Contents lists available at ScienceDirect

Forest Ecology and Management

The distinct fruit size and physical defense promote divergent secondary seed dispersal strategies of three oak species

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ARTICLE INFO

ABSTRACT

Secondary seed dispersal is one of the most important factors contributing to the co-existence of plant species. Variations in fruit properties including fruit size, physical defense and chemical composition influence seed foraging and secondary dispersal, but the details remain unclear. Here, we focused on three common nut-bearing tree species (*Quercus aliena* Blume, *Q. dentata* Thunb., and *Q. variabilis* Blume), which often co-occur in mixed deciduous forest in northern China. We estimated their acorn properties and evaluated their effects on the secondary dispersal patterns. We found similar chemical profiles but different acorn sizes and physical defense among these three species. Moreover, we detected distinct secondary seed dispersal strategies in relation to their acorn properties: *Q. dentata* produced the smallest-sized acorns with the lowest physical defense, which had shorter dispersal range but the highest survival rate; *Q. variabilis* generated the largest-sized acorns with the highest physical defense, which suffered the lowest survival rate but benefited from the longer dispersal range; and an intermediate survival rate existed in *Q. aliena* with the intermediate-sized acorns. In addition, Père David's rock squirrel (*Sciurotamias davidianus* Milne-Edwards, Sciuridae) and brown rat (*Rattus norvegicus* Berkenhout, Muridae) are secondary seed dispersal agents for three oak species. Brown rats not only disperse more acorns than Père David's rock squirrels, they also create different dispersal distance for the acorns of three species, which enhance three species' niche separation. Our results therefore revealed that differentiations in acorn properties have derived distinct trade-offs in secondary seed dispersal strategies, likely facilitating the coexistence of the three examined species.

1. Introduction

Understanding the mechanisms behind plant species co-existence is an enduring challenge for ecologists. To date, competition driven by abiotic (such as nitrogen and phosphorous) and biotic factors (such as plant interactions) had been extensively examined in plant coexistence studies (Craine and Dybzinski, 2013). However, empirical studies on how multitrophic interactions such as secondary seed dispersal shape plant coexistence are scarce (Bartomeus and Godoy, 2018). Secondary seed dispersal is an important biotic interaction representing mutualism: plants provide foods to animals, meanwhile animals promote plant regeneration by dispersing the seeds in favorable locations (Ruxton and Martin Schaefer, 2012; Chang and Zhang, 2014; Ong et al., 2022).

Characterized by dispersers removing the seeds from the parent plant (Padilla et al., 2012), secondary dispersal affecting habitats' colonization, population spread and distribution, as well as the flow of individuals between populations to achieve genetic connectivity, which in turn facilitates plant coexistence (Snyder and Chesson, 2004; Crawley, 2000; Vander Wall, 2001).

The process of seed predation and dispersal is complex, as the seed fate is influenced by a diverse group of factors such as varied fruit characteristics and crop yield (Zhang et al., 2008; Pérez-Ramos et al., 2008; Wróbel and Zwolak, 2019). Fruit characteristics, including fruit size, physical defense and chemical composition, are considered influential factors impacting secondary seed dispersal. Fruit size represents nutrient reserve, its effects on secondary seed dispersal are still under

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debate: some studies indicate larger fruits have lower post-dispersal survivorship (e.g. Boman and Casper, 1995; Kollmann et al., 1998; Blate et al., 1998); some suggest larger fruits are more likely to be dispersed with longer distance (e.g. Jansen et al., 2004; Stapanian and Smith, 1978; Xiao et al., 2013); while others found the medium-sized fruits are more likely to be dispersed (e.g., Theimer, 2003; Wang and Chen, 2009). Fruit husk, seed coat and other appendages (spines and cupules) are effective physical defenses for predation risks (Vander Wall, 2010). In addition, seed antifeedants, such as tannins, fibers, and terpenoids are chemical defenses to reduce the attractiveness of the seeds (Steele et al., 1993; Robbins, 1994). On the other hand, macronutrients including protein, lipid and carbohydrates are vital nutrition for seed predators (Vander Wall, 2001). Therefore, fruit size, physical defense and seed chemistry together contributed to seed predation and seed dispersal (Jansen et al., 2004). However, the detailed impact of variations in these fruit characteristics on secondary seed dispersal are scarce.

