seeds but cache more dormant seeds [25]. Although we have no solid evidence, changes in smell and taste of acorns after germination will account for the rodents' preference for acorns [41]. Translocation of carbohydrate reserves in the nondormant acorns is also expected to interfere acorn selection of rodents [42]. This may well explain why dormant acorns were more likely to be dispersed by seed-eating animals compared to nondormant acorns. On the contrary, acorns of *Q. accutissima* and *C. glauca* established less seedlings than *Q. variabilis* and *Q. serrata*, although seed dormancy has been also considered an alternative adaptation to escape seed predators [43]. This discrepancy can be attributed to the neglected survey on the final stage of seedling establishment in previous studies [25,34], reflecting the significance of temporal dispersal in manipulating spatial dispersal between the two mutualist partners in seed dispersal processes.

Our results may have underestimated the possibility of seedling establishment from the nondormant acorns of *Q. variabilis* and *Q. serrata* in the field. Our recent studies provide solid evidence that the robust taproots of nondormant oak acorns show the potential to regenerate into normal seedlings even if the cotyledons are detached by seed predators [21,22,24]. However, the taproots of dormant oak species failed to regenerate into normal seedlings [21]. Moreover, young seedlings of nondormant oaks tolerate cotyledon damage better than those of dormant species [37]. Given that seed-eating animals detached the cotyledons from the germinating acorns in their caches in the following visits, the regenerated seedlings from the robust taproots might have been neglected because the plastic tags were usually taken away together with the detached cotyledons and remained unseen to the investigators. In fact, we found a large proportion of seedlings of *Q. variabilis* and *Q. serrata* originated directly from the pruned taproots in the artificial caches, although the cotyledons have already been detached by seed-eating animals (Figure S3). Therefore, it is safe to predict that acorns of nondormant *Q. variabilis* and *Q. serrata* will produce more seedlings than dormant *Q. accutissima* and *C. glauca* in the field, reinforcing the role of temporal dispersal in enhancing spatial dispersal fitness of nondormant seed species.

5. Conclusions

In summary, our study shows a clear tendency for nondormant acorns of *Q. variabilis* and *Q. serrata* to have high dispersal effectiveness than dormant *Q. accutissima* and *C. glauca*. Rapid germination may benefit nondormant plants by increasing cache survival and seedling establishment, shifting conditional mutualism towards more mutualistic between the two mutualist partners. On the contrary, seed-eating animals impose continuous predation pressure on dormant acorns of *Q. accutissima* and *C. glauca*, providing limited spatial dispersal service. Our results support our hypothesis that nondormancy enhances seed dispersal advantage and promotes mutualism between nondormant seeds and scatter-hoarding animals, providing insight into the co-evolution of temporal and spatial dispersal of oaks exhibiting contrasting life-history traits.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data is deposited in the Figshare Repository www.figshare.com (accessed on 3 June 2022).

Conflicts of Interest: The authors declare no conflict of interest.

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