ORIGINAL ARTICLE

Effects of fragmentation on the seed predation and dispersal by rodents differ among species with different seed size

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Abstract

Fragmentation influences the population dynamics and community composition of vertebrate animals. Fragmentation effects on rodent species in forests may, in turn, affect seed predation and dispersal of many plant species. Previous studies have usually addressed this question by monitoring a single species, and their results are contradictory. Very few studies have discussed the fragmentation effect on rodent–seed interaction among tree species with different seed sizes, which can significantly influence rodent foraging preference and seed fate. Given that fruiting periods for many coexisting plant species overlap, the changing foraging preference of rodents may substantially alter plant communities. In this study, we monitored the dispersal and predation by rodents of 9600 seeds, belonging to 4 Fagaceae species with great variation in seed size, in both the edge and interior areas of 12 tropical forest fragments ranging in area from 6.3 to 13872.9 ha in Southwest China. The results showed that forest fragmentation altered the seed fates of all the species, but the intensity and even the direction of fragmentation effect differed between species with large versus small seeds. For the seeds harvested, fragment size showed negative effects in forest interiors but positive effects at edges for the 2 large-seeded species, but showed little effect for the 2 small-seeded species. For the seeds removed, negative effects of fragment size only existed among the small-seeded species. The different fragmentation effect on seed dispersal and predation among plant species may, in turn, translate into the composition differences of the regeneration of the whole fragmented forest.

Key words: edge effect, forest fragmentation, plant–rodent interaction, seed size

INTRODUCTION

Fragmentation is a major threat to biodiversity in forests (Fahrig 2003; Laurance et al. 2006). Populations of many animals and plants have declined as forest fragmentation has increased (Laurance 1994; Cordeiro & Howe 2001; Da Silva Jr & Pontes 2008), and regional populations of several large mammals have been extirpated (Terborgh et al. 2001; Crooks 2002; Foley et
However, some small mammals, especially certain rodent species, may benefit from fragmentation because of the loss of predators and competitors, and their quick breeding ability (Laurance et al. 2002; Gibson et al. 2013; Morán-López et al. 2015; Mendes et al. 2016).

Rodents are both seed predators and seed dispersers in forests, thus influencing seedling regeneration, spatial distribution and diversity of trees (Hirsch et al. 2012; Jansen et al. 2012; Xiao et al. 2013; Sidhu & Datta 2015; Zhang et al. 2016; Cao et al. 2017). Therefore, changes to rodent populations and their foraging preferences in fragments may influence the whole structure and diversity of plant communities (Cordeiro et al. 2009; Zhang et al. 2016). Fragment size and edge effects are usually considered as the 2 most important fragmentation parameters for plant–rodent interactions (Kollmann & Buschor 2003; Fleury & Galetti 2006; Aliyu et al. 2014; Mendes et al. 2016), but previous work on these interactions in forest fragments has yielded contradictory results. For example, in 2 separate studies in eastern Brazil, Andreazzi et al. (2012) showed that seeds of Attalea humilis were scatter-hoarded more frequently in the large fragments than small ones, but seed predation by rodents did not relate to fragment size, whereas Mendes et al. (2016) observed greater seed predation in smaller fragments. Aliyu et al. (2014) also found that seeds suffered more predation in small fragments and forest edges than in the continuous forest interior, which they attributed to greater fruit production at forest interior sites. Fleury and Galetti (2006) found that the seed predation was more common in medium-sized fragments than both small and large ones. Forest fragmentation also decreased the distance of seeds dispersed by rodents (Cramer et al. 2007; Aliyu et al. 2014; but see Morán-López et al. 2015).