Oak genus (*Quercus* L.) is one of the most diverse trees genera in the Northern Hemisphere, with high species diversity in southeast Asia, Central and North America (Denk et al., 2018). The fruit of oak, acorn, is a single nut subtended by cupule structure are attractive food for many wild animals (Lambert et al., 2004). As one of the classical models for examining secondary seed dispersal, acorn dispersal rely almost entirely on nut-caching animals, and this dispersal in turn reflects structure, composition and evolutionary process in forest ecosystems (Steele, 2021). Meanwhile, the sympatry and co-occurrence of varied oak species is very common in the deciduous forests (Damesin et al., 1998; Xiao et al., 2006b). Investigating animal-mediated acorn dispersal of the co-occurred *Quercus* species is important in understanding the factors that drive their co-occurrence, which would promote conservation of oak forests.

Three oak species, *Quercus aliena* Blume, *Q. dentata* Thunb. and *Q. variabilis* Blume, coexist in mixed deciduous temperate or warm-temperate forests in East Asia (Chen et al., 2022; Huang et al., 2000). Among them, *Q. aliena* and *Q. dentata* belong to a small monophyletic group nested within section *Quercus* (white oaks), while *Q. variabilis* belongs to section *Cerris* (Box, 2015; Du et al., 2022; Hubert et al., 2014; Hipp et al., 2020; Vander Wall, 2001). The secondary seed dispersal of three species directly impacts on their distribution and in turn influence their co-occurrence, but how the fruit characteristics relate to seed predation and dispersal of three species remains unclear.

In this study, we measured the fruit characteristics, i.e., fruit size, physical defense and seed chemistry of three oak species. In addition, we depicted the secondary seed dispersal patterns of above species by field surveys and seed dispersal experiments, to infer the potential impacts of fruit characteristics on their secondary seed dispersal.

2. Methods

2.1. Study site and fruit collection

Our study site, Shangfang Mountain National Forestry Park, is located in the southwest of Beijing Municipality, P. R. China (115°48′E, 39°39′N). Mount Shangfang is a part of the Taihang Mountains with around 353 ha of well-preserved secondary forest covering an elevation range from 110 to 1500 m (Lyu et al., 2018). The common tree species here are from genus *Quercus* L., *Platycladus* Spach, *Larix* Mill. and *Pteroceltis* Maxim. Among them, *Q. aliena*, *Q. dentata* and *Q. variabilis* are three dominant oak species. *Q. dentata* habitats open conditions on the top of the hills, whereas *Q. aliena* with higher density is growing at the bottom and along the hillside. The third species, *Q. variabilis*, is distributed from the bottom to the top of the mountain. Genetic study based on neutral nuclear marker in this site had shown clear species boundaries existed among the three species (Lyu et al., 2018). Some of the common seed dispersers in this region includes rhesus macaque (*Macaca mulatta* Zimmermann, Cercopithecinae), Père David's rock squirrel (*Sciurotamias davidianus* Milne-Edwards, Sciuridae), Korean

field mouse (*Apodemus peninsulae* Thomas, Muridae), brown rat (*Rattus norvegicus* Berkenhout, Muridae) and flying squirrel (*Trogopterus xanthipes* Milne-Edwards, Sciuridae) (Gong et al., 2020).

After flowering, the acorns of three oak species mature in autumn of the same year (*Q. aliena* and *Q. dentata*) or the next year (*Q. variabilis*). We collected fresh acorns of the three oak species from the ground during the fruiting period in 2018. For each species, we chose 1, 000 sound acorns by seed floatation test and stored fresh acorns in a refrigerator at 4° C, which were used in the following experiments within five months.

