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

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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*

al. 2005; Newbold *et al.* 2013). 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-

proximately 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 confucianus*, *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 rodents 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 edge transects were parallel to the forest fragment edge, with the distances being 3 and 18 m to the edge, respectively. 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 camera (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 after 20 days, and the seed fates were checked. Small rodents (88.8%, $n = 9018$ camera triggers), especially the nocturnal species (96.9%, $n = 8008$ camera triggers), were the dominant predators and dispersers of our experimental seeds. Seed fates were considered at several hierarchical levels: first, seeds were divided into those ignored and those harvested by rodents; next harvested 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 radius of the seed release plot (Wang & Yang 2014). For each removed seed that could be located, we also measured 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 distributions, we using mixed effects models as formulated in the package *lme4* (Bates *et al*. 2014). Three analyses were conducted to evaluate seed fate categories at different stages during the rodent scatter-hoarding process: 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 (analysis 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 binomial responses, so these were fitted using a generalized linear mixed effects model (GLMM). The fourth analysis involved exponentially distributed continuous data, which was log-transformed and fitted using a linear 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, forest edge or interior) and species (factor, *C. echidnocarpa*, *C. hystrix*, *C. mekongensis* and *Q. acutissima*). Random effects were considered in a nested structure (seed release plot was nested in fragment, which was nested in forest type). Models were evaluated using likelihood ratio tests (LRTs) on nested models (all compared to χ^2-values with appropriate degrees of freedom for the number of parameter changes). Model subsetting was terminated where significant interactions were encountered 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. hystrix* and *C. echidnocarpa*, respectively) ($\chi^2 = 298.85$, 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. mekongensis* (94.01% *vs* 5.99%, $n = 1536$) were more likely to be removed rather than eaten *in situ* than *C. hystrix* (50.36% *vs* 49.64%, $n = 1650$) and *C. echidnocarpa* (44.96% *vs* 55.04%, $n = 1657$) ($\chi^2 = 1237.20$, df = 3, $P < 0.001$). Of the 4008 removed seeds, 57.21% were retrieved 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. echidnocarpa* (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. echidnocarpa* (97.42% *vs* 2.58%, *n* = 581) (χ^2 = 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. echidnocarpa* and *C. hystrix*) in both edge and interior locations (analysis I) (Fig. 1). By contrast,
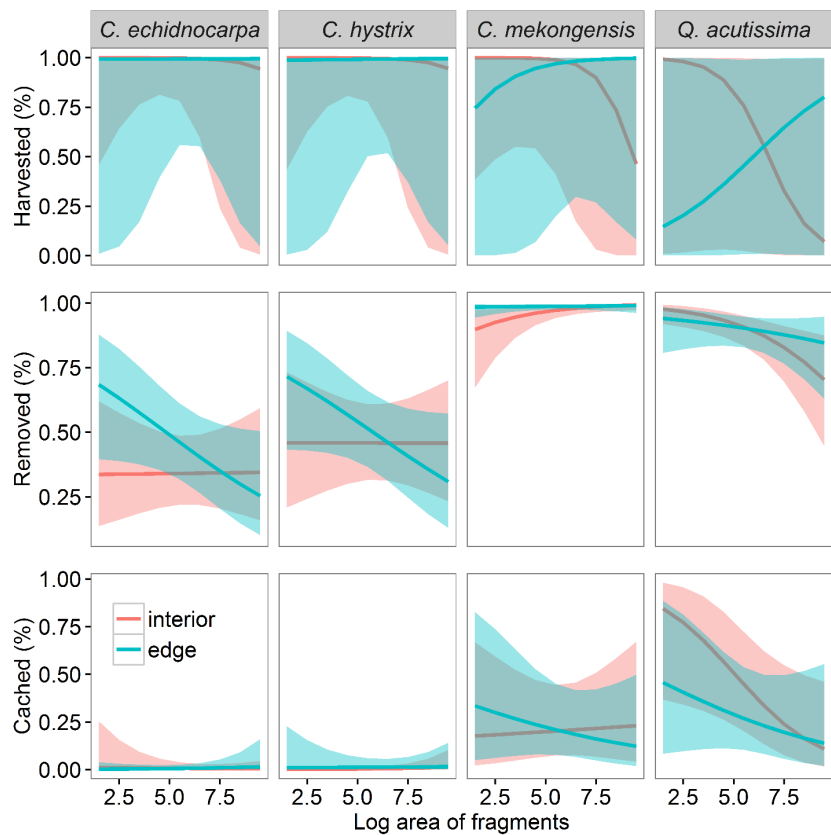

