



Ecological succession drives the structural change of seed-rodent interaction networks in fragmented forests



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ABSTRACT

While deforestation and fragmentation can cause massive species loss in forest ecosystems, forest regeneration can also drive successional changes in species composition. Although studies have sometimes documented the effects of these compositional changes on interspecific interactions, few studies have investigated changes in the structure of plant-animal networks. We investigated how interaction networks of assemblages of rodents and tree seeds changed with forest fragmentation and succession in a subtropical region. We compared seed-rodent interactions between 14 secondary forest patches that ranged in area from 2 to 58 ha, and from 10 to at least 100 years old, representing a successional gradient. We expected that deforestation and fragmentation would reduce seed production and diversify rodent communities, resulting in higher interaction strengths and connectivity, but weak nestedness (i.e., specialists interact with subsets of the species interaction of generalists). We measured the frequency of rodents eating and removing seeds (interaction strength) in each patch during 3 successive years, using seed tagging and infrared camera trapping, and calculated the properties of the seed-rodent networks. We found that the relative abundances of seeds and rodents changed with stand age not patch size, as did seed-rodent interactions: older patches produced more seeds, contained fewer individuals and species of rodents, and had seed-rodent networks with lower connectance and interaction strength, but higher nestedness. Connectance and interaction strength decreased with metabolic per capita seed availability (as measured by seed energy value); nestedness increased with seed richness, but decreased with rodent abundance. At species level, we found stand age and patch size showed significant effects on seed or rodent abundance of a few species. We also found seed coat thickness and starch contents had significant effects on network metrics. Our results suggest that during succession after deforestation, seed-rodent interactions in these sub-tropical forests change from a state dominated by high seed removal and highly connected seed-rodent networks to a state with more seeds and highly nested networks. From a management perspective of our study region, succession age, not fragment size, and network structure should be paid more attention so as to facilitate the restoration processes of degraded forests. Rodent management should be applied to protect native forest species and exclude invasive ones from farmlands and human residences at early succession stage.

1. Introduction

Anthropogenic change in forested landscapes often represents a dynamic mix of habitat loss and fragmentation alongside habitat regeneration from both human-assisted plantings and natural succession (Chazdon, 2008). Many studies have shown that habitat loss and fragmentation have large negative effects on species and community abundance (Aguilar et al., 2006). Other studies have shown changes in

species composition due to natural succession in re-growing areas (Lohbeck et al., 2013; Whitehead et al., 2014; Martínez-Ramos et al., 2016). In areas undergoing a mix of habitat fragmentation and re-growth it is not clear which process will dominate in changing species composition. Fragmentation has also been reported to modify species interactions (Magrath et al., 2014). Recent studies have found that mutualisms, such as pollination and seed dispersal, are particularly sensitive to the negative effects of forest fragmentation (Aguilar et al.,

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2006; Fortuna and Bascompte, 2006; Uriarte et al., 2010; Magrath et al., 2014). Disentangling the consequences of fragmentation and regeneration for the structure of species interaction networks has been crucial for forest management.

One way of understanding the consequences of changing community composition for species interactions and community functioning is to study interaction networks, such as food webs, mutualistic networks (e.g., flower-pollinator and seed dispersal by birds) and bipartite antagonistic networks (e.g., plant-herbivore and host-parasite interactions) (Schleuning et al., 2011; Dattilo et al., 2014; CaraDonna et al., 2017). Two basic metrics for characterizing such ecological networks are connectance (probability of realized interaction) and interaction strength (which can be measured empirically by visiting frequency, predation efficiency, etc.) (May, 1972). A highly connected architecture promotes persistence and resilience in mutualistic networks (Thebault and Fontaine, 2010). Weak interaction strength is widely seen as a potential mechanism for maintaining diversity and stability (Berlow, 1999). Likewise, nestedness (i.e., specialists interact with subsets of the species interaction of generalists) and modularity (i.e., compartmentation of species interactions) have been identified as properties that could promote stability (Bascompte et al., 2003; Bascompte et al., 2006; Bascompte and Jordano, 2007; Olesen et al., 2007; Rohr et al., 2014; Gilarranz et al., 2017). Thus, network metrics could be used to quantify the consequences of changes in species composition for the structure and stability of natural communities.

Seed-rodent networks are an important type of interaction in forest ecosystems, playing an important role in the maintenance of biodiversity and ecosystem services (Zhang et al., 2016a). The majority of seeds in forests are typically consumed by rodents, yet a small proportion may be dispersed by rodents and facilitated to germinate and establish seedlings (Jansen and Forget, 2001; Vander Wall, 2010). Consequently, interactions between tree seeds and rodents vary between being antagonistic and mutualistic (Theimer, 2005; Garzon-Lopez et al., 2015; Xiao and Zhang, 2016; Zhang et al., 2016b). Both the abundance and functional traits of rodents and seed species are key factors in the formation of mutualistic and antagonistic interactions between seeds and rodents (Wang et al., 2014; Garzon-Lopez et al., 2015; Zhang et al., 2015). Previous studies have evaluated specific seed-rodent interactions in semi-natural enclosures (Wang et al., 2014; Zhang et al., 2016b), but less considered multi-species interaction networks in field conditions because of a lack of methods for measuring seed-rodent interaction strength. Therefore, how natural seed-rodent interaction networks are structured and how this structure is affected by deforestation, forest fragmentation and succession remains unknown.

Many studies have found that deforestation significantly affects species composition and abundance (Brook et al., 2003; Fisher and Wilkinson, 2005; Benchimol et al., 2017). Deforestation has been shown to decrease seed species richness and abundance by removing large trees (Laurance, 1999; Benchimol et al., 2017). Deforestation or fragmentation also creates suitable open habitats for incursion of non-native rodents, increasing both species richness and abundance (Duntan and Fox, 1996; Shenko et al., 2012). These contrasting changes of seed-predator/disperser abundance and species richness would be expected to alter the strength of seed-rodent interactions (i.e., the frequency of seed removal by rodents). Likewise, in studies of succession saw changes in both plants and rodents. For instance, in an old-field system small patches maintained earlier successional states and were dominated by grassland rodent species, whereas larger patches contained more woody vegetation and contained forest rodent species (Schweiger et al., 2000). Outside of a fragmentation context, studies have demonstrated that seed availability, predator satiation or dispersal behavior, can affect the strength of interactions between seeds and rodents (Yi et al., 2011; Xiao et al., 2013). Optimal foraging theory and optimal diet selection theory describe potential mechanisms (Emlen, 1966), e.g., low food availability makes predators increase predation

efficiency and expand diet. Expansion of animal generalists' diet often leads to more connections in plant-animal networks, and for rodent-seed networks with all rodents as generalists, a highly-connected network should have low nestedness. We expect that in more disturbed or younger forest patches with less seed species but more rodents, rodents have stronger predation/hoarding effects on seeds and expand diet due to relatively low seed availability for rodents, so seed-rodent interactions are stronger and the connectance of seed dispersal networks is higher with lower nestedness.

