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RESEARCH ARTICLE

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Cascading effects of forested area and isolation on seed dispersal effectiveness of rodents on subtropical islands

Di Zeng[1] | **Robert K. Swihart**[2] | **Yuhao Zhao**[1] | **Xingfeng Si**[1,3] | **Ping Ding**[1]

[1]College of Life Sciences, Zhejiang University, Hangzhou, Zhejiang, China
[2]Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana
[3]School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China

Correspondence
Ping Ding
Email: dingping@zju.edu.cn

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Abstract

1. Habitat loss and fragmentation often leads to defaunation of large-bodied mammals, and their loss could trigger release from top-down control or food resource competition for small mammal seed dispersers, which in turn may affect the effectiveness of seed dispersal by altering the number of dispersed seeds or the manner in which they are dispersed. Although rodents are primary seed dispersers in habitat subjected to defaunation, changes in seed dispersal effectiveness of rodents along mammalian defaunation gradients, and empirical support for mechanisms underlying alteration of this ecological process, are unclear.
2. We assessed the direct and indirect effects of forested area and isolation on seed dispersal effectiveness of rodents on 21 study islands with varying levels of defaunation in the Thousand Island Lake, China. We used camera sampling, live traps and semi-quantitative acorn counts to assess occurrence of large-bodied mammal species, relative abundance of small rodent species and seed crop size respectively. Seed dispersal, post-dispersal seed survival, seedling emergence, and seedling survival were estimated by tracking fates of tagged acorns and by planting acorns in exclosures.
3. Forested area had positive indirect effects on seed dispersal effectiveness through defaunation and rodent competition for acorns, whereas isolation had negative direct and weaker positive indirect effects on seed dispersal effectiveness mediated by loss of large-bodied mammals and rodent competition for acorns. Loss of large-bodied mammals negatively affected seed dispersal effectiveness indirectly by virtue of its impact on rodent competition for acorns. Seed dispersal effectiveness exhibited a unimodal relationship with intensity of rodent competition for acorns, peaking at intermediate levels.
4. *Synthesis*. Indirect effects of island attributes mediated by defaunation of large-bodied mammals on small or isolated islands appear to drive altered competition for food among rodents and decreased seed dispersal effectiveness. Altered interactions between acorns and their rodent consumers/dispersers can substantially affect oak population demography in the Thousand Island Lake system. More broadly, our findings highlight the importance to the seed dispersal process of multiple interwoven effects between habitat fragmentation and defaunation of large-bodied mammals.

KEYWORDS
defaunation, forested area, indirect effects, isolation, scatter-hoarding rodent–oak interaction, seed dispersal effectiveness, Thousand Island Lake

1 | INTRODUCTION

Human-induced habitat loss and fragmentation have substantial implications for biodiversity conservation (Fahrig, 2003; Laurance et al., 2006). Considerable evidence exists for the negative effects of habitat loss and fragmentation on ecological processes such as seed dispersal by animals (Galetti et al., 2013; Mendes, Ribeiro, & Galetti, 2016).

In systems characterized by animal-dispersed seeds, interactions between plants and scatter-hoarding vertebrates often are likely to constitute a conditional mutualism (Kellner, Lichti, & Swihart, 2016; Lichti, Steele, Zhang, & Swihart, 2014) that depends on foraging behaviours of dispersers (Morán-López et al., 2015). Because dispersers' foraging behaviours can vary with seed availability, interactions among dispersers and predation pressure (Lichti et al., 2014; Pesendorfer, Sillett, Morrison, & Kamil, 2016), habitat loss and fragmentation could impact the outcomes of conditional mutualisms between plants and scatter hoarders by modifying factors that affect foraging behaviours of seed dispersers. For instance, small forested fragments in central Spain exhibited lower levels of intraspecific competition for acorns among *Apodemus* mice, reduced levels of concealment cover from predators and altered mouse foraging behaviours, with a net effect of decreased seed dispersal effectiveness of these rodents (Morán-López et al., 2015). Moreover, per capita seed availability, which is a proxy for intensity of rodent competition for seeds, significantly affected seed dispersal by scatter-hoarding rodents and seedling establishment in subtropical forests of China (Xiao, Zhang, & Krebs, 2013). Therefore, we expect that habitat loss and fragmentation can affect outcomes of conditional mutualisms between seeds and scatter-hoarding rodents by altering competition for food resources among rodents.