As discussed above, the current studies do not tell a consistent story about how fragmentation affects seed predation and dispersal by rodents. This is very likely due to differences in the plant–animal systems being studied in these different locations. One source of variation is that fragmentation may change rodent community composition (Suzán et al. 2008), and different species of rodents often show different seed preferences during foraging (Munoz & Bonal 2008; Tamura & Hayashi 2008). A second source of variation may result from differences in seed characteristics of tree species studied at each site, as rodents predate seeds differently based on their characteristics. Numerous studies have demonstrated that seed size can significantly influence rodent foraging preference and, thus, seed fate (Moore et al. 2007; Wang & Chen 2009; Vander Wall 2010; Lichti et al. 2017). Most previous studies have targeted a single plant species in their experiments (Xiao et al. 2013; Mendes et al. 2016; Zhang et al. 2017). However, many coexisting species in forests fruit during similar periods, which may increase the role of rodent preference in seed fate, and, thus, forest composition (Garzon-Lopez et al. 2015; Yi & Wang 2015a). Changes of rodent foraging preference upon seed size may, in turn, lead to different effects on seed fate among plant species. However, very few studies have discussed this question. In this study, we monitored the seed dispersal and predation of 4 fagaceae species with great variation in seed size (2 large, 2 small), in 12 different sized tropical fragmented forests. We attempted to answer 2 questions. First, do forest fragmentation effects on rodent–plant interaction (i.e. seed dispersal and predation by rodents) differ significantly among plant species? Second, if so, does seed size partly explain this interspecific variation?

MATERIALS AND METHODS

Study site

This study was conducted in the dry season (from December 2015 to April 2016) in the Xishuangbanna region, the northern edge of tropical Southeast Asia where the largest tropical rainforest in China is found. The annual mean temperature is 15.10–21.70 °C, and the annual precipitation is 1200–2500 mm, more than 80% of which occurs in the rainy season between May and October (Cao et al. 2006). Twelve fragmented forests were selected around Xishuangbanna Tropical Botanical Garden in Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, Southwest China (21°55′N, 101°15′E). Our target fragments ranged in size from 6.30 to 13 872.87 ha and contained all the dominant forest types in this region (tropical rainforest, seasonal broadleaf forest and monsoon forest over limestone) (Table S1) (Cao & Zhang 1997; Liu & Slik 2014).

Study species

Four fagaceae species were selected for the study, including 2 large-seeded species, Quercus acutissima (seed mass 3.91 ± 1.01 g, mean ± SD, n = 2400) and Castanopsis mekongensis (3.37 ± 0.89 g); and 2 small-seeded species, Castanopsis hystrix (0.74 ± 0.21 g) and Castanopsis echidnocarpa (0.51 ± 0.13 g). All the species are common in our study area, except Q. acutissima, for which seeds were collected in Menghai County, ap-
approximately 80 km away from our study fragments. All
the species have similar fruiting phenology and share
the same rodent seed dispersal agents (e.g. Niviventer
conflucianus, Niviventer fulvescens, Rattus flavipectus
and Maxomys surifer; Chen & Huang 1998; Wang
et al. 2014). All the experimental seeds were weighed
and tagged using a modification of the methods of Xiao
et al. (2006). A 0.6-mm diameter hole was drilled at
the base of each seed, and a small white plastic tag (2.5 ×
3.6 cm) with an individual number was tied through the
hole with a thin steel thread (15 cm in length). When ro-
dents cached the seed in the soil, the tags were usually
left on the forest floor, making the seeds or seed fates
easy to detect.

Experimental design

In each fragmented forest, 2 parallel transects were
established in both the edge and interior area. The 2
transects were parallel to the forest fragment edge, with
the distances being 3 and 18 m to the edge, respec-
tively. The interior transects were at least 200 m from
each edge of the forest, while for small fragments, the
interior transects were established in the center of the
forest with a distance to the edges being approximately
100 m. Five 20 × 20-cm plots were set up at intervals of
20 m along each transect.