This study aimed to determine how forest fragmentation and succession affect seed-rodent interaction networks. Our approach was to quantify seed abundance, the rodent community, and seed removal by rodents across 14 patches of subtropical forest that differed in successional age and size. Specifically we had the following predictions: (1) in younger or smaller patches, there would be higher rodent species richness and abundance, and vice versa; (2) in younger or smaller patches, there would be increased interaction strength and connectance but reduced nestedness; (3) lower seed abundance and/or higher rodent abundance would increase interaction strength and connectance but decrease nestedness.

2. Materials and methods

2.1. Study site

The study was performed in the deforested and fragmented subtropical evergreen broad-leaf forest, located in the Dujiangyan region (altitude 600–1000 m, 31°04' N–31°05' N, 103°42' E–103°43' E) of Sichuan Province, southwest China. It lies in the transition zone between the Qinghai-Tibetan Plateau and the plains of Chengdu. The climate is subtropical, with a mean annual temperature of 15.2 °C, and annual precipitation of 1200–1800 mm. The Dujiangyan region is a hotspot of biodiversity in China.

Our study was conducted in 14 forest patches annually from 2014 to 2017. Most of forest was cleared in the 1980s–2000s, and subsequently forest fragments of 2–58 ha were allowed to regrow on hilltops while flatter areas were maintained in cultivation or became roads under the management of Dujiangyan city government (Zhao et al., 2016). These forest patches were classified into three kinds based on stand age, and also varied in patch size. Experiments were conducted in 14 forest patches (labeled as A, B1, B2, C, D, F, H, K, L, M, R, S, U and V; Fig. 1; Table S1). Forests in patch B1 and B2 are at least 100 years old, and we refer to them as old patches, because of their age and protection from the nearby Banruosi Temple. The other forest patches have undergone extensive logging and destruction in the 1980s–2000s and represent early or middle succession stages. The stand age was categorized into young, middle and old forests based on survey of local people, and represents a gradient of succession from early to late stages because the accurate year of deforestation was unknown (Table S1). We did not consider the distance between patches (or their isolation) because distances are relatively short and exploratory analyses ruled out inter-patch distance as a determinant of abundance and species richness (Table S2).

In the study site, the common tree species include *Lithocarpus hancei*, *Quercus acutissima*, *Q. serrata*, *Q. variabilis*, *Cyclobalanopsis glauca*, *L. megalophyllus*, *Choerospondias axillaris*, *Castanopsis fargesii*, *C. ceratocantha* and *Camellia oleifera*. We recorded 11 sympatric rodent species in this region, including South China field mice (*Apodemus draco*), Chevrier's field mice (*A. chevrieri*), Sichuan field mice (*A. latronum*), Edward's long-tailed rats (*Leopoldamys edwardsi*), Chestnut rats (*Niviventer fulvescens*), Chinese white-bellied rats (*N. confucianus*), Norway rats (*Rattus norvegicus*), Himalayan rats (*R. nitidus*), Pere David's vole (*Eothenomys melanogaster*), Harvest mice (*Micromys minutus*) and House mice (*Mus musculus*) (Xiao et al., 2013). These rodent species either feed on tree seeds such as nuts and acorns or hoard them. Thus, rodent seed dispersers potentially play a significant role in forest

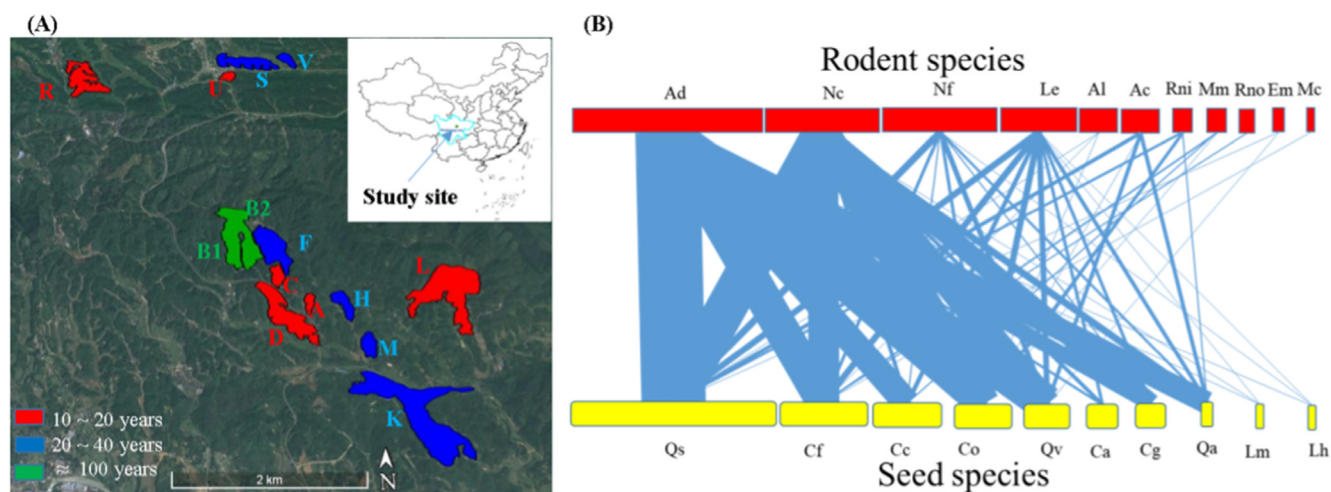


Fig. 1. The 14 experimental plots with different size and succession age (A) and aggregated rodent-seed interaction network of all the plots over three years (B). In the interaction network, the length of rectangles indicates the relative abundance of rodent or seed species, and the thickness of links indicates the relative interaction strength between each pair of rodent and seed species. Rodents: Ac-*A. chevrieri*, Ad-*A. draco*, Al-*A. latronum*, Le-*L. edwardsi*, Nf-*N. fulvescens*, Nc-*N. confucianus*, Rni-*Rattus nitidus*, Rno-*R. norvegicus*, Em-*E. melanogaster*, Mc-*Mus musculus* and Mm-*M. minutus*, respectively. Seeds: Qa-*Q. acutissima*, Qs-*Q. serrata*, Qv-*Q. variabilis*, Cg-*C. glauca*, Lm-*L. megalophyllus*, Ca-*C. axillaris*, Cf-*C. fargesii*, Cc-*C. ceratocantha*, Co-*C. oleifera*, and Lh-*L. hancei*, respectively.

seed regeneration. All recorded rodent species are nocturnal.