2.2. Fruit characteristics estimation

We applied two fruit morphometrics, i.e., the fresh fruit mass and husk thickness/seed width ratio to represent the fruit size and seed physical defense respectively. Mean fruit fresh mass and mean husk thickness (measured by vernier caliper on the dissected fruit) was averaged for 200 sound acorns of each species.

The seed chemical properties including macronutrients and antifeedants of each species were estimated at the Grain Testing Center of the Chinese Academy of Agricultural Sciences in March 2019. In details, crude protein was determined by semi-micro Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Pierce and Haenisch, 2010). Crude starch, reduced sugar, crude fiber, crude lipids and tannin were quantified, according to the People's Republic of China National Standard (GB 5006–85, GB 5009.7–2016, GB 6193–86, GB 2906–82 and GB/T 15686–2008 respectively).

2.3. Seed dispersal experiment

We conducted the seed dispersal experiment in six plots on Mount Shangfang from October 2018 to February of 2019. The minimum interval between any two plots was 100 m, and each plot was located at least 30 m away from the nearest pedestrian trail. A hole with a diameter of 0.2 mm was punctured on the bottom of each acorn using a small electric drill, to avoid damaging the embryo. The punctured acorn was then tagged with a plastic label (3.6 cm × 2.5 cm) attached to an 8 cm long stainless wire, which has been validated to be light enough to not impact on predators' choice and decision (Lu and Zhang, 2005; Xiao et al., 2006a). Fifty tagged acorns for each species were released for two times at each plot, with the first in October and the second in November (Perea et al., 2011). In total, 1, 800 acorns were placed (50 acorns by 3 species by 6 plots by 2 times). The acorn removal *in situ* was monitored by the infrared cameras LTL-6310MC attached to a nearest standing tree trunk 0.4 m above the ground. Both pictures and 10 s' video recording were taken triggered by animal movement.

The acorns were searched within the area with a radius of 30 m after acorn placement. Both the removal distance and survival seeds were measured and recorded. We categorized seed fates into five situations (Chang et al., 2012): i) remained *in situ*; ii) eaten *in situ* (including both complete and partial consumption); iii) cached after removal; iv) eaten after removal and v) missing. The seed fate related to different predators was based on camera data. The acorn status was monitored from September 21st 2018 to Feb 24th 2019 for a total of 126 days. As we did not detect seedlings emergence by the end of the observation, the seed survival in our analysis was represented by acorn survival.

2.4. Data analysis

We performed all the statistical analyses in R version 3.6.1 (R Core Team, 2019). We first try to compare the fruit characteristics differences among threes species. We carried out Shapiro–Wilk test and Levene test (package *car*, Fox and Weisberg, 2019) to explore data distribution and homogeneity respectively. We found that the data of fruit morphometrics and seed chemistry were not normally distributed nor homogeneous, therefore, we performed Kruskal-Wallis rank sum test and

multiple comparison test by applying each characteristic (the fresh fruit mass, seed physical defense represented by husk thickness and seed width ratio, as well as the content of crude protein, crude fat, reducing carbohydrates, crude starch, crude fiber and tannin) as response variable and three species as categorical independent variable (package *pgirmess*, Giraudoux, 2018).

As most acorns were effectively eaten or relocated by the first 24 h from the placement based on camera recording data, we chose 24 h as the time point to apply Generalized Linear Mixed Model (GLMM) with Poisson-distributed errors to explore differences of four different seed fates, i.e., remained *in situ*, eaten *in situ*, cached, and eaten after dispersal among three species. The acorn count of each fate was set as response variable, and three species were categorical independent variables. Plot one to six were applied as random intercept to incorporate the spatial correlation. To untangle two dispersers' decision making towards three species, we also applied GLMM with Poisson-distributed errors to explore differences of two seed fate counts relate to two dispersers (eaten *in situ*, dispersal seed count by brown rats and Père David's rock squirrel respectively as response variables) among three species (as categorical independent variables), by applying plots as random intercept. We applied Akaike Information Criterion (AIC) afterwards to compare the model of seed fate counts and plot intercept with the model of plot intercept only. The significance of the independent variables for the selected model was then tested by type I Wald Chi-square test (package *car*). When a significant result was found by running the models, the pairwise GLMM analysis was further performed to clarify the seed fate count variation among the three species.