Defaunation, the loss of animal species from natural communities (Dirzo & Miranda, 1991), often is linked to habitat loss and fragmentation (Corlett, 2007; Dirzo et al., 2014; Wright, 2003). Many studies considered defaunation to understand the effects of large vertebrate extinction on key ecological processes, such as seed dispersal and predation by rodents (Fleury, Rodrigues, Couto, & Galetti, 2014; Galetti, Donatti, Pires, GuimarÃEs, & Jordano, 2006; Galetti, Guevara, et al., 2015; Wright, 2007). These studies indicated that defaunation of large-bodied mammals could further affect the outcome of conditional plant-scatter-hoarder mutualisms, by either indirect or direct pathways. For example, large predators often play an important role in structuring communities by top-down control, and loss of predators may have indirect effects on seed dispersal effectiveness by releasing rodents from top-down limitation causing higher seed mortality (Terborgh et al., 2001). Large herbivores may also affect the structure and composition of small mammal communities directly, via interference competition by trampling (Keesing, 1998), or indirectly via exploitative competition for food resources and habitat transformation (Foster, Barton, & Lindenmayer, 2014; Galetti, Guevara, et al., 2015; Ripple et al., 2015). Thus, loss of large herbivores may positively affect populations of small rodents (Galetti, Guevara, et al., 2015) or alter rodent foraging behaviours (Puerta-Piñero, María Gómez, & Schupp, 2010) and thereby negatively affect seed dispersal effectiveness (Galetti, Bovendorp, & Guevara, 2015). Although previous studies have assessed the indirect or direct impact of defaunation of large-bodied animals on seed dispersal and plant recruitment, they exhibit multiple limitations (Kurten, 2013). In particular, many studies have relied on proxies of defaunation intensity without a quantitative assessment of animal communities (Kurten, 2013) and failed to assess how seed dispersal effectiveness changes along gradients of defaunation intensity. In addition, studies of effects of defaunation on interactions between plants and scatter hoarders have rarely considered multiple stages of plant recruitment. Previous studies have tended to focus on negative effects on plant regeneration caused by loss of large-bodied seed dispersers, such as African elephants (*Loxodonta africana*), tapir (*Tapirus*), large primates (i.e. *Ateles* or *Lagothrix*) and agoutis (*Dasyprocta*) (Kurten, 2013). In contrast to such direct effects, the loss of large-bodied mammals could cause trophic cascades due to release from top-down control by predators or resource competition, leading to indirect effects on populations and behaviours of small scatter-hoarding rodents and concomitant change in the outcomes of rodent-plant interactions (Galetti, Bovendorp, & Guevara, 2015). Unfortunately, few studies have assessed the indirect effects of defaunation.

Creation of archipelagos of land-bridge islands from former hilltops following dam construction and inundation can provide natural ecological laboratories (Jones, Bunnefeld, Jump, Peres, & Dent, 2016; Wu, Huang, Han, Xie, & Gao, 2003) to assess the impacts of area, isolation and biodiversity loss on ecological processes such as seed predation (Tong, Zhang, Wang, Inbar, & Chen, 2017) and rodent-mediated seed dispersal (Terborgh et al., 2001). We conducted our study in Thousand Island Lake (TIL), China, a system of land-bridge islands created by construction of a hydroelectric dam. The islands in our system are biologically simpler than mainland ecosystems (Chen, Holyoak, Si, Wang, & Ding, 2018) and share a common and short (59 years) isolation history and regional species pool (Si, Baselga, & Ding, 2015).

We conducted seed dispersal and seedling establishment experiments to estimate seed dispersal effectiveness of rodents on islands of varying sizes, levels of isolation and defaunation intensity of large-bodied (>1 kg) mammals. The contribution of dispersers to plant recruitment can be estimated by seed dispersal effectiveness, which is the product of quantitative and qualitative components (Schupp, Jordano, & Gómez, 2010): The probability of dispersal emphasizes the quantity of seed dispersal, whereas the cumulative effects of factors that affect the probability of a dispersed seed surviving to germinate and, ultimately, reproduce constitute the quality of seed dispersal. Our objective was to assess how forested area and isolation affected the effectiveness with which rodents dispersed acorns of *Quercus serrata* var. *brevipetiolata*. In addition to direct effects, we assessed cascading effects on rodent seed dispersal effectiveness due to defaunation of large-bodied mammals and competition among rodents for acorns (Figure 1). Specifically, we ask:

1. Does defaunation of large-bodied mammals vary with forested area and isolation in Thousand Island Lake? Large-bodied mammals require more food and habitat, and small islands may provide insufficient resources for their long-term survival. In addition, isolation of islands by water may limit recolonization following local extinction. We thus predicted that loss of large-bodied mammals would be higher on smaller or more isolated islands. We tested this prediction by quantifying a defaunation index for study islands that varied in area and isolation.
2. Does rodent competition for acorns vary with degree of defaunation? Large-bodied mammals can function as predators and competitors of rodents. Hence, loss of large-bodied mammals could remove agents that limit the abundance of rodents (Galetti, Bovendorp, et al., 2015; Galetti, Guevara, et al., 2015) resulting in higher rodent abundance relative to seed availability. We thus predicted that higher levels of defaunation would lead to greater rodent competition for acorns. To test this prediction, we estimated rodent abundance relative to seed availability as a proxy for the intensity of rodent competition for acorns on study islands exhibiting a gradient of defaunation intensity.
3. Does the intensity of rodent competition for acorns affect seed dispersal effectiveness on study islands? When rodent abundance is very low relative to seed availability, satiation of scatter hoarders leads to a smaller fraction of dispersed seeds (Lichti, Steele, & Swihart, 2017; Moore, McEuen, Swihart, Contreras, & Steele, 2007) that tend to be deposited closer to mother trees and with more clumping (Puerta-Piñero et al., 2010), all of which are factors that reduce seed dispersal effectiveness. At the other extreme, when rodent abundance is very high relative to seed availability, rodents may disperse more seeds (Ouden, Jansen, & Smit, 2005), but they ultimately either consume or recover/pilfer most cached seeds to satisfy energy needs, leading to lower post-dispersal seed survival (Soné & Kohno, 1999; Wang et al., 2017) that also negatively affects seed dispersal effectiveness. Thus, the limiting cases of per capita seed availability are predicted to elicit low seed dispersal effectiveness due to lack of dispersal (when availability is high) or lack of survival (when availability is low). At an intermediate intensity of rodent competition for acorns, higher seed dispersal effectiveness is expected due to increased probability of caching and higher post-dispersal survival. Therefore, we predicted that over a range of per capita seed availability, seed dispersal effectiveness should exhibit a unimodal pattern in relation to intensity of rodent competition for acorns, peaking at intermediate levels. To test this prediction, we conducted seed dispersal experiments and seed planting experiments on study islands that varied in intensity of rodent competition for acorns.
4. Do forested area and isolation affect seed dispersal effectiveness both directly and indirectly? Habitat loss and isolation may affect seed dispersal effectiveness by directly altering rodent species composition (Lambert et al., 2003; Vieira et al., 2009), or by altering suitability of microsites for seed germination and seedling survival. Island area and isolation may also influence seed dispersal effectiveness indirectly by altering rodent abundance via reductions in the assemblage of large-bodied predators and competitors. We thus predicted that forested area and isolation would alter seed dispersal effectiveness, both directly and indirectly, via their effects on diversity of larger fauna.