2.2. Sampling design

2.2.1. Seeds

Seed fall was measured using seed traps made of Vinyon (New Agricultural Net Factory, Dujiangyan, China, mesh size = 2 mm) (Zhang et al., 2016b; Zhao et al., 2016). Each trap sampled a 1 × 1 m area (Fig. 2A). In late August 2014, we set up 178 traps suspended 0.8-m above the ground using bamboo or trunk posts. Considering different sizes of patches, 3–7 seed traps were placed in a plot, in 2 or 4 sampling lines with a spacing of 10 m between adjacent traps. In each year, we collected fallen seeds every 2 weeks from early September to late December when seeds became mature. During the peak period of seed rain, fresh and intact seeds of each species were collected for seed-

dispersal experiments.

2.2.2. Rodents

We used wire live traps (30 × 13 × 12 cm), baited with fresh chestnuts to trap small rodents (Zhao et al., 2016). We placed them into 4 × 10 grids with intervals of 10 m in each plot (Fig. 2B) for five consecutive nights (200 trap nights) during October to November each year. Traps were placed at 15:00–17:00 h in the afternoon and were checked at 7:00–9:00 h the next morning. All captured animals were weighed and identified to species, sex and reproductive status (females pregnant, lactating or not; males with testes descended or not). Different species were also marked with distinguishable patterns (such as “|”, “+”, “—”, etc.) on their back with wine-red human hair dye (Zhao et al., 2016; Gu et al., 2017) and then released *in situ*. Color labeling was used to estimate abundance (minimum number alive) and identify

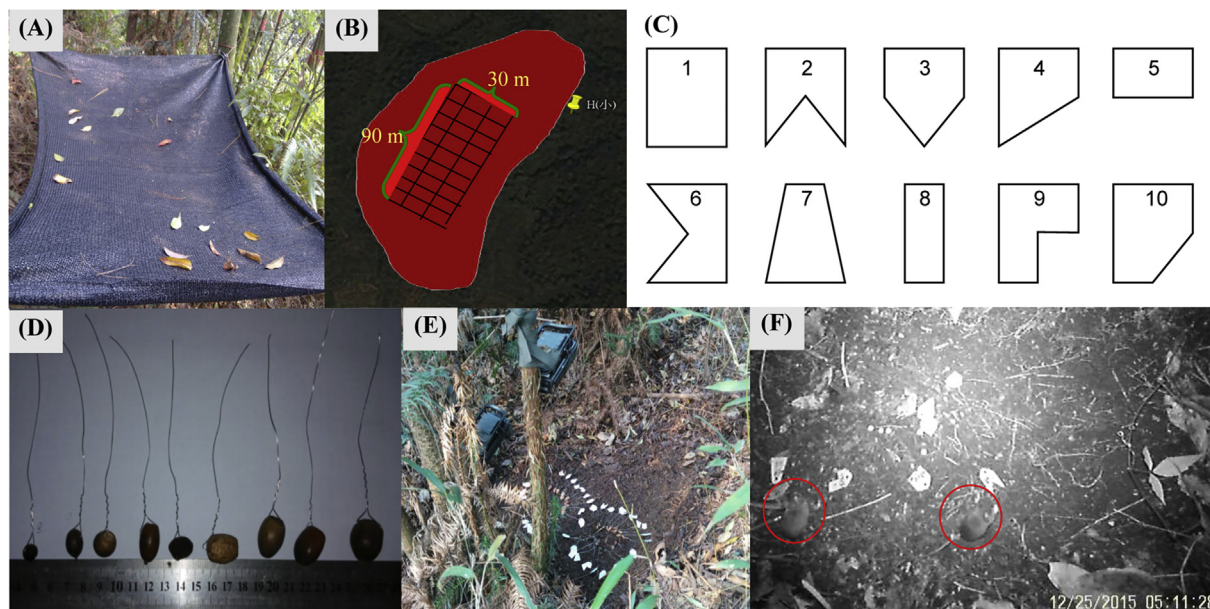


Fig. 2. Illustrations of seed traps, infrared (IR) camera and seed tagging method for measuring seed-rodent interaction strength. (A) Seed trap. (B) Rodent trap grids. (C) Shapes of seed tags. Each shape was used to mark different individuals within a seed species. (D) Released tagged seeds. (E) Setting of IR camera traps nearby the seed station. (F) Two rodent individuals (*Apodemus draco*) recorded by an infrared camera. Different rodent species were distinguished by different patterns on their back with wine-red human hair dye. Plastic seed tags with different shapes were used to distinguish different seed species.

species on infrared cameras and determine if they ate *in situ* or removed seeds at the seed stations (Zhao et al., 2016; Gu et al., 2017). Procedures for capturing and raising animals were in accordance with the regulations of the Institute of Zoology, Chinese Academy of Sciences.

2.2.3. Seed-rodent interactions

Seed removal trials were carried out from August 2014 to April 2017 in the 14 forest patches of Dujiangyan region. In previous studies, plastic tags have been used for tagging seeds (Forget, 1990; Zhang and Wang, 2001; Xiao et al., 2006). Here, we used plastic tags with different shapes representing different seed individuals, and applied IR cameras (Jansen et al., 2002) to record individual seeds visited (removed or eaten) by rodents, which enable us to measure the interaction strength between rodents and tree seeds, as follows (also see: Zhao et al., 2016; Gu et al., 2017). We selected seeds of 10 common tree species: *L. hancei*, *Q. acutissima*, *Q. serrata*, *Q. variabilis*, *C. glauca*, *L. megalophyllus*, *C. axillaris*, *C. fargesii*, *C. ceratocantha*, and *C. oleifera*. The seed rain periods of these tree seeds generally overlapped, with only minor variation in peak time (Zhao et al., 2016). During the time when various seeds were mature, fresh and intact seeds were collected from the ground or trees outside of the experimental patches, and air dried in a cool place.

We labeled seeds using the tagging methods of Zhao et al. (2016). A 0.5-mm diameter hole was drilled through the husk near the germinal disc of each seed. Though the cotyledons were partly damaged (except for *L. hancei* nuts), the embryo remained intact and was capable of germinating. A small, light white plastic tag (3.6×2.5 cm, < 0.1 g) with different shapes was tied through the hole using a thin steel wire 10 cm long (Fig. 2C, D). Each weighed seed was given a unique code by writing on the tag using a marker pen. When rodents buried the seeds in the soil, the plastic-tags were often left on the surface, making them easy visually relocate.

In November or December of 2014, 2015 and 2016, 2–8 seed species were released depending on the availability of seed species in each patch. Each species including 10 tagged seeds with unique codes reflected in different tag shapes, spaced evenly on the soil surface within 1–2 m² (Fig. 2C, D). IR camera traps (Ltl -5210A, Zhuihai Ltl Acorn Electronics Co., Ltd, Zhuihai, China) were tied to a tree adjacent to each seed station (0.4–0.7 m high) and set on video record mode (Video Size: 640 × 480; PIR sensitivity: High; Video Length: 20 s; Trigger Interval: 0 s) to monitor seeds removed or eaten by small rodents for three days (Fig. 2E, F). We released 90 seeds per tree species per forest patch every year, and 13,830 seeds in total. We randomly searched a 25-m radius around each station with equal effort (2–3 h by two people for each plot visit), and recorded the fate of the tagged seeds or whether seeds were missing with unknown fate. In the lab, we systematically analyzed the video recordings (all capacity 537.3 gigabytes) and identified rodent and seed species for each interaction.