At each plot, 40 tagged seeds (10 seeds × 4 plants
species) were placed along a circle (approximately 15
cm in diameter), and then an infrared-triggered cam-
era (Ltl-6210MC) was positioned at a height of 10 to 50
cm above ground to monitor the visiting animals. All
the debris in the vision of the cameras was cleaned up to
avoid false triggers. All the cameras were taken back af-
after 20 days, and the seed fates were checked. Small ro-
dents (88.8%, n = 9018 camera triggers), especially the
nocturnal species (96.9%, n = 8008 camera triggers),
were the dominant predators and dispersers of our ex-
perimental seeds. Seed fates were considered at several
hierarchical levels: first, seeds were divided into those
ignored and those harvested by rodents; next harvest-
ed seeds were divided into those eaten in situ and those
removed by rodents; then removed seeds were divided
into: seeds cached; seeds eaten after being transported;
and missing seeds that were not found within a 20-m ra-
adius of the seed release plot (Wang & Yang 2014). For
each removed seed that could be located, we also mea-
sured the distance to its original release plot.

Data analysis

All statistical analyses were conducted using the R
statistical software version 3.2.5 (R Development Core
Team 2016, www.R-project.org). As our data was nested
in random effects and mostly followed non-normal dis-
tributions, we using mixed effects models as formulat-
ed in the package lme4 (Bates et al. 2014). Three anal-
yses were conducted to evaluate seed fate categories at
different stages during the rodent scatter-hoarding pro-
cess: first, seeds harvested versus ignored at the original
plots (analysis I); second, of the harvested seeds, those
removed versus eaten at the plot site (analysis II); third,
of the removed seeds, those cached versus eaten (analy-
sis III). A fourth analysis was conducted to evaluate how
far removed seeds were transported from their original
location (analysis IV). The first 3 analyses involved bi-
nominal responses, so these were fitted using a general-
ized linear mixed effects model (GLMM). The fourth
analysis involved exponentially distributed continuous
data, which was log-transformed and fitted using a lin-
ear mixed effects model (LMM). The fixed and random
effects terms included in the models were identical in all
4 analyses: fixed effects were fragment size (numeric,
log transformed), location of seeds released (factor, for-
est edge or interior) and species (factor, C. echidnocar-
pa, C. hystric, C. mekongensis and Q. acutissima). Ran-
dom effects were considered in a nested structure (seed
release plot was nested in fragment, which was nest-
ed in forest type). Models were evaluated using likeli-
hood ratio tests (LRTs) on nested models (all compared
to χ²-values with appropriate degrees of freedom for the
number of parameter changes). Model subsetting was
terminated where significant interactions were encoun-
tered following the principle of marginality.

RESULTS

Overall pattern of seed fate

After 20 days, 62.47% of the seeds were harvested
(n = 9600). Seeds of Q. acutissima (48.08%, n = 2400)
were harvested less than those of the other 3 species
(64.00%, 68.75% and 69.04%, for C. mekongensis, C.
hystric and C. echidnocarpa, respectively) (χ² = 298.85,
df = 3, P < 0.001). Of the 5997 harvested seeds, 66.68%
were removed and 33.32% were eaten in situ. Seeds of
Q. acutissima (84.84% vs 15.16%, n = 1154) and C. me-
kongensis (94.01% vs 5.99%, n = 1536) were more like-
ly to be removed rather than eaten in situ than C. hy-
stric (50.36% vs 49.64%, n = 1650) and C. echidnocarpa
(44.96% vs 55.04%, n = 1657) (χ² = 1237.20, df = 3, P
< 0.001). Of the 4008 removed seeds, 57.21% were re-
trieved with the mean removal distance being 3.91 ± 4.28
m (mean ± SD). Seeds of *Q. acutissima* (4.92 ± 4.98 m, *n* = 495) and *C. mekongensis* (5.57 ± 5.36 m, *n* = 603) were moved a greater distance than those of *C. hystrix* (2.89 ± 2.83 m, *n* = 614) and *C. echinocarpa* (2.42 ± 2.45 m, *n* = 581) (*F* = 116.90, *P* < 0.001). Of the 2293 removed seeds that were retrieved, 83.99% were eaten and 16.01% seeds were cached by rodents. Seeds of *Q. acutissima* (62.42% vs 37.58%, *n* = 495) and *C. mekongensis* (75.95% vs 24.05%, *n* = 603) were more likely to be cached after being removed than those of *C. hystrix* (96.74% vs 3.26%, *n* = 614) and *C. echinocarpa* (97.42% vs 2.58%, *n* = 581) (χ² = 353.20, df = 3, *P* < 0.001).