Figure 1 Fragment effects on seed harvested, removed and cached by rodents, as predicted by mixed effects linear models. The colored strips represent 95% confidence intervals around the predictions.

Table 1 Summary of the linear mixed effects model analyses. All models had significant 3-way interactions as assessed by likelihood ratio tests (LRTs)

Analysis	Response	Highest significant interaction	LRT df	χ^2-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 var-

ied 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 (Andreazzi *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
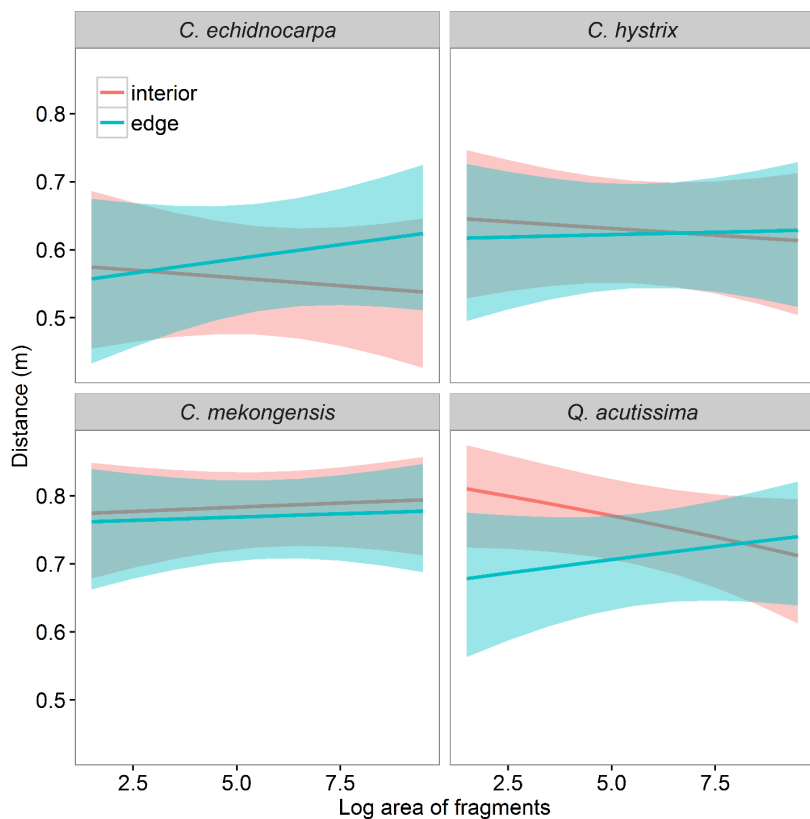

Figure 2 Fragment effects on the distance of seeds transported by rodents, as predicted by a mixed effects linear model. The colored strips represent 95% confidence intervals around the predictions.

& Batzli 2004; Morán-López *et al*. 2015). 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. echidnocarpa* 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. *Niviventer fulvescens*, *Rattus flavipectus*, *Maxomys surifer*, *Niviventer confucianus* and 1 unidentified 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-

Table 2 Morphological (mean ± SD, *N* = 2400) and nutritional traits of the 4-seed species

Seed species	Fresh weight (g)	Coat thickness (mm)[†]	Crude protein (%)[†]	Crude fat (%)[†]	Crude starch (%)[†]	Tannins (%)[†]	Germination schedule
Castanopsis echidnocarpa	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

[†]Coat thickness (mm), crude protein (%), crude fat (%), crude starch (%) and tannins (%) (Wang *et al*. 2014). [‡]The crude starch (%) of *Q. acutissima* (Wang *et al*. 2016).

dents. Because of resource limitations we did not monitor the germination and survival of the cached seeds to investigate the longer-term effects on juvenile tree recruitment. However, many studies have found that seed dispersal and predation by rodents can significantly affect the composition and distribution pattern of the seedling community (Hirsch *et al.* 2012; Jansen *et al.* 2014; Garzon-Lopez *et al.* 2015).