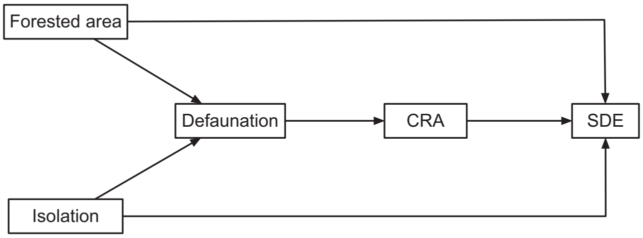

FIGURE 1 Conceptual path diagram predicting hypothesized direct and indirect relationships among forested area, isolation, defaunation, rodent competition for acorns (CRA) and seed dispersal effectiveness (SDE). Arrows indicate hypothesized causality. The one-way arrow between CRA and SDE represents a predicted quadratic relationship between rodent competition for acorns and seed dispersal effectiveness, as described in the text

We incorporated predictions arising from our hypotheses into a conceptual model (Figure 1), and used path analysis to quantify direct and indirect effects between forested area, isolation and defaunation intensity on seed dispersal effectiveness.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

The Thousand Island Lake, eastern China (29°22′–29°50′N, 118°34′–119°15′E) was created in 1959 by the construction of the Xin'anjiang Dam for hydroelectric production and resulted in the flooding of an area of approximately 580 km^2 (Figure 2). The lake created 1,078 islands with areas >0.25 ha when the water, which fluctuates annually, reaches its highest level (108 m). Currently, 88.5% of the land area on the islands is covered by forest (Yu, Hu, Feeley, Wu, & Ding, 2012). The vegetation on the islands is a mix of subtropical deciduous and coniferous forest, mainly of *Pinus massoniana*, with many broad-leaved trees and shrub species (Si, Pimm, Russell, & Ding, 2014), including *Cyclobalanopsis glauca*, *Castanopsis sclerophylla*, *Quercus fabric*, *Quercus serrata* var. *brevipetiolata*, *Lithocarpus glaber*, *Loropetalum chinense* and *Schima superba*. The lake region has

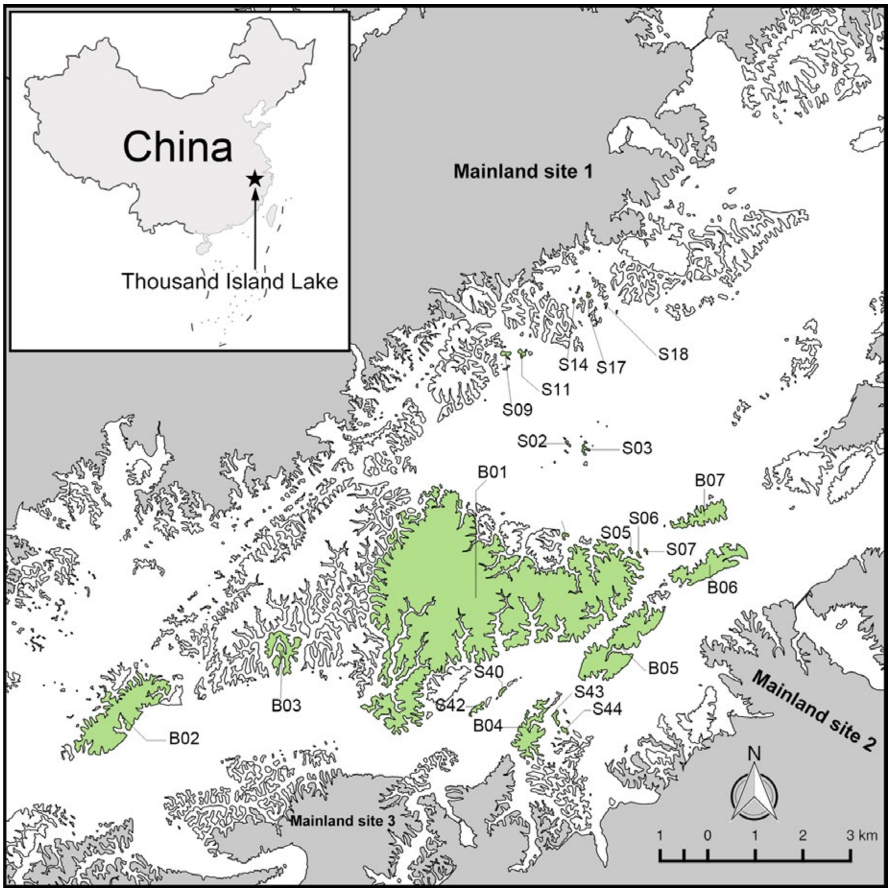

FIGURE 2 The map of research sites (21 study islands and three mainland sites) in the Thousand Island Lake region, Zhejiang Province, eastern China

a typical subtropical monsoon climate, with marked seasonality. The annual precipitation of the region is 1,430 mm, mainly concentrated in a rainy season between April and June. The average annual temperature is 17.0°C, and the daily temperature ranges from −7.6°C in January to 41.8°C in July (Si et al., 2015).