2.3. Data analysis

2.3.1. Measures of seeds and rodents

As no single index can capture all the characteristics of species assembly, we here considered multiple species indices for testing the impact of fragmentation and succession as well as their associations with network metrics. Species richness of seeds (SR) was measured as the number of species observed in each forest patch. Seed abundance (SA) was measured as the total number of seeds produced by a patch. Due to energetic value of different seed species varied greatly, it is necessary to use the metabolic seed abundance (estimated by the seed calorific value per seed species, MSA): $MSA = (\sum_{i=1}^S n_i CV_i) / S$, where S = the number of seed species; n_i = the number of a given seed species; CV_i = the average calorific value of a given species i .

Species richness of rodents (RR) was measured by number of species observed in each forest patch. Rodent abundance (RA) was estimated using the minimum number alive (MNA) by the live trapping method described above for each plot and year. Because the body mass of

different species varied greatly, it is necessary to measure the metabolism-related metrics by considering both abundance and body mass of rodents so as to represent the food availability per capita (Xiao et al., 2013). Metabolic rodent abundance (the sum of metabolic-scaling body mass from each rodent species each year, MRA) was calculated as: $MRA = \sum_{i=1}^S n_i BM_i^{0.75}$, where S = the number of rodent species; n_i = the population size (here MNA) of a given rodent species i ; $BM_i^{0.75}$ = the average metabolic-scaling body mass of a given species i . Per capita seed availability (PCSA): $PCSA = SA / RA$. Metabolic per capita seed availability (MPCSA): $MPCSA = MSA / MRA$ (Xiao et al., 2013).

To test the effects of seed traits on network metrics, the morphological traits, nutrient composition and caloric value of seeds were measured (see Zhang and Zhang, 2008). Chemical analysis was conducted in duplicates on a mixture of seed kernel for each tree species; seed nutrient compositions were measured by the Measure Center of Grain Quality, Ministry of Agriculture, China. The dry-kernel caloric values were calculated by the average gross-energy equivalents of protein (17.2 kJ/g), fat (38.9 kJ/g) and starch (17.2 kJ/g). The seed sizes were calculated by multiplying seed length with seed width.

2.3.2. Network measures

Among various network measures, we only considered several measures that are mostly related to structure and interaction strength of seed-rodent interactions in this study. Optimal diet theory predicts food availability can induce diet expansion or shifting, thus we chose connectance to quantify the probability of interactions in each seed-rodent network. Changes in connectance should reflect the degradation or restoration of seed predation and dispersal function in forests. Connectance was measured by the proportion of realized links in a network (Dunne et al., 2002). The second set of network metrics quantifies nested architecture including nestedness and weighted nestedness. The latter takes into account the weight of the interaction strength (Galeano et al., 2009). They were chosen because they are related to network stability (Bascompte et al., 2003; Burgos et al., 2007) and also reflect the structure of seed-rodent interactions as rodents, as generalists, might shift their diets as species composition changes. The last network metric is interaction strength (IS) between seed and rodent species, which is a direct measure of seed dispersal and predation by rodents, calculated as $IS = \text{overall number of seeds eaten and removed by rodents} / \text{total number of tagged seeds released} \times 100\%$ (Vazquez et al., 2005).

To detect the effect of seed traits or rodent traits (only body mass) on metric of aggregated network (Fig. 1), we selected 6 network metrics: (1) species degree, which is the number of species associated with other related species in the network (Bascompte et al., 2006; Bascompte and Jordano, 2007); (2) species strength, which is the sum of the dependence or the intensity of an animal species or plant species (Bascompte and Jordano, 2007); (3) interaction asymmetry, depicting the relative dissimilarity between the two mutual dependencies (Bascompte et al., 2006); (4) nested rank, it means that the species has a higher or lower generality (Alarcon et al., 2008); (5) species specificity, or specificity, which is used to measure the specificity of a species (Bluthgen et al., 2006); (6) partner diversity, which is the diversity of the associates of a species, and can measure the extent of the generality of the species (Bersier et al., 2002; Bascompte and Jordano, 2007). The *bipartite* package was used for calculation of network measures in the R program (R Development Core Team, 2014).

2.3.3. Statistical analysis

To identify the associations of post-deforestation succession and fragmentation with seed-rodent interactions, we used linear mixed models to test: (1) The degree to which stand age and patch size explained variation in the different species indices of seeds and rodents (SR, SA, MSA, RR, RA, MRA, PCSA or MPCSA) across the 14 patches, with year and patch as random factors. (2) The degree to which stand

age and patch size explained variation in the different network metrics (connectance, nestedness, weighted nestedness and interaction strength), with year and patch as random factors. (3) The degree to which species indices explained variation in network metrics, with year and patch as random factors. As species indices are inter-dependent (e.g., RR, RA and MRA are correlated rodent indices), we only considered model formulations (here y indicates response variable) like: $y = f(RR, SR)$, $f(RA, SA)$, $f(MRA, MSA)$, $f(PCSA)$, or $f(MPCSA)$ to avoid collinearity in models. The variables were log-transformed to meet assumptions of the statistical models if necessary. In order to see the effects of the functional traits of rodents and seeds on network structure, Spearman's rank correlation was used to test the relationships between rodents or seeds functional traits and network metrics. We also detect the effects of stand age and patch size on seed and rodent abundance of different species. All linear mixed models were performed by *lme4* and *lmerTest* in the R program 3.3.3 (R Development Core Team, 2014).

3. Results

3.1. Forest stand age, size and species richness or abundance

Rodent species richness ranged from 1 to 6 species, and rodent abundance ranged from 3 to 19 individuals across the 14 forest patches. Rodent species richness ($\chi^2 = 15.29$, $P < 0.001$) and rodent abundance ($\chi^2 = 17.20$, $P < 0.001$) significantly decreased with stand age (Fig. 3; Table S3). The abundance of *A. draco*, *A. latronum*, *N. confucianus* and *R. nitidus* was significantly decreased with stand age (*A. draco*: $\chi^2 = 8.93$, $P = 0.01$; *A. latronum*: $\chi^2 = 8.93$, $P = 0.01$; *N. confucianus*: $\chi^2 = 16.56$, $P < 0.01$; *R. nitidus*: $\chi^2 = 6.14$, $P = 0.04$).