In conclusion, we have shown a complex influence of forest fragmentation on the rodent–seed interaction. Forest fragmentation affected the seed fate of all the species; however, the intensity and even the direction of this effect differed greatly among different species, and differed between species with small versus large seeds. The different effects of fragmentation on seed dispersal and predation among plant species may, in turn, translate into the recruitment differences across the whole fragmented forest.

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REFERENCES

Aliyu B, Adamu H, Moltchanova E, Forget PM, Chapman H (2014). The interplay of habitat and seed type on scatterhoarding behavior in a fragmented afromontane forest landscape. *Biotropica* **46**, 264–7.

Andreazzi CS, Pimenta CS, Pires AS, Fernandez FA, Oliveira-Santos LG, Menezes JF (2012). Increased productivity and reduced seed predation favor a large-seeded palm in small Atlantic forest fragments. *Biotropica* **44**, 237–45.

Bates D, Maechler M, Bolker B, Walker S (2014). lme4: Linear mixed-effects models using S4 classes. *R package* version 1.1-7. [Cited 4 May 2017.] Available from URL: http://cran.r-project.org/web/packages/lme4/index.html.

Cao L, Guo C, Chen J (2017). Fluctuation in seed abundance has contrasting effects on the fate of seeds from two rapidly geminating tree species in an Asian tropical forest. *Integrative Zoology* **12**, 2–11.

Cao M, Zhang J (1997). Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. *Biodiversity and Conservation* **6**, 995–1006.

Cao M, Zou X, Warren M, Zhu H (2006). Tropical forests of Xishuangbanna, China. *Biotropica* **38**, 306–9.

Chen H, Huang C (1998). *Flora Republicae Popularis Sinicae*, vol. **22** Fagaceae. Science Press, Beijing, pp. 28–221. (In Chinese.)

Cordeiro NJ, Howe HF (2001). Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* **15**, 1733–41.

Cordeiro NJ, Ndangalasi HJ, McEntee JP, Howe HF (2009). Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* **90**, 1030–41.

Cramer JM, Mesquita RCG, Williamson GB (2007). Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation* **137**, 415–23.

Crooks KR (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* **16**, 488–502.

Da Silva AP Jr, Pontes ARM (2008). The effect of a mega-fragmentation process on large mammal assemblages in the highly-threatened Pernambuco Endemism Centre, north-eastern Brazil. *Biodiversity and Conservation* **17**, 1455–64.

Fahrig L (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**, 487–515.

Fleury M, Galetti M (2006). Forest fragment size and microhabitat effects on palm seed predation. *Biological Conservation* **131**, 1–13.

Foley JA, DeFries R, Asner GP *et al.* (2005). Global consequences of land use. *Science* **309**, 570–74.

Garzon-Lopez CX, Ballesteros-Mejia L, Ordoñez A, Bohlman SA, Olff H, Jansen PA (2015). Indirect interactions among tropical tree species through shared rodent seed predators: A novel mechanism of tree species coexistence. *Ecology letters* **18**, 752–60.

Gibson L, Lynam AJ, Bradshaw CJA *et al.* (2013). Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* **341**, 1508–10.

Hirsch BT, Kays R, Pereira VE, Jansen PA (2012). Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letters* **15**, 1423–9.

Jansen PA, Hirsch BT, Emsens WJ, Zamora-Gutierrez V,

Wikelski M, Kays R (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences* **109**, 12610–5.

Jansen PA, Visser MD, Joseph Wright S, Rutten G, Muller-Landau HC (2014). Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecology Letters* **17**, 1111–20.

Johnson AM, Karels TJ (2015). Partitioning the effects of habitat fragmentation on rodent species richness in an urban landscape. *Urban Ecosystems* **19**, 547–60.