We selected *Q. serrata* var. *brevipetiolata* as our study species, the most common Fagaceae species in our study sites (Yu et al., 2012). Its flowering period is from April to May with nut-ripening periods from September to October (Flora of China Editorial Committee, 1994–2013). Based on infrared camera photos taken in preliminary seed dispersal experiments, rodents were the main seed predators of *Q. serrata* var. *brevipetiolata*. At least nine rodent species occur in our study sites: *Niviventer confucianus*, *N. fulvescens*, *Apodemus draco*, *A. agrarius*, *Leopoldamys edwardsi*, *Berylmys bowersi*, *Rattus norvegicus*, *R. tanezumi* and *Eothenomys melanogaster* (Wang, Bao, Yu, Xu, & Ding, 2010). Six of these nine rodent species are usually considered as scatter hoarders, and two *Rattus* species are both larders. In this work, the dominant species was *Niviventer confucianus*, a scatter hoarder (see Section 3). The squirrel *Callosciurus erythraeus* occurred in the area but was not commonly seen on our study islands and thus was excluded from our data analysis.

2.2 | Island attributes

We conducted our experiments on 21 islands and three mainland sites chosen as reference study sites to quantify defaunation intensity on study islands (Figure 2). We used the forest area covered on the islands as our measure of forested area, because rodents often avoid open sites with high predation risk (Hulme & Kollmann, 2005), such as seasonal inundated zones along island perimeters. As the measure of isolation, we used the Euclidean edge-to-edge distance to the nearest neighbouring island. We think this metric is more proper because small islands presumably could facilitate dispersal of mammal species from large islands or the mainland, which are called stepping stones (Gilpin, 1980; MacArthur & Wilson, 1967; Thornton et al., 2002). Forested area of study islands ranged from 0.4 to *c*. 1,159 ha, and isolation from 14 to 121 m (Supporting Information Table S1). Forested areas of each island and mainland borders were digitized at 1:5000 scale from SPOT-6 imagery (website: https://www.intelligence-airbusds.com/en/147-spot-6-7-satellite-imagery). Digitized maps were then rasterized and processed using FRAGSTATS 4.2 (McGarigal, Cushman, & Ene, 2012). Isolation was calculated using the Near tool in ArcGIS 10.4 (website: http://support.esri.com/Products/Desktop/ArcGIS-desktop/arcmap/10-4-1).

2.3 | Defaunation of large-bodied mammals on islands

To assess species composition of large-bodied mammals, we set camera traps on study islands and mainland sites from 2015 to 2017.

The number of cameras was roughly proportional to forested area ($\log_e$-transformed) with a maximum of eight cameras on the largest island (Island B01, Supporting Information Table S1). When multiple cameras were deployed, we distributed them across the study island spaced more than 200 m apart. On the mainland reference sites, we deployed a total of 10 cameras, each separated by >200 m. The infrared digital cameras (Ltl-5210MC; Ltl Acorn Electronic Co., Ltd., Zhuhai, China) were locked to trees at heights of 40–50 cm above the ground. Cameras faced north or south to avoid triggering caused by sunlight, and vegetation was removed in front of cameras to further minimize false triggering events (Si, Kays, & Ding, 2014). We set cameras to take three photos after each trigger and the time interval between each trigger was 15 s. All cameras were operated 24 hr a day. We downloaded photos and checked batteries every 2–3 months. We identified animals recorded in each photo to species when possible.

We used the defaunation index (Giacomini & Galetti, 2013) on occurrence data to assess the loss of larger bodied species of mammals on study islands relative to mainland sites. Thus, the defaunation index provides a quantitative measure of dissimilarity between the community on each focal island and the mainland mammal community, which serves as a reference (Giacomini & Galetti, 2013):

$$\text{defaunation} = \frac{\sum_{k=1}^{S} w_k \left(P_{k,r} - P_{k,f}\right)}{\sum_{k=1}^{S} w_k \left(P_{k,r} + P_{k,f}\right)},$$

where r is the reference mainland community, f is the community on a focal island, S is the total number of species, P is occurrence (presence = 1, absence = 0) of species k, and w_k is the importance (weight) assigned to species k in terms of its functional impact on defaunation. To assign species importance (w_k), we used body mass (M, kg) because body mass is an important determinant of species' life history and ecological interactions (Brown, Gillooly, Allen, Savage, & West, 2004; Giacomini & Galetti, 2013; Woodward et al., 2005). We converted M to metabolic scaling ($M^{3/4}$) to more accurately reflect the size-dependent impact of species on communities (Brown et al., 2004; Giacomini & Galetti, 2013).

2.4 | Quantifying crop size and rodent abundance

Crop size was estimated 2 weeks before the peak seedfall using a composite index in 2015 and 2016. The composite index of crop size was comprised of two components: the relative amount of a tree's acorn crop and the average acorn size. The former was estimated with a semi-quantitative rating method (Morán-López et al., 2015), ranging from 0 (no acorns on the canopy) to 4 (>90% of canopy with acorns). The average acorn size was visually estimated on a scale from 0 (smallest) to 6 (largest) based on the seed length. Thus, the crop size index ranged from 0 to 24. In this study, we estimated crop size index for each experimental tree and its four nearest reproductively mature conspecifics on each island, and thus calculated their means as the crop size index for each island. Because variation in tree density across islands could affect the reliability of our crop size index, we also calculated tree density of *Q. serrata* var. *brevipetiolata* from tree community data collected on a subset of 29 islands in the Thousand Island Lake (Yu et al., unpubl. data). Incorporation of tree density had no relationship with the crop size index ($r^2 = 0.09$, $p = 0.186$) and was not considered further.