Seed species richness ranged from 1 to 7 species, and seed abundance ranged from 0.72 to 63.88 across the 14 forests. Stand age had a significant positive association with seed species richness ($\chi^2 = 7.29$, $P = 0.03$) and MPCSA ($\chi^2 = 14.63$, $P < 0.001$), but no significant association with seed abundance or MSA (Fig. 3; Table S3). The abundance of *C. ceratocantha*, *Q. variabilis* and *C. oleifera* was significantly increased with stand age (*C. ceratocantha*: $\chi^2 = 9.94$, $P = 0.01$; *Q. variabilis*: $\chi^2 = 6.26$, $P = 0.04$; *C. oleifera*: $\chi^2 = 6.98$, $P = 0.03$).

Patch size had no significant association with species richness or pooled abundance of either rodent or seed species (all $P > 0.05$), but the abundance of *R. nitidus* and *Q. acutissima* was positively associated with the patch size (*R. nitidus*: $\chi^2 = 4.31$, $P = 0.04$; *Q. acutissima*: $\chi^2 =$

6.77, $P = 0.01$)

3.2. Forest stand age, size and network metrics

Connectance ranged from 0.44 to 1, interaction strength ranged from 0.07 to 1, and nestedness ranged from 0 to 35.32 across the 14 forest patches. Stand age had significant negative associations with connectance ($\chi^2 = 8.89$, $P = 0.01$) and interaction strength ($\chi^2 = 9.52$, $P = 0.009$; Figs. 3 and 4; Table S3). Stand age had a significant positive association with nestedness ($\chi^2 = 19.77$, $P < 0.001$; Figs. 3F and 4; Table S3). Patch size had no significant association with any network metric examined (all $P > 0.05$; Table S3).

3.3. Species abundance or richness and network metrics

Rodent abundance showed a significant positive association with interaction strength ($t = 2.451$, $P = 0.02$), and a significant negative association with nestedness ($t = -2.649$, $P = 0.014$; Fig. 4; Table S4).

Seed richness had a significant positive association with nestedness ($t = 2.77$, $P = 0.048$) (Fig. 4; Table S4). MSA showed a significant positive association with weighted nestedness ($t = 4.32$, $P < 0.001$) and a significant negative association with connectance ($t = -2.87$, $P = 0.007$; Fig. 4; Table S4). MPCSA had significant negative associations with connectance ($t = -2.23$, $P = 0.032$) and interaction strength ($t = -2.047$, $P = 0.048$; Fig. 4; Table S4).

3.4. Effects of seed or rodent traits on metrics of aggregated network

Body mass of rodents had insignificant effects on metrics of aggregated network (all $P > 0.05$, Table S5). The coat thickness of seeds was positively correlated with the nested rank, and negatively correlated with species degree and interaction asymmetry; crude starch was positively correlated with species specificity ($P < 0.05$ for all; Table 1).

4. Discussion

Deforestation or fragmentation (Duntan and Fox, 1996; Brook et al., 2003; Fahrig, 2003), and the successional age of forests (Schweiger et al., 2000; Peñaclaros, 2003) can cause substantial change in species composition and abundance. However, the consequences of such changes for interaction networks in ecosystems and communities are largely unknown. By using a combination of seed tagging and IR

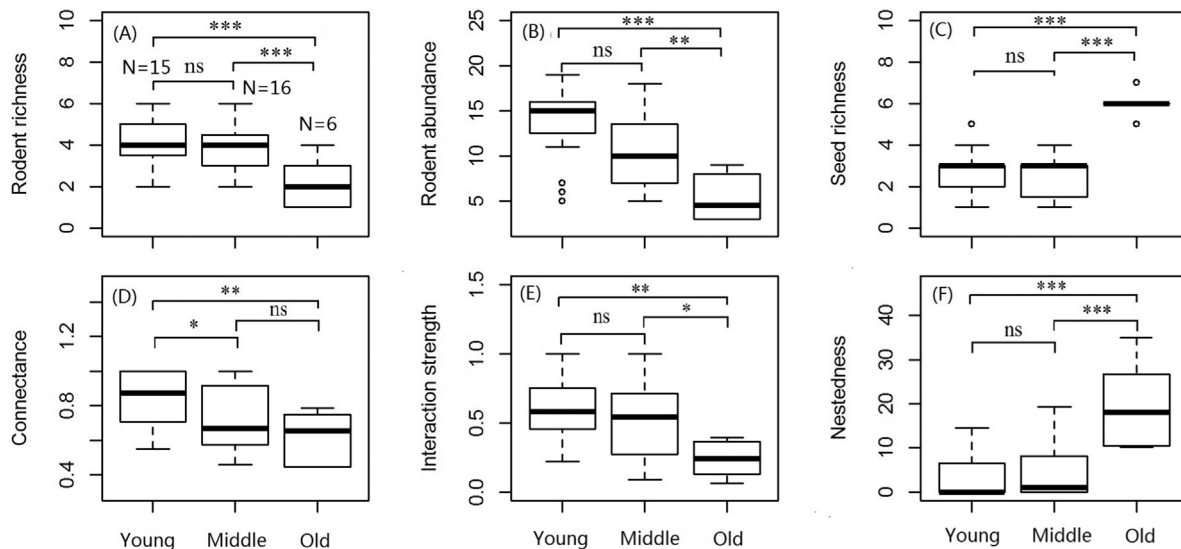


Fig. 3. Relationship between stand age and species richness, abundance (A, B, rodents; C, seeds), or network metrics (D–F). *, **, *** indicate $P < 0.05$, 0.01, 0.001, respectively, and ns indicates non-significant effect ($P > 0.05$). The bottom and top limits of each box are the lower and upper quartiles, respectively; the horizontal black band within each box is the median; and error bars equal ± 1.5 times the interquartile range. N in (A) indicates the sample size, the same for others.