Kollmann J, Buschor M (2003). Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecology* **164**, 249–61.

Laurance WF (1994). Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation* **69**, 23–32.

Laurance WF, Lovejoy TE, Vasconcelos HL *et al.* (2002). Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* **16**, 605–18.

Laurance WF, Nascimento HEM, Laurance SG *et al.* (2006). Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences* **103**, 19010–4.

Lichti NI, Steele MA, Swihart RK (2017). Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Reviews* **92**, 474–504.

Liu JJ, Slik JWF (2014). Forest fragment spatial distribution matters for tropical tree conservation. *Biological Conservation* **171**, 99–106.

Matlack GR (1994). Vegetation dynamics of the forest edge-trends in space and successional time. *Journal of Ecology* **82**, 113–23.

Mendes CP, Ribeiro MC, Galetti M (2016). Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. *Ecography* **39**, 465–75.

Moore JE, McEuen AB, Swihart RK, Contreras TA, Steele MA (2007). Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology* **88**, 2529–40.

Morán-López T, Fernández M, Alonso CL, Flores-Rentería D, Valladares F, Díaz M (2015). Effects of forest fragmentation on the oak-rodent mutualism. *Oikos* **124**, 1482–91.

Munoz A, Bonal R (2008). Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Animal Behaviour* **76**, 709–15.

Newbold T, Scharlemann JPW, Butchart SHM *et al.* (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20122131.

Nupp TE, Swihart RK (2000). Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy* **81**, 512–26.

Sidhu S, Datta A (2015). Tracking seed fates of tropical tree species: Evidence for seed caching in a tropical forest in North-East India. *PLoS ONE* **10**, e0134658.

Suzán G, Armién A, Mills JN *et al.* (2008). Epidemiological considerations of rodent community composition in fragmented landscapes in Panama. *Journal of Mammalogy* **89**, 684–90.

Tamura N, Hayashi F (2008). Geographic variation in walnut seed size correlates with hoarding behavior of two rodent species. *Ecological Research* **23**, 607–14.

Terborgh J, Lopez L, Nunez P *et al.* (2001). Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–6.

Vander Wall SB (2010). How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **365**, 989–97.

Wang B, Chen J (2009). Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. *Ecology* **90**, 3023–32.

Wang B, Yang X (2014). Teasing apart the effects of seed size and energy content on rodent scatter-hoarding behavior. *PLoS ONE* **9**, e111389.

Wang Z, Cao L, Zhang Z (2014). Seed traits and taxonomic relationships determine the occurrence of mutualisms versus seed predation in a tropical forest rodent and seed dispersal system. *Integrative Zoology* **9**, 309–19.

Wolf M, Batzli G (2004). Forest edge-high or low quality habitat for white-footed mice (*Peromyscus leucopus*)? *Ecology* **85**, 756–69.

Xiao Z, Jansen PA, Zhang Z (2006). Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *Forest Ecology and Management* **223**, 18–23.

Xiao Z, Zhang Z, Krebs CJ (2013). Long-term seed survival and dispersal dynamics in a rodent-dispersed

tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. *Journal of Ecology* **101**, 1256–64.

Yi X, Wang Z (2015a). Context-dependent seed dispersal determines acorn survival of sympatric oak species. *Plant Ecology* **216**, 123–32.

Yi X, Wang Z (2015b). Dissecting the roles of seed size and mass in seed dispersal by rodents with different body sizes. *Animal Behaviour* **107**, 263–7.

Zhang H, Chu W, Zhang Z (2017). Cultivated walnut trees showed earlier but not final advantage over its wild relatives in competing for seed dispersers. *Integrative zoology* **12**, 12–25.

Zhang H, Yan C, Chang G, Zhang Z (2016). Seed trait-mediated selection by rodents affects mutualistic interactions and seedling recruitment of co-occurring tree species. *Oecologia* **180**, 475–84.

Zhang Y, Yu J, Sichilima AM, Wang W, Lu J (2016). Effects of thinning on scatter-hoarding by rodents in temperate forest. *Integrative Zoology* **11**, 182–90.

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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