We estimated the relative abundance of rodents by live-trapping along transects from July to September before seed dispersal experiments in 2015 and 2016. Sampling effort for each island was roughly proportional to forested area ($\log_e$-transformed), resulting in one transect on the small forested islands and 4–8 transects on the large forested islands. On each transect, 10 steel-wired small mammal live traps without trigger pans (7.5 × 8.75 × 22.5 cm) were placed at 15-m intervals, baited with peanuts, and operated for four consecutive nights. Traps were checked each morning. Newly captured individuals were identified to species, marked with uniquely numbered ear tags, and released immediately after measurement.

We used a modified index of per capita seed availability to assess competition for acorns among rodents on each island. Rodent competition for acorns was calculated based on the sum of metabolically scaled body mass for each rodent species, namely, metabolically scaled rodent biomass (MR) to reflect size-dependent caloric intake (Clauss, Schwarm, Ortmann, Streich, & Hummel, 2007; Xiao et al., 2013) and crop size index (CSI). Specifically, rodent competition for seeds on a focal island is given by $\mathrm{MR/CSI} = \sum_{i=1}^{k} N_i M_i^{3/4} / \mathrm{CSI}$, where k is the number of rodent species on the focal island, N_i is the relative abundance (individuals per 100 trap nights) of rodent species i found there, and $M_i^{3/4}$ is the average metabolically scaled body mass of species i. Higher values of rodent competition for acorns thus indicate greater intensity of competition for rodents on the acorn crop (Morán-López et al., 2015; Theimer, 2005; Xiao et al., 2013).

2.5 | Seed dispersal experiments

We selected 63 mature *Q. serrata* var. *brevipetiolata* trees as focal sites for seed dispersal experiments on 21 study islands during winters in 2015 and 2016. Three focal trees were chosen on each study island, separated by >25 m. Mature, fresh acorns were collected from underneath or on non-focal trees when seeds began to fall in late October in 2015 and 2016. Acorns were floated in water to exclude insect-damaged/empty seeds (Gribko & Jones, 1995). Experimental acorns were marked individually by attaching a coded plastic tag (3 × 2 cm) with a 12-cm thin steel thread (Xiao, Jansen, & Zhang, 2006) to facilitate our relocation of acorns following removal and caching by rodents. Plastic tags have a negligible effect on patterns of seed dispersal by rodents (Xiao et al., 2006).

We placed 30 tagged acorns under the canopy of each focal tree in each year. We randomly searched a 30-m radius around focal trees with equal effort (0.5 hr for two people each visit) and recorded fates of all detected seeds. Searches were done 1, 2, 3, 10, 24, 54, 114 and 140 day(s) after placement of acorns, and we repeated the searches again in spring of the following year. Detected seeds were categorized as intact (not handled by rodent in situ), predation in situ (predated by rodent in situ) or dispersed (seed displaced from its initial site of placement by >0.5 m). Dispersed seeds were further categorized as cached (i.e. buried intact in the soil, under leaves or deposited intact on the surface), consumed after dispersal (i.e. leaving only tags and seed fragments) or missing (because the tag was visually obstructed, hoarded in burrows or dispersed >30 m).

When we found a cache or seed fragment, we recorded the tag's code, dispersal distance and direction from the original seed source. To facilitate relocation, we marked each cache site using a white plastic stick (15 cm in height) with the code for acorns in the cache. All sticks were set 10 cm away from the seed cache to reduce potential cues for pilferers. We checked all caches periodically in subsequent visits until cached acorns were recovered by animals or had germinated with a taproot. Nutrients of seeds gradually transfer into a dormant taproot after seed germination, so the appearance of a taproot reduces a seed's value to rodents and increases the likelihood of seedling development (Cao et al., 2016). Therefore, we defined cache survival as seeds in a cache surviving to germinate with taproots or seeds that remained intact in a cache at the end of the dispersal experiments. If a tagged seed was removed from a cache by a rodent, we searched at least a 15-m radius around the cache. When we found a cached seed was subsequently re-cached, we measured again the distance and direction from its original seed source.

2.6 | Seedling emergence and survival: Sowing experiments

Independent of the seed dispersal study, seedling emergence and survival were assessed experimentally in 2015 and 2016 with artificial caches in metal, rodent-proof exclosures (Calvino-Cancela, 2011). Seeds in sowing experiments were tagged in the same manner as those in the dispersal experiment. We constructed eight metal exclosures (0.3 × 0.3 × 0.2 m) on each island (total 168 on all study islands) to exclude seed predation of rodents. In each exclosure, 10 tagged seeds were sown at 5 cm spacing at a depth of 0.5 cm to simulate actual rodent caches. Seed germination and seedling survival were monitored biweekly for the first 2 months and bimonthly thereafter, until autumn of the following year. The fraction of seedlings that germinated the following spring was computed for each enclosure, and seedling survival was computed as the fraction of germinated seedlings that survived to the end of their first summer.

2.7 | Seed dispersal effectiveness of acorns by rodents

To obtain overall seed dispersal effectiveness by rodents, we calculated the probability of seed dispersal and conditional probabilities for caching survival, emergence and establishment for each of the 21 study islands. The product of seed dispersal and seed caching probabilities represents the quantitative component of seed dispersal effectiveness, whereas the qualitative component of seed dispersal effectiveness is the product of the conditional probabilities of cache survival, seedling emergence and seedling survival. Seed dispersal effectiveness was computed as the product of its quantitative and qualitative components (Schupp et al., 2010).