Both nocturnal (e. g. mice and rats) and diurnal (e. g. squirrels) animals are known to be seed dispersers of acorns (Muñoz and Bonal, 2008; Pérez-Ramos and Maranon, 2008; Lichti et al., 2017). Examining their difference in seed predation and dispersal would be important in evaluating their seed dispersal efficiency. By setting plots as random intercept and day/night as independent variable, we applied mixed effect cox regression (package *coxme*) to entangle the differences in acorns death (eaten *in situ* and after removal) and survival (remain *in situ* and cached after removal) from seed releasing till complete seed removal (Therneau, 2015).

To compare the dispersal distance variation, we plotted the dispersal distance in relation to the number of acorns for the three oak species by SigmaPlot 12.0. As the dispersal distance was not normally distributed nor homogeneous by Shapiro–Wilk test and Levene test (package *car*, Fox and Weisberg, 2019), by applying different dispersal distance as response variable and three species as categorical independent variable, we carried out Kruskal-Wallis rank sum test and multiple comparison test in package *pgirmess* (Giraudoux, 2018) to compare the dispersal

distance among the three species.

3. Results

3.1. The variation in fruit morphometrics and seed chemical attributes

We found that both fruit mass and husk thickness/seed width ratio were significantly different among three species: *Q. variabilis* > *Q. aliena* > *Q. dentata* (Kruskal-Wallis chi-squared is 393.44 and 257.23 respectively, both $p < 0.001$) (Fig. 1, Table 1). However, these three species were not significantly different in terms of their seed chemical attributes, including both macronutrients (i.e., crude protein, crude lipid, crude starch and reducing carbohydrates) and antifeedants (i.e., crude fiber and tannin) (Table 1).

3.2. Seed predation and dispersal of three species

Among the total 600 released acorns per species, the caching rate of *Q. aliena*, *Q. dentata* and *Q. variabilis* were 21 %, 28 % and 46 % respectively (Table A. 1); total consumption rate (eaten *in situ* plus eaten after dispersal) of *Q. aliena*, *Q. dentata* and *Q. variabilis* were 79 %, 70 % and 54 % respectively; the remain *in situ* rate of *Q. aliena*, *Q. dentata* and *Q. variabilis* were 0 %, 2 % and 0 % respectively.

After releasement, the acorns were either dispersed (n = 1014), remained *in situ* (n = 13) or eaten *in situ* (n = 770), and only 3 were missing. By the first 24 h from the placement, as very few acorns were remained *in situ*, most acorns of all three species were effectively eaten or dispersed (Fig. 2a and 2b). The caching of three species peaked after 48 h and declined afterwards (Fig. 2c), and consumption of the removed acorns reached the maximum by the end of the week (Fig. 2d). Based on the results of the model with less AIC value, GLMM analysis at 24 h time point revealed that the acorns of *Q. aliena* and *Q. dentata* not only had lower caching rates and higher remained *in situ* count, but were also more likely to be eaten after dispersal compared to the acorns of *Q. variabilis* (Table 2). These results were largely congruent to the overall caching rate (Table A. 1). We did not find a significant difference among three species in the acorn eaten *in situ* count at the 24 h time point.