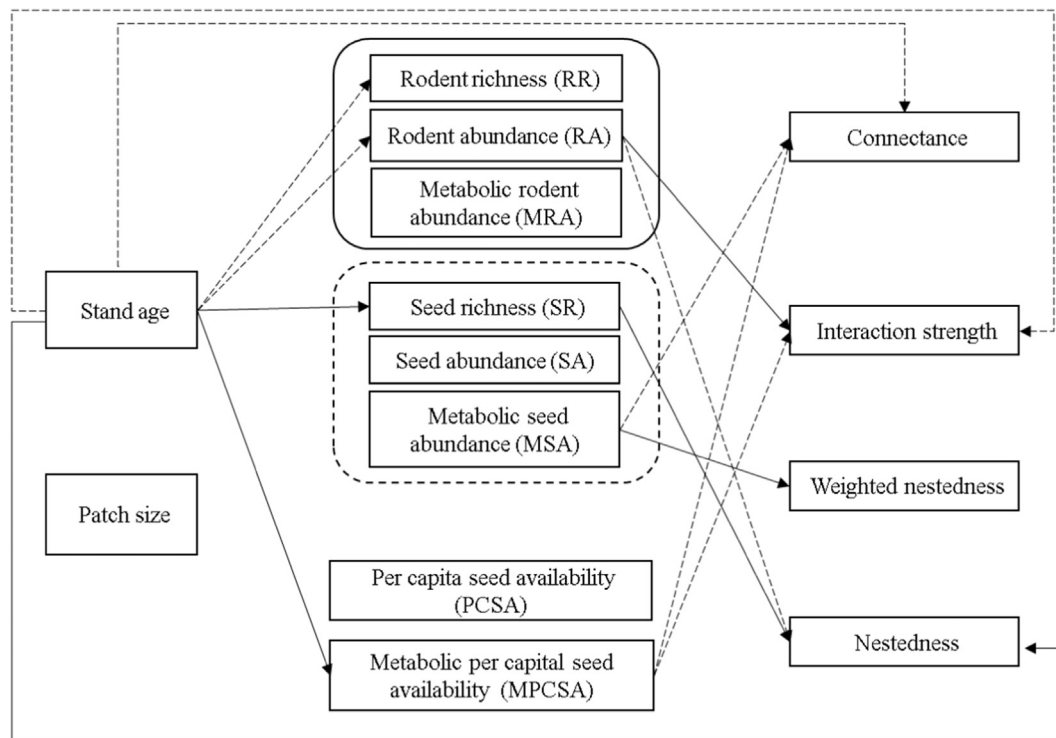


Fig. 4. Relationship of stand age and patch size with network metrics via species indices of rodents and seeds. Solid black lines represent significant positive associations, and dashed black lines represent significant negative associations. The solid line box represents rodent species indices, and the dotted line box represents seed species indices. PCSA = SA/ RA; MPCSA = MSA/ MRA.

camera tracking, we were able to measure the interaction strength between seeds and rodents, and therefore, to quantify the impacts of human deforestation on the mutualistic relationship between plants and their seed dispersers.

We found that tree seed-rodent network metrics changed significantly with stand age (regrowth time since deforestation), but not with fragment patch size. In younger forest patches, interaction strength was stronger and nestedness was lower than in either older patches or old stands. These results suggest changes in network structure were mediated by changes in seed and rodent species richness as well as rodent abundance, generally supporting the idea that seed availability relative to rodents changes the structure of seed-rodent networks. Because network metrics are important indicators for diversity and stability of ecosystems, the network architecture favoring stability fundamentally differs between food webs and mutualistic networks (Thebault and Fontaine, 2010). Our results provide new insights into the relationship between diversity and stability in forest ecosystems, and have implications for restoring degraded ecosystems.

We speculate that early during succession, the production of seeds by tree species may be offset by the high seed predation rates by the abundant rodents.

Several previous studies indicated that species richness and diversity of small mammals were higher in young stands than old growth areas (Duntan and Fox, 1996; Sullivan et al., 2000). This might be because deforestation creates open habitats that benefit non-native rodents (Fisher and Wilkinson, 2005). Our results are generally consistent with these observations. We found in younger stands, rodent species richness and abundance (or metabolic rodent abundance) were both higher (Fig. 3), supporting our Prediction 1. The increase of richness was mainly due to incursion of rodents that are active in farmlands and human residences, such as *M. minutus*, *M. musculus*, *R. nitidus* and *R. norvegicus*. Meanwhile, the increase of abundance for common forest rodent species (e.g., *A. draco* and *N. confucianus*) was probably caused by higher environmental heterogeneity and diversified food resources at early succession age. Seed species richness was lower in younger patches (Fig. 3). In our study region, deforestation mainly

Table 1
Effects of seed traits on aggregated network metrics.

Species traits	Species degree	Species strength	Interaction asymmetry	Nested rank	Species specificity	Partner diversity
Seed fresh weight	−0.117	−0.189	−0.166	0.232	−0.287	0.300
Seed size	−0.096	−0.243	−0.217	0.232	−0.485	0.473
Coat thickness	−0.667*	−0.500	−0.674*	0.747*	−0.422	−0.118
Seed dry weight	−0.144	−0.201	−0.179	0.253	−0.242	0.232
Kernel weight	0.169	0.034	0.145	−0.102	−0.034	0.295
Crude protein	−0.452	−0.383	−0.490	0.382	−0.532	0.077
Crude fat	0.026	−0.156	−0.134	−0.040	−0.488	0.332
Crude starch	0.001	0.189	0.178	0.002	0.726*	−0.619
Crude fiber	−0.362	−0.279	−0.366	0.268	−0.404	0.040
Tannin	0.198	0.160	0.222	−0.204	0.067	0.154
Caloric value	−0.094	−0.179	−0.187	0.051	−0.272	0.008
Caloric value per seed	0.213	0.021	0.138	−0.113	−0.038	0.245

* $P < 0.05$ (2-tailed).

happened in 1980s–2000s, and many large trees like *Q. variabilis*, *C. fargesii* and *Cerasus pseudocerasus* were cut. In young stands, *Q. serrata* was the dominant tree species. With forest protection during the last three decades, the forest composition has begun to recover. Although total seed abundance was not affected by succession or patch size, additional analysis at species level indicated that the abundance of *C. ceratocantha*, *Q. variabilis* and *C. oleifera* was significantly increased with stand age; the abundance of *Q. acutissima* was positively associated with the patch size.

Human disturbance may impact species interactions involved in seed dispersal in a variety of ways. For example, Wright and Duber (2001) reported that poachers and habitat fragmentation indirectly altered the spatial pattern of seed dispersal, seed predation, and seedling recruitment in the palm *Attalea butyraceae* in central Panama when humans disrupted mammal communities. Spotswood et al. (2012) demonstrated that the presence of invasive fruit-bearing plants and introduced frugivores altered seed dispersal networks, and found that the patterns of alteration depended on both the frugivore community and the relative abundance of available fruit. In plant-herbivore and host-parasitoid food webs, network structure was altered by habitat fragmentation, with different metrics such as connectance, vulnerability and generality being affected depending on interaction type (Valladares et al., 2012). However, the effects of human activities such as deforestation on seed-rodent interaction networks are poorly understood (Zhao et al., 2016). We found that the interaction strength and connectance were larger but nestedness was smaller in younger stands, as compared older stands, supporting our Prediction 2. Our results suggest that forest succession after deforestation would increase ecosystem stability according to previous studies showing nestedness (Bascompte et al., 2003; Bascompte et al., 2006; Pawar, 2014; Rohr et al., 2014) and weak interactions (Berlow, 1999) enhanced local stability of networks in theory by avoiding strong positive or negative feedback on population dynamics.