2.8 | Data analysis

Data from each island were averaged between years for analyses. Before analysis, we transformed forested area ($\log_e$), defaunation (arcsine square-root) and seed dispersal effectiveness (arcsine square-root) to reduce skewness and to normalize the residuals. After transformation we standardized all variables. All statistical analyses were conducted in R version 3.4.2 (R Development Core Team, 2017).

To assess main components that determine rodent competition for acorns, we fitted patterns of metabolically scaled rodent biomass, crop size index, and rodent competition for acorns as a function of the defaunation index. We also evaluated the relative importance of metabolically scaled rodent biomass and crop size index to rodent competition for acorns via multiple regression in R package *relaimpo* (Groemping, 2006) version 2.2-3.

We constructed models via confirmatory path analysis, a type of structural equation modeling (SEM) approach without unmeasured (latent) variables (Lefcheck, 2016; Shipley, 2009) to investigate the hypothesized causal relationships among these variables. Piecewise SEM incorporates several linear or nonlinear models into a single analysis pathway using directional separation (d-separation) tests to statistically identify causal relationships and missing links (i.e. pathways) in a directed acyclic graph (Shipley, 2009). In the piecewise SEM method, paths are structured as a set of separate linear equations, which are evaluated individually using local estimation, allowing for fitting more data distributions and sampling designs (Lefcheck, 2016). In particular, piecewise SEM can accommodate smaller sample sizes, which is more proper for our case. An initial path model was built based on our conceptual path diagram (Figure 1). Specifically, we hypothesized that the relationship between seed dispersal effectiveness and island attributes would be mediated by loss of large-bodied mammals and there would be a quadratic relationship between rodent competition for acorns and seed dispersal effectiveness. Shipley's d-separation test was used to assess model fit via a Fisher's *C* statistic and χ^2-based *p*-value (Shipley, 2009). We refined the original model by dropping non-significant links, beginning with the least significant, and continuing stepwise until the change in AIC_c associated with one step was less than 2. Path analysis and model testing were conducted in the R package *piecewiseSEM* (Lefcheck, 2016), version 2.0.0.

3 | RESULTS

We identified 11 large-bodied mammal species (Supporting Information Table S2) from 2,493 usable photos. Rarefaction results indicated that camera-trapping effort was sufficient to characterize assemblage richness (Supporting Information Figure S1).

Live-trapping captured 533 individual rodents. The scatter hoarders *N. confucianus* and *N. fulvescens* were the two most abundant rodent species and comprised 84.0% and 11.1% of captured individuals respectively. The metabolically scaled rodent biomass ranged from 44.52 to 729.41. It had no relationship with forested area (Spearman correlation, $r = -0.21$, $p = 0.361$, Supporting Information Figure S2) but was positively correlated with isolation (Spearman correlation, $r = 0.59$, $p = 0.005$). The index of crop size ranged from 0.38 to 6.13, and competition among rodents for acorns on study islands ranged from 27.3 to 880.8. Along a gradient of defaunation, rodent competition for acorns displayed a pattern more similar to metabolically scaled rodent biomass than seed crop size (Supporting Information Figure S3), presumably because the former explained roughly three times more variation in rodent competition for acorns than the latter (Supporting Information Figure S4).

A total of 3,780 tagged seeds were released in our experiments, and we successfully located 82.28% of these. Overall, only 6.77% of tagged seeds ($n = 256$) were not harvested by rodents. Of released seeds, 39.97% ($n = 1,511$) were predated in situ and 53.25% ($n = 2,013$) were dispersed by rodents. Of dispersed seeds, only 4.37% ($n = 88$) survived in caches and germinated. The highest seed dispersal effectiveness of rodents on islands was 3.52%.

Most of our predictions were confirmed by our path analysis, especially for some indirect effects that were not detected by partial regression models (Table 1; Figure 3). The final model resulted in a good overall model fit and explained 66% of the variation in seed dispersal effectiveness (Fisher's $C_{[10]} = 10.441$, $p = 0.403$, $AIC_c = 73.441$). In the final path model, forested area had an overall positive effect on seed dispersal effectiveness by virtue of an indirect effect mediated through defaunation intensity and competition for seed among rodents. In contrast, isolation had a net negative effect on seed dispersal effectiveness due to a strong negative direct effect and a weak positive indirect effect mediated through defaunation and rodent competition for acorns (Table 1; Figure 3). Defaunation intensity affected seed dispersal effectiveness negatively via competition among rodent for acorns, albeit with an unexpected direct negative relationship between defaunation and rodent competition (Table 1; Figure 3). The path model also confirmed the predicted unimodal pattern between seed dispersal effectiveness and rodent competition for acorns (Figure 3).

TABLE 1 Direct, indirect and total standardized effects of forested area, isolation, defaunation, rodent competition for acorns (CRA) and quadratic term of competition among rodents on acorns (CRA^2) on seed dispersal effectiveness (SDE) in our final path model

Predictors	Pathway to SDE	Effect
Forested Area	Direct	—
	Indirect through defaunation and CRA	0.340
	Total effect	0.340
Isolation	Direct	−0.453
	Indirect through defaunation and CRA	0.149
	Total effect	−0.304
Defaunation	Direct	—
	Indirect through CRA	−0.394
	Total effect	−0.394
CRA	Direct	0.849
	Total effect	0.849
CRA^2	Direct	−0.953
	Total effect	−0.953

4 | DISCUSSION

Our path models showed that forested area and isolation affect the seed dispersal effectiveness of rodents on islands in TIL. As expected, seed dispersal effectiveness was greatest for larger, less isolated islands. Both forested area and isolation have indirect effects on seed dispersal effectiveness through their effects on the loss of large-bodied mammal species and per capita availability of acorns to rodents. Our findings highlight the potential synthetic effects of top-down control by predators and competition for food by large-bodied primary consumers on seed dispersal by rodents, albeit in unexpected ways. Our study also provides an empirical example of how habitat loss and fragmentation can cascade through ecological systems to have important consequences for ecosystem functioning.