### Fragment effects on seed fates

Likelihood ratio tests confirmed that there were significant 3-way interactions between species, fragment size and location in all 4 analyses conducted (Table 1, Fig. 1). Thus, the full interaction model was evaluated in each case. Seed harvesting of the 2 large-seeded species, *C. mekongensis* and *Q. acutissima*, decreased with increasing fragment size at interior plots and increased at edge plots, whereas the effect of fragmentation on seed harvesting was much weaker for the 2 small-seeded species (*C. echinocarpa* and *C. hystrix*) in both edge and interior locations (analysis I) (Fig. 1). By contrast,

![Figure 1](image-url)

**Figure 1** Fragment effects on seed harvested, removed and cached by rodents, as predicted by mixed effects linear models. The colored strips represent 95% confidence intervals around the predictions.

| Analysis | Response | Highest significant interaction | LRT df | χ²-value | Probability |
|----------|----------|---------------------------------|--------|----------|-------------|
| Harvested | Binomial | species × area × location | 3      | 23.518   | <0.001      |
| Removed  | Binomial | species × area × location | 3      | 24.049   | <0.001      |
| Cached   | Binomial | species × area × location | 3      | 11.909   | 0.007       |
| Distance | Gaussian | species × area × location | 3      | 11.855   | 0.009       |
Fragment size had a negative effect on seed removal of the small-seeded species at edge locations but not at interior locations, whereas it had no effect on removal of the 2 large-seeded species in either edge or interior locations (analysis II) (Fig. 1). Fragment size had a negative effect on seed caching of *Q. acutissima* in both edge and interior locations, and on seed caching of *C. mekongensis* at edge locations, but had no effect on caching of the 2 small species at either edge or interior locations (Fig. 1).

Fragment size had a negative effect on dispersal distance of *C. echidnocarpa* seeds in interior locations but a positive effect in edge locations; however, an opposite pattern was shown for seeds of *Q. acutissima* (analysis IV). Fragment size showed little effect on dispersal distance of *C. hystrix* and *C. mekongensis* (Fig. 2).

**DISCUSSION**

In this study, both fragment size and forest edge showed some effects on each step of the foraging processes of scatter-hoarding rodents, but these effects varied greatly among different plant species.

As discussed in the Introduction, many studies have shown that forest fragmentation has significant effects on seed dispersal and predation by rodents, but they have found contradictory results. Some studies found that seeds were more likely to be removed and cached in large fragments than small fragments (Andreaazzi *et al.* 2012), possibly because there are more species of rodents in large fragments (Nupp & Swihart 2000; Johnson & Karels 2015), while other studies found the opposite result, and their explanation was that more rodents existed in small fragments because of increased seed production and decreased population of predators (Morán-López *et al.* 2015; Mendes *et al.* 2016). Some studies found that seeds were predated more frequently in fragment edges than in forest interiors, which they attributed to greater understory vegetation in fragment edges, providing harvesters increased shelter from predators (Matlack 1994; Kollmann & Buschor 2003), but other studies observed less seed removal at forest edges and proposed that this was due to lower cover at forest edges affording less protection from predators (Wolf...
However, in our study we have shown that patterns of seed foraging differ among species when they are released simultaneously in fragments of different sizes and in edge versus interior locations, suggesting that parsimonious interpretations such as those provided previously are not tenable.

Our study also provides some evidence that one seed characteristic that might mediate these patterns is seed size, as there were clear differences during the foraging behavior at each step (harvesting, removing and caching) between large-seeded and small-seeded species. Seed size has been demonstrated to play an important role in mediating rodent foraging behavior upon seeds (Wang & Chen 2009; Vander Wall 2010; Lichti et al. 2017). In our study, the 2 large-seeded species *Q. acutissima* and *C. mekongensis* were more likely to have their seeds being removed and cached and transported to a further distance than the small-seeded species, *C. echinocarpa* and *C. hystrix* (Figs 1 and 2).