Based on the camera image and video recording, we found Père David's rock squirrels and brown rats are seed predators as well as dispersers for the three species (Table A. 2). Père David's rock squirrels sought acorns during daytime (7 am to 6 pm) whereas brown rats foraged at night (7 pm to 6 am the next day). Based on GLMM, the eaten *in situ* acorn count by Père David's rock squirrel was not significantly different among the three species (Table 3). However, we found a different eaten *in situ* acorn count by brown rat, i.e., *Q. aliena* and


Fig. 1. Acorn morphology of *Q. aliena*, *Q. dentata* and *Q. variabilis*.

Table 1

The differences in fruit morphometric and seed chemical attributes among three species.

Attributes	Traits	QA	QD	QV	χ^2	*p*-value	Rank
Fruit morphometrics	Husk thickness (mm) / seed width (mm)	0.30	0.20	0.40	257.23	< 0.001	QV > QA > QD
	Fruit mass (g)	3.65	1.79	4.29	393.44	< 0.001	QV > QA > QD
Seed chemistry	Crude protein (%)	5.91	4.93	4.83	4.57	0.10	NA
	Crude fat (%)	2.26	4.69	3.21	4.57	0.10	NA
	Reducing carbohydrates (%)	3.67	4.60	4.82	4.57	0.10	NA
	Crude starch (%)	59.75	56.10	56.94	4.57	0.10	NA
	Crude fiber (%)	1.94	2.12	2.25	3.71	0.16	NA
	Tannin (%)	1.59	1.68	1.54	2.57	0.28	NA

QV, QA and QD represented *Q. variabilis*, *Q. aliena* and *Q. dentata* respectively. The differences of each trait among species were tested by Kruskal-Wallis rank sum test. NA stands for non-significant pairwise relationship among three species.
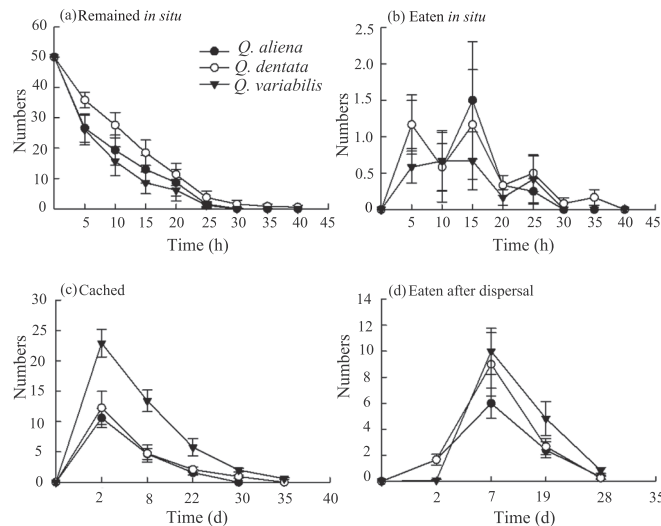
Fig. 2. Dynamic of acorns fates of three oak species. Acorns (a) remained *in situ*, (b) eaten *in situ*, (c) cached and (d) eaten after dispersal. (a) and (b) the time is shown in hours, (c) and (d) the time is shown as in days.

Table 2

The variation in different seed fates among three species by generalized linear mixed model (GLMM).

Seed fate counts	*Q. aliena*	*Q. dentata*	*Q. variabilis*	*p*-value	Chisq-value
Eaten after dispersal	−0.31	−0.31	−3.30	0.013	8.756
Cached	2.34	2.49	3.12	< 0.001	67.758
Remained *in situ*	−0.81	−0.01	−0.81	< 0.001	17.568

The appeared coefficients are significant based on model selection by Akaike's Information Criterion (AIC). The *p* and Chi-square values were based on type I Wald chi-square test to check the significance of three species as categorical factors in the GLMM model.

Q. dentata > *Q. variabilis*. There were also significantly differences in dispersed acorn count by both predators respectively: the dispersal preference of brown rat was *Q. dentata* > *Q. aliena* > *Q. variabilis*; whereas Père David's rock squirrel prefers to disperse *Q. variabilis* more than *Q. dentata* and *Q. aliena*.