The path model revealed significant effects of area and isolation on the loss of large-bodied mammals. Small islands seldom have enough resources to maintain a stable population of large-bodied mammals (Okie & Brown, 2009). Our finding that small islands suffered greater defaunation is consistent with prior findings and theoretical expectations. In contrast to expectations, we found a weak but significant negative partial correlation between isolation and defaunation. We suspect that the range of isolation for TIL islands was too small to truly serve as an isolating mechanism for larger mammals. Previous studies have shown that the loss of non-volant mammals increased with isolation and concluded that colonization ability via overwater dispersal can play a significant role (Hoekstra & Fagan, 1998; Lomolino, 1994). However, isolation in TIL ($M = 52$ m) was about 100 times less on average than found in these earlier studies, suggesting that the isolation of islands in TIL might not limit dispersal for larger mammals. Differences among isolation metrics offer another possible explanation for the observed isolation effects on defaunation. We could have used other isolation metrics based on distance to mainland, proximity of neighbouring islands in buffer zones or ecologically scaled indices of connectivity (Gehring & Swihart, 2003; Moilanen & Nieminen, 2002; Vos, Verboom, Opdam, & Ter Braak, 2001; Weigelt & Kreft, 2013). We believe our isolation metric more properly reflects mammalian movements, because islands presumably facilitate dispersal of mammal species in a stepping-stone process (Gilpin, 1980; MacArthur & Wilson, 1967; Thornton et al., 2002). Future work is needed with fine-scale

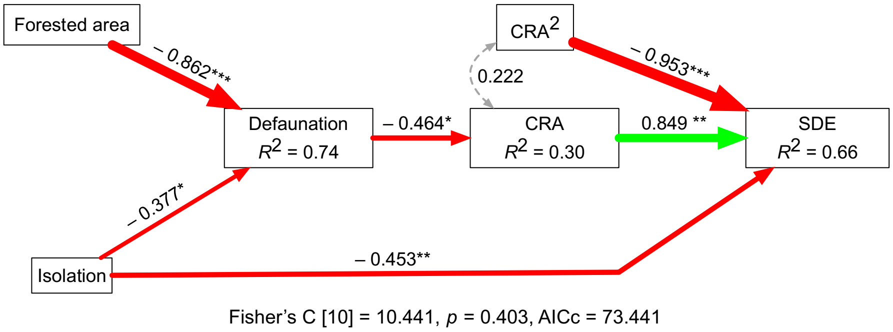

FIGURE 3 Path analysis diagram for forested area, isolation, defaunation, rodent competition for acorns (CRA) and its quadratic term (CRA^2) and seed dispersal effectiveness (SDE) and intermediate factors. Boxes represent measured variables. Arrows represent unidirectional relationships among variables, and the standardized regression coefficient is indicated above paths. Significant effects are depicted for $p<0.05$ (*), <0.01 (**) and <0.001 (***). Arrow size is proportional to the absolute value of the coefficient for each pairwise relationship. The dashed grey arrow represents a non-significant path. Red depicts negative effects and green depicts positive effects. The variance explained (R^2) is shown in the box of each response variable

movement data to systematically assess the concordance between various measures of isolation and actual patterns of inter-island movement by mammals.

Defaunation of large-bodied mammals, such as predators or ungulates, can change abundance and composition of seed-dispersing rodents (Galetti, Bovendorp, et al., 2015; Galetti, Guevara, et al., 2015) and consequently alter rodent competition for acorns. Some previous studies noted that habitat fragmentation reduced rodent competition for acorns (Morán-López et al., 2015). However, few studies focused on the effects of fragmentation-induced defaunation on rodent competition for acorns. Our path model indicated a negative effect of defaunation on rodent competition for acorns (Figure 3). Closer inspection of this unexpected effect showed that the metabolically scaled rodent biomass (MR) shared a similar unimodal relationship with rodent competition for acorns (CRA) along a gradient of defaunation intensity (Supporting Information Figure S3). When large carnivores or ungulates exist, the biomass of rodents likely is restricted by predation or competition by food resource (Foster et al., 2014; Ripple et al., 2015; Young et al., 2014). Therefore, the per capita availability of acorns should be higher at low levels of defaunation intensity. Rodent competition for acorns should increase as defaunation intensity increases due to concomitant loss of top-down control. However, at the highest levels of defaunation intensity, which are associated with small islands, rodents may be unable to sustain larger populations even with increases in seed crop size (Supporting Information Figure S3), resulting in lower competition for acorns among rodents. Rodent density often fails to increase on smaller islands, presumably because the islands are too small to support a viable population and hence rely on periodic rescue via colonization (Adler & Levins, 1994). Our empirical data also supported a tendency for relative abundance of rodents on the smaller islands to decrease (Supporting Information Figure S2), but larger samples are needed to examine this relationship more closely.