Why did forest fragmentation effects on seed fate differ between large-seeded and small-seeded species? Different species of rodents usually show different foraging preferences during their scatter-hoarding processes (Yi & Wang 2015b), and rodent body size has often been considered as an important factor influencing the seed size-foraging preferences of scatter-hoarding rodents (Munoz & Bonal 2008; Tamura & Hayashi 2008). Forest fragmentation may influence the rodent community. For example, in North America the density of small-bodied white-footed mouse (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) declined with forest area, whereas large-bodied gray squirrels (*Sciurus carolinensis*) increased with forest area (Nupp & Swihart 2000; Johnson & Karels 2015). The changes of relative density of different rodent species in the fragments may, in turn, lead to different effects on seed fate among different plant species. In our study, the camera trap data showed that neither fragment size nor forest edge significantly affected the relative abundance of the whole rodent community (unpublished data from 8 of our 12 fragments). This does not exclude that possibility that species composition is affecting the seed fate at each site. There were at least 5 rodent species (i.e. *Ni-viventer fulvescens*, *Rattus flavipictus*, *Maxomys surifer*, *Niviventer confucianus* and 1 unidentifiable species) in our study fragments, with body mass ranging from 60.30 to 238.70 g (unpublished data). These different rodent species have been shown to have different preferences on different sized seeds, including the species used in this study (Wang et al. 2014). However, we could not assess the effects of different rodent species compositions, because it was difficult to identify rodent species from our camera traps due to the low quality of the pictures. Live-traps or high definition cameras are recommended in future studies.

In this study, we have mainly discussed the effects of seed size, but other seed traits, such as germination schedule, nutrition level and secondary metabolites, could also influence seed predation and dispersal by rodents (Vander Wall 2010; Lichti et al. 2017; Zhang et al. 2017). Most of these traits differed among our study species, but there was no apparent relationship between seed size and any of these traits (Table 2). Furthermore, our results showed no obvious differences of forest fragmentation effects on seed fate between seeds with different levels of tannin, fat, starch, protein content or coat thickness. However, we could not test the difference in forest fragmentation effects on seed fate between seeds with different germination schedules, as all the species used in this study are recalcitrant seeds and show no apparent dormancy.

In our study, quite a number of seeds (especially for *Q. acutissima* and *C. mekongensis*) were cached by ro-

| Seed species               | Fresh weight (g) | Coat thickness (mm) | Crude protein (%) | Crude fat (%) | Crude starch (%) | Tannins (%) | Germination schedule |
|----------------------------|------------------|--------------------|-------------------|---------------|-----------------|-------------|---------------------|
| *Castanopsis echinocarpa*  | 0.51 ± 0.13      | 0.43 ± 0.01        | 3.8               | 0.4           | 73.5            | 0.15        | No dormancy         |
| *Castanopsis hystrix*      | 0.74 ± 0.21      | 0.34 ± 0.01        | 3.08              | 0.25          | 75.86           | 0.15        | No dormancy         |
| *Castanopsis mekongensis*  | 3.37 ± 0.89      | 1.07 ± 0.01        | 6.75              | 0.13          | 66.28           | 0.17        | No dormancy         |
| *Quercus acutissima*       | 3.91 ± 1.01      | 0.62 ± 0.01        | 3.42              | 3.13          | 69.58           | 10.7        | No dormancy         |

1Coat thickness (mm), crude protein (%), crude fat (%), crude starch (%) and tannins (%) (Wang et al. 2014). 2The crude starch (%) of *Q. acutissima* (Wang et al. 2016).
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**SUPPLEMENTARY MATERIALS**

Additional supporting information may be found in the online version of this article at the publisher’s website.

**Table S1** Background information of our 12 forest fragments

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