Different plots did not impact on acorn survival count significantly (Table 4). The negative coefficient of *Q. dentata* indicated its higher survival count compared to *Q. aliena*, whereas the positive coefficient of *Q. variabilis* indicated its higher death count compared to *Q. aliena*. The overall survival possibility of three species increased with their fruit mass: *Q. dentata* (smallest acorn) > *Q. aliena* > *Q. variabilis* (largest acorn). The negative coefficient between day and night indicated a higher survival possibility at night time compared to day time.

Table 3

The variation in different seed caching and dispersal count among three species by different predators by Generalized Linear Mixed Model (GLMM).

| Seed fate counts	*Q. aliena*	*Q. dentata*	*Q. variabilis*	*p*-value	Chisq-value
Dispersal by Père David's rock squirrel	2.98	2.94	3.34	< 0.001	27.55
Dispersal by brown rat	1.69	1.97	1.19	< 0.001	18.296
Eaten *in situ* by brown rat	1.74	1.56	1.14	0.005	10.482

The appeared coefficients are significant based on model selection by Akaike's Information Criterion (AIC). The *p* and Chi-square values were based on type I Wald chi-square test to check the significance of three species as categorical factors in the GLMM model.

Table 4

Mixed Effects Cox Models on acorn survival along time by setting plot as random factor.

Covariates	Z	Coef	Exp (coef)	*p*-value
Q. dentata	10.50	−0.641	0.527	< 0.001
Q. variabilis	2.66	0.161	1.174	< 0.001
day/night	−5.51	−0.394	0.675	< 0.001

We categorized eaten *in situ* and eaten after removal as acorns death, caching and remain *in situ* as survival. Z: The wald statistic, which corresponds to the ratio of each regression coefficient to its standard error. Coef: The coefficient of the explanatory variable. Exp (coef): The risk ratio which is the degree of estimation of the increased or decreased predicted risk.

The acorns were relocated within a 25 m radius range from the releasing points (searching radius 30 m). 78 %, 71 %, 60 % of *Q. dentata*, *Q. aliena* and *Q. variabilis* acorns were dispersed within 10 m,
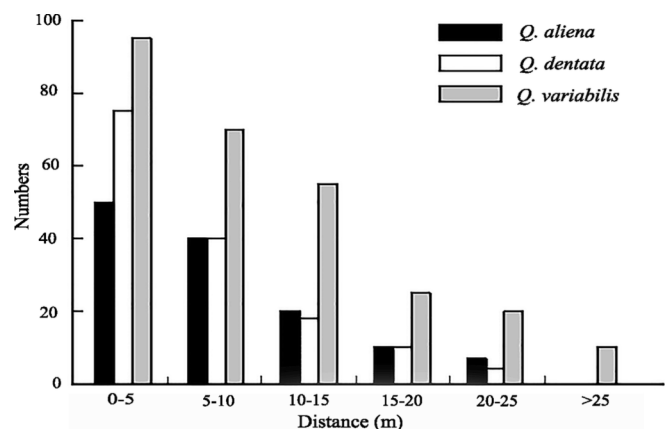
Fig. 3. Dispersal distance of acorns of three species from the releasing point.

respectively (Fig. 3). The average dispersal distance of *Q. dentata* (the smallest acorn), *Q. aliena* and *Q. variabilis* (the largest acorn) was 6.8 m, 8.2 m and 9.6 m, respectively, with significant differences among the three species (Kruskal-Wallis chi-squared = 18.8, $p < 0.001$).