Habitat fragmentation has been reported to affect species interactions (Fahrig, 2003). The components of fragmentation generally include changes in fragment size, isolation, edge effects and habitat degradation (Fahrig, 2003; Magrath et al., 2014). Recent studies suggest that mutualisms, such as pollination and seed dispersal, were more sensitive to the negative effects of forest fragmentation than antagonisms, such as predation or herbivory (Aguilar et al., 2006). Applying meta-analytical techniques, Magrath et al. (2014) demonstrated that the effects of fragmentation on mutualisms were primarily driven by habitat degradation, edge effects, and fragment isolation, with little effect of fragment size. Dattilo et al. (2015) found that fragment size did not affect the topological structure of the individual-based palm-pollinator network. However, Aguirre and Dirzo (2008) reported pollinator abundance was negatively affected by fragment size. In our study, although no significant effects of patch size on pooled rodent abundance was found, but we found the abundance of *A. draco*, *A. latronum*, *N. confucianus* and *R. nitidus* was significantly decreased with stand age, supporting our prediction 1. We did not find significant effects of fragment size on the species richness and network metrics. This was likely because isolation had little effect for rodents and seeds. In our study area, the fragmented forests were isolated by the small and narrow farmlands or roads in the valleys. Rodents might easily move across these farmlands, and disperse seeds among patches in dry season (Jorge and Howe, 2009).

Most mutualistic networks may be shaped by differences in species abundance among interacting species (Vazquez et al., 2005; Gleditsch and Carlo, 2011; Verdu and Valiente-Banuet, 2011; Dattilo et al., 2014). For seeds and rodents, interaction strength may be affected by many factors, such as seed abundance, rodent abundance, or seed availability (Schleuning et al., 2011; Xiao et al., 2013; Cao et al., 2017). Our study showed that rodent abundance had a significant positive association with interaction strength, but a negative association with nestedness; metabolic seed abundance (MSA) had a significant negative association

with connectance; metabolic per capita seed availability (MPCSA) had a significant negative association with connectance and interaction strength (Fig. 4; Table S4). These results generally support our Prediction 3. These observations also supported the predictions of optimal foraging theory and optimal diet selection theory that interaction degree or diet breadth would increase because of stronger competition for food resources with fewer seed resources or more predators (Emlen, 1966; Araujo et al., 2008; Bolnick et al., 2010). Several studies quantitatively assessed interaction strength between tree seed species and rodent species by using enclosures in field stations, and found functional traits of seeds and rodents played a significant role in the formation of mutualism and predation of the seed-rodent dispersal system (Wang et al., 2014; Zhang et al., 2015).

Seed traits also play a significant role in shaping the network structure. Previous studies have indicated that many seed traits (e.g. coat thickness, nutrition value, tannin content, etc.) affect seed-rodent interactions (Zhang et al., 2016a, 2016b). Our previous studies in the study region indicated that small rodents like *Apodemus* species prefer to hoard high starch with soft seed coat, instead of seeds with hard or thick seed coat in the study region (Chang and Zhang, 2014). In this study, we found coat thickness was positively correlated with nested rank, and negatively correlated with species degree and interaction asymmetry; crude starch was positively correlated with species specificity of aggregated network (Table 1), suggesting hard seed coat or high starch content may facilitate the formation of structure. We found the abundance of two plant species (i.e. *C. ceratocantha*, *Q. variabilis*) with high starch contents was significantly increased with stand age, which may partially explain the increased nestedness and decreased connectance in old stands.

Robust estimates of the actual number of interactions (links) within diversified ecological networks require adequate sampling effort that needs to be explicitly gauged (Jordano, 2016). Biodiversity sampling is a labor-intensive activity, and sampling is often not sufficient to detect all or even most of the species present in an assemblage (Gibson et al., 2011). Many previous studies focused on the interaction between plants and pollinators (CaraDonna et al., 2017) or frugivorous birds (Schleuning et al., 2011), but few have considered the interaction between plant fruits (seeds) and small mammals in natural conditions (but see Jansen et al., 2012; Zhao et al., 2016; Gu et al., 2017). One reason is that it is difficult to identify the seed-rodent interactions at species level. A combination of seed tagging and IR camera tracking allowed us to quantify seed-rodent interactions. However, our methods still have some limitations. Occasionally, a small proportion (3.7%) of rodents could not be identified due to their quick movement or failure of cameras. In the future, to clearly and more efficiently determine the individual relationship between seeds and rodents, it is necessary to use passive integrated transponder (PIT) tags to identify seeds and rodents (Shenko et al., 2012). More detail ecological parameters of both rodents and seeds, such as rodent individual behavior and seed dispersal, storage, germination and survival, should be further analyzed and researched in seed-rodent interaction networks to improve forest ecosystem management.

Our results highlight that forest succession after deforestation played a significant role in determining network structure, which may affect diversity and stability of seed-dispersal networks in fragmented ecosystems. Therefore, to facilitate the restoration processes of degraded forests, it is necessary to protect old-growth forests that provide seed sources, and reduce human disturbances (such as cutting, grazing and farming). Human intervention may be necessary if rodent density is too high, or seed source is too low. In such conditions, it would likely be beneficial to supply external seed resources by planting large trees or spraying seeds, and by managing the abundance of rodent species that contribute significantly to seed predation/dispersal in forests. Exclusion of non-native rodent species from farmlands and human residences could be important in early succession stage after deforestation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.03.023>.