We found a unimodal relationship between seed dispersal effectiveness and intensity of rodent competition for acorns, as inferred indirectly from acorn crop size and rodent relative abundance. Prior studies have assessed differences in caching probability and seed survival for binary categories such as seed-rich versus seed-poor years (Jansen, Bongers, & Hemerik, 2004; Li & Zhang, 2007; Wang et al., 2017) or have assumed a linear effect of per capita seed availability (Xiao et al., 2013). Our analysis suggests that if seed production or rodent density span a sufficiently large range, trade-offs between satiation of consumers (at high availability) and competition for limiting resources among dispersal agents (at low availability) can yield intermediate regions of per capita seed availability where seed dispersal effectiveness is greatest. In our study, intensity of competition for acorns is likely related to direct competition for food between individuals as well as the likelihood of cache pilferage (Theimer, 2005; Vander Wall, 2010) because of food limitation on islands. At low levels of competition intensity, rodents invest less effort to cache seeds (Lichti et al., 2017; Moore et al., 2007) and more seeds are deposited closer to mother trees (Morán-López, Wiegand, Morales, Valladares, & Díaz, 2016; Puerta-Piñero et al., 2010). In addition, a higher proportion of seeds remain beneath mother trees, where seeds tend to suffer higher mortality because of higher densities of host-specific seed predators, pathogens and herbivores (Connell, 1971; Janzen, 1970; Wright, 2003). At the other extreme, high competition for acorns or pilferage pressure results in greater seed dispersal (Ouden et al., 2005; Puerta-Piñero et al., 2010), but lower seed survival after scatter-hoarding (Soné & Kohno, 1999), because lower seed availability may force rodents to consume cached seeds to satisfy energy needs (Wang et al., 2017). Our results are consistent with operation of these two mechanisms on seed dispersal effectiveness by rodents in the Thousand Island Lake ecosystem.

Importantly, our path model revealed significant indirect effects of habitat loss and fragmentation on seed dispersal effectiveness through defaunation of large-bodied mammals and rodent competition for acorns. Losses in habitat area can alter the abundance of seed predators/dispersers directly by reduced carrying capacity and increased stochastic population fluctuations (Karr, 1982; Terborgh, 1992) to affect dispersal quantity and consequently seed dispersal effectiveness (Morán-López et al., 2015). In our study, there was no relationship between forested area and metabolic biomass of rodents (Spearman correlation, $r = -0.21$, $p = 0.36$). Thus, direct effects of forested area on seed dispersal effectiveness were not detected. Instead, area effects were indirect (Adler & Levins, 1994) and mediated by altered trophic interactions (Feeley & Terborgh, 2008). Smaller islands lacked a full complement of primary consumer competitors (i.e. large ungulates) and mammalian predators, which presumably released rodents from these limiting factors (Adler & Levins, 1994; Foster et al., 2014). Diverse assemblages of predators, particularly carnivorous mammals, can regulate rodent population dynamics and depress population growth of rodents (Adler & Levins, 1994; Sundell, 2006; Terborgh et al., 2001). Previous experimental studies of the role of predation in vole population dynamics found that predation limits population growth and, in some circumstances, even regulates population fluctuations (Sundell, 2006). Reductions in predators on islands, by releasing rodents from top-down control, could alter outcomes of the oak–rodent conditional mutualism that result in lower seed dispersal effectiveness. Our models are somewhat consistent with this explanation.

Unlike forested area, our path model showed that isolation had both direct and indirect effects on seed dispersal effectiveness. Isolation can affect populations of rodents on islands directly by limiting individual dispersal, leading to “fence effects” (Adler & Levins, 1994). Moreover, isolation can select for a more sedentary lifestyle (Adler & Levins, 1994), resulting in greater social stability and reduced aggressive interactions via greater neighbour familiarity and kin recognition (Charnov & Finerty, 1980; Kawata, 1990; Lambin & Krebs, 1991). On our study islands, isolation was significantly correlated with metabolically scaled biomass of rodents (Spearman correlation, $r = 0.59$, $p = 0.005$), which for a given level of acorn production should increase seed predation, reduce caching rate, and consequently lower seed dispersal effectiveness. We also found a considerably weaker and unexpected positive indirect effect of isolation on seed dispersal effectiveness via loss of large-bodied mammals on competition for acorns among rodents (Table 1, Figure 3). Further study is warranted to assess the generality and nature of this indirect effect of isolation.

5 | CONCLUSIONS

Isolation directly and negatively affected the conditional mutualism between acorns and rodents on subtropical land-bridge islands. The effect of habitat loss was also negative but subtler, as it was mediated by consequences of defaunation of large-bodied mammals to rodent populations on smaller islands. Habitat fragmentation and subsequent mammalian defaunation thus exhibited interwoven effects on seed dispersal and consumption by rodents that could have important implications for plant demography in this and other systems subjected to landscape-scale modification of habitat. In particular, cascading effects of fragmentation on seed dispersal processes may be driven by mechanisms that differ with fragmentation severity and history. In general, we expect rodent–seed interactions on oceanic islands or insular systems with a highly impermeable matrix to be more directly affected by island area and isolation, especially for long elapsed times since fragmentation (Swihart et al., 2003). In contrast, rodent–seed interactions on terrestrial or land-bridge islands with greater matrix permeability might be more greatly influenced by life-history traits related to niche breadth that influence use of resources following release from limiting interactions such as competition or predation by larger vertebrates, especially in systems with short elapsed times since fragmentation. Similar studies in systems spanning a range of ages and severity of fragmentation are needed to more fully appreciate the direct and indirect effects of fragmentation on conditional mutualisms between plants and rodents.

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AUTHORS' CONTRIBUTIONS

D.Z. and P.D. conceived the ideas and designed the study. D.Z., Y.Z. and P.D. collected field data. D.Z. and R.K.S. analysed the data. D.Z. and R.K.S. led the writing of the first draft of the manuscript. P.D. and X.S. substantially contributed to revise the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data associated with this study are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.db3q9t0 (Zeng, Swihart, Zhao, Si, & Ding, 2018).

ORCID

Di Zeng https://orcid.org/0000-0003-2780-3738
Xingfeng Si https://orcid.org/0000-0003-4465-2759

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SUPPORTING INFORMATION

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