4. Discussion

The complex suit of chemical, physical, morphological characteristics of a fruit affects animals' foraging decisions and behaviors (Van Soest, 1994; Vander Wall, 2001), so comparing secondary seed dispersal pattern among plant species owning different fruit characteristics is crucial in facilitating understanding of species coexistence. In this study, we found that the three oak species were similar in all examined acorn chemical attributes, but were significantly different in fruit size and physical defense (Fig. 1, Table 1). Moreover, species with different acorn characteristics displayed distinct secondary dispersal patterns, showing a tradeoff between dispersal distance and survival given that all three species were served by the same dispersers. As fruit size represents reproductive energy, the overall difference in fruit characteristics of three sympatric oaks are mainly the reproductive energy per nut and relative physical defense, but not nutrient composition nor chemical defense. We therefore propose that the seed fate variation among the three species is mainly contributed by their fruit size and physical defense.

The high acorn eaten *in situ* and removal rate (Fig. 2a and 2b, Table A. 1) indicated that the acorns of these three species were favorable and essential food for the animals. In our study, Père David's rock squirrels and brown rats were identified as seed predators and dispersers for three species during day and night time, respectively (Table A. 2). Two dispersers were distinctly different in their acorn consumption and dispersal preference, Père David's rock squirrel preferred to disperse bigger fruits (*Q. variabilis*) more often than smaller fruits (*Q. dentata and Q. aliena*); whereas brown rats eat more smaller fruits *in situ*. Moreover, brown rats are better at distinguish three different-sized species: they disperse the smallest-fruited and largest-fruited *Q. dentata* and *Q. variabilis* most and least respectively, leave the dispersal rate of the medium-sized *Q. aliena* in between (Table 3). Moreover, these two animals were also different in the seed dispersal quantity: Père David's rock squirrels caused a significantly higher number of acorn death, whereas brown rat dispersed more acorns (Table 4). Belonging to the rodent family Sciuridae and Murine respectively, Père David's rock squirrels and brown rats are both recognized as seed-dispersing scatter-hoarders (Vander Wall, 1990). However, other studies suggest their role in seed dispersing could be disputable. For instance, Père David's rock squirrels were identified to remove embryos of large non-dormant acorns (Xiao et al., 2013). Another study suggests brown rats not only bury large number of acorns in unfavorable environment for seedling establishment such as dark burrows, but also consume most of them afterwards (Shepherd and Ditgen, 2013). In our study, we often found a single acorn or 2–3 acorns hoarded per site, suggesting two rodents are scatter-hoarders for the three species. Further examining the seed dispersal quality of these two kinds of rodents by tracking the seedlings establishment in the future would be necessary to evaluate their seed dispersal effectiveness for these three species.

Both the physical defense and fruit size impact on foraging decisions: rodents prefers consuming seeds costing less handling time *in situ*, and the seeds with better physical protections which cost longer time to open are more often cached (Jacobs, 1992; Vander Wall, 2001); larger fruit represented higher nutrition value to foragers (Jansen et al., 2004), so they were more likely to be removed and cached, rather than be eaten *in situ* (Wang and Chen, 2009; Vander Wall, 2010). At the first 24 h after placement, we found that the seed fates of three species corresponded to their fruit size and physical defense (Table 2): the biggest-fruited *Q. variabilis* with strongest physical protection was dispersed and cached more often, as well as consumed less after dispersal; the smaller-sized *Q. aliena* and *Q. dentata* with less physical defense had higher

remain *in situ* count, lower cache rate and higher consumption after dispersal.

The fruit size and physical defense also influence the long-term survivorship and dispersal distance of seeds for three species (Table 4). Consistent with many previous seed dispersal studies (Forget et al., 1998; Stapanian and Smith, 1978; Xiao et al., 2005), we also found a positive correlation between fruit size and dispersal distance: the dispersal distance is longer for biggest-fruited *Q. variabilis*, and the smaller-sized *Q. dentata* and *Q. aliena* had shorter dispersal distance. Meanwhile, the overall survivorship of three species was negatively related to their fruit mass: the smallest- and largest-sized *Q. dentata* and *Q. variabilis* had the highest and lowest survival rate, and the survivor rate of the intermediate-sized *Q. aliena* was in between (Table 4). This indicated that despite the stronger physical protection, larger fruits representing bigger energy reserve were subject to higher death risks (Kelrick et al., 1986; Willson and Whelan, 1990; Boman and Casper, 1995; Gomez, 2004). Combining with the fruit characteristic analysis, we conclude that the fruit size and physical defense variation among three species contribute to their distinctive seed dispersal mechanisms: the smallest-sized *Q. dentata* fruits with lowest physical protection have shorter dispersal distance, which will be compensated by their highest survival rate; *Q. variabilis* with the biggest fruits and highest physical defense has highest death rate, but their longer dispersal distance would be vital for seedling establishment; the intermediate-sized *Q. aliena* with intermediate physical protection has intermediate survival rate.

High consumption rate of acorns was observed in many studies (Crawley, 2000; Pérez-Ramos et al., 2013; Sun et al., 2004). The estimated consumption rate (eaten *in situ* plus eaten after dispersal) of *Q. aliena*, *Q. dentata* and *Q. variabilis* were 79 %, 70 % and 54 % respectively in our study (Table A. 1). We should note that the real acorn loss should be higher than our estimation. The cached acorns could be recovered and consumed by same predators or different animals (pilferage) later (Cao et al., 2018), which would represent acorn death. Moreover, the drought-sensitive acorns need to survived through the varied post-dispersal conditions. Representing recalcitrant seeds, the seeds of acorns are very sensitive to dehydration. Dehydration negatively impacts on oak seed vigor, which makes it the main abiotic cause for seed mortality, seed germination and seedling establishment failure (Xia et al., 2012; 2022). An acorn starts to lose water from the moment of its' fall, and the survival of which is greatly influenced by the humidity of the microenvironment after dispersal. The high consumption rate and the unpredictable environment could negatively impact on plant regeneration, so the diverged seed dispersal strategies of three *Quercus* species would be vital in maintaining their distribution and coexistence.

At local scale, species coexistence is often ensured by two opposing forces (Chesson, 2000). First, the fitness difference among species drives the best-adapted species to exclude others. The second is stabilizing mechanisms which limit dominance and enhance diversity through niche separation. Previous studies suggested that different dispersal distance could lead to species coexistence (Snyder and Chesson, 2003, 2004). We found plant species' coexistence could be enhanced by the trade-off in both dispersal distance and surival rate: the small-fruited species with lowest physical protection survived best but was dispersed closer to the mother tree; the big-fruited species with the highest physical defense died most but was dispersed farther; and the survival rate of the species with intermediated-sized acorns with medium-leveled physical defense were in between. Even though Père David's rock squirrel do not differentiate the smaller- and medium-fruited species, brown rat, on the other hand, could play a vital role in the three species niche separation by giving them distinctt dispersal distance. The trade-off between dispersal distance and survival rate among three species, combining with the help of altered behavior of two dispersers, allows th three oaks to escape competition by increasing environmental heterogeneity, which in turn contribute to their coexistence. Instead of passively chosen by animals, our study identified that

plants try to manage their own seed fates and their survival with others by modulating varied fruit properties to manipulate animals foraging behavior and decisions.

Species coexistence is essential of the maintenance of biodiversity, and therefore revealing the underlying mechanisms is important in plant conservation and community management (Lichti et al., 2017). The coexistence of three oak species is important in maintaining the stability and functioning of the ecosystem, as they represent essential carbon storage, as well as habitats and food source for the animals. Our study not only provides empirical evidence of how biotic interactions contribute to diversity, but also raise a new perspective in comprehending species coexistence via secondary seed dispersal. Our work thus improves our understanding of species coexistence across trophic levels and will assist forest management and conservation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared the link to my data/code at the Attach File step

Data availability statement

Data of fruit characteristics estimation and seed dispersal experiment can be obtained in https://doi.org/10.6084/m9.figshare.19767058.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120642.

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