References

- Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* 9, 968–980.
- Aguiar, A., Dirzo, R., 2008. Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest. *Biol. Conserv.* 141, 375–384.
- Alarcon, R., Waser, N.M., Ollerton, J., 2008. Year-to-year variation in the topology of a plant-pollinator interaction network. *Oikos* 117, 1796–1807.
- Araujo, M.S., Guimaraes, P.R., Svanback, R., Pinheiro, A., Guimaraes, P., Dos Reis, S.F., Bolnick, D.I., 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology* 89, 1981–1993.
- Bascompte, J., Jordano, P., 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38, 567–593.
- Bascompte, J., Jordano, P., Melian, C.J., Olesen, J.M., 2003. The nested assembly of plant-animal mutualistic networks. *P. Natl. Acad. Sci. USA* 100, 9383–9387.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Benchimol, M., Talora, D.C., Mariano-Neto, E., Oliveira, T.L.S., Leal, A., Mielke, M.S., Faria, D., 2017. Losing our palms: the influence of landscape-scale deforestation on Arecaceae diversity in the Atlantic forest. *For. Ecol. Manage.* 384, 314–322.
- Berlow, E.L., 1999. Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334.
- Bersier, L.F., Banasek-Richter, C., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. *Ecology* 83, 2394–2407.
- Bluthgen, N., Menzel, F., Bluthgen, N., 2006. Measuring specialization in species interaction networks. *Bmc Ecol.* 6, 9.
- Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L.K., Lau, O.L., Paull, J.S., 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proc. Royal Soc. B* 277, 1789–1797.
- Brook, B.W., Sodhi, N.S., Ng, P.K.L., 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* 424, 420–423.
- Burgos, E., Ceva, H., Perazzo, R.P.J., Devoto, M., Medan, D., Zimmermann, M., Delbue, A.M., 2007. Why nestedness in mutualistic networks? *J. Theor. Biol.* 249, 307–313.
- Cao, L., Guo, C., Chen, J., 2017. Fluctuation in seed abundance has contrasting effects on the fate of seeds from two rapidly germinating tree species in an Asian tropical forest. *Integr. Zool.* 12, 2–11.
- CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., Sanders, N.J., 2017. Interaction rewiring and the rapid turnover of plant-pollinator networks. *Ecol. Lett.* 20, 385–394.
- Chang, G., Zhang, Z., 2014. Functional traits determine formation of mutualism and predation interactions in seed-rodent dispersal system of a subtropical forest. *Acta Oecol.* 55, 43–50.
- Chazdon, R.L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320, 1458.
- Dattilo, W., Aguiar, A., Quesada, M., Dirzo, R., 2015. Tropical forest fragmentation affects floral visitors but not the structure of individual-based palm-pollinator networks. *PLoS One* 10, e0121275.
- Dattilo, W., Marquitti, F.M.D., Guimaraes, P.R., Izzo, T.J., 2014. The structure of ant-plant ecological networks: is abundance enough. *Ecology* 92, 475–485.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567.
- Duntan, C.E., Fox, B.J., 1996. The effects of fragmentation and disturbance of rainforest on ground-dwelling small mammals on the Robertson Plateau, New South Wales, Australia. *J. Biogeogr.* 23, 187–201.
- Emlen, J.M., 1966. The role of time and energy in food preference. *Am. Nat.* 100, 611–617.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515.
- Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev.* 35, 51–81.
- Forget, P.M., 1990. Seed-dispersal of *Vouacapoua americana* (Caesalpinaceae) by caviomorph rodents in French Guiana. *J. Trop. Ecol.* 6, 459–468.
- Fortuna, M.A., Bascompte, J., 2006. Habitat loss and the structure of plant-animal mutualistic networks. *Ecol. Lett.* 9, 281–286.
- Galeano, J., Pastor, J.M., Iriondo, J.M., 2009. Weighted-Interaction Nestedness Estimator (WINE): a new estimator to calculate over frequency matrices. *Environ. Modell. Software* 24, 1342–1346.
- Garzon-Lopez, C.X., Ballesteros-Mejia, L., Ordóñez, A., Bohlman, S.A., Olff, H., Jansen, P.A., 2015. Indirect interactions among tropical tree species through shared rodent seed predators: a novel mechanism of tree species coexistence. *Ecol. Lett.* 18, 752–760.
- Gibson, R.H., Knott, B., Eberlein, T., Memmott, J., 2011. Sampling method influences the structure of plant-pollinator networks. *Oikos* 120, 822–831.
- Gilarranz, L.J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J., Gonzalez, A., 2017. Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science* 357, 199–201.
- Gleditsch, J.M., Carlo, T.A., 2011. Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Divers. Distrib.* 17, 244–253.
- Gu, H., Zhao, Q., Zhang, Z., 2017. Does scatter-hoarding of seeds benefit cache owners or pilferers? *Integr. Zool.* 12, 477–488.
- Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Ouden, J.D., Wieren, S.E.V., 2002. The role of seed size in dispersal by a scatter-hoarding rodent. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal & Frugivory Ecology Evolution & Conservation*. CABI, Wallingford, UK, pp. 209–225.
- Jansen, P.A., Forget, P.M., 2001. Scatterhoarding rodents and tree regeneration. In: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, M. (Eds.), *Dynamics and Plant-Animal Interactions in a Neotropical Rainforest*. Springer, Netherlands, Netherlands, pp. 275–288.
- Jansen, P.A., Hirsch, B.T., Emsens, W.J., Zamora-Gutierrez, V., Wikelski, M., Kays, R., 2012. Thieving rodents as substitute dispersers of megafaunal seeds. *Proc. Natl. Acad. Sci. USA* 109, 12610–12615.
- Jordano, P., 2016. Sampling networks of ecological interactions. *Funct. Ecol.* 30, 1883–1893.
- Jorge, M.L.S.P., Howe, H.F., 2009. Can forest fragmentation disrupt a conditional mutualism? A case from central Amazon. *Oecologia* 161, 709–718.
- Laurance, W., 1999. Reflections on the tropical deforestation crisis. *Biol. Conserv.* 91, 109–117.
- Lohbeck, M., Poorter, L., Lebriajtrejos, E., Martínezramos, M., Meave, J.A., Paz, H., Pérezgarcía, E.A., Romeropérez, I.E., Tauro, A., Bongers, F., 2013. Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology* 94, 1211.
- Magrach, A., Laurance, W.F., Larrinaga, A.R., Santamaría, L., 2014. Meta-analysis of the effects of forest fragmentation on interspecific interactions. *Conserv. Biol.* 28, 1342–1348.
- Martínez-Ramos, M., Pingarrón, A., Rodríguez-Velázquez, J., Toledo-Chelala, L., Zermeno-Hernández, I., Bongers, F., 2016. Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica* 48, 745–757.
- May, R.M., 1972. Will a large complex system be stable. *Nature* 238, 413–414.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. *Proc. Natl. Acad. Sci. USA* 104, 19891–19896.
- Pawar, S., 2014. Why are plant-pollinator networks nested? *Science* 345, 383.
- Peñalcaros, M., 2003. Changes in forest structure and species composition during secondary forest succession in the bolivian amazon. *Biotropica* 35, 450–461.
- R Development Core Team, 2014. R: a language and environment for statistical computing, version 3.3.3. R Foundation for Statistical Computing, Vienna, Austria.
- Rohr, R.P., Saavedra, S., Bascompte, J., 2014. On the structural stability of mutualistic systems. *Science* 345, 416–426.
- Schleuning, M., Bluthgen, N., Florchinger, M., Braun, J., Schaefer, H.M., Bohning-Gaese, K., 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. *Ecology* 92, 26–36.
- Schweiger, E.W., Diffendorfer, J.E., Holt, R.D., Pierotti, R., Gaines, M.S., 2000. The interaction of habitat fragmentation, plant, and small mammal succession in an old field. *Ecol. Monogr.* 70, 383–400.
- Shenko, A.N., Bien, W.F., Spotila, J.R., Avery, H.W., 2012. Effects of disturbance on small mammal community structure in the New Jersey Pinelands, USA. *Integr. Zool.* 7, 16–29.
- Spotswood, E.N., Meyer, J.Y., Bartolome, J.W., 2012. An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. *J. Biogeogr.* 39, 2007–2020.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2000. Small mammals and stand structure in young pine, seed-tree, and old-growth forest, southwest Canada. *Ecol. Appl.* 10, 1367–1383.
- Thebault, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856.
- Theimer, T.C., 2005. Rodent scatterhoarders as conditional mutualists. In: Forget, P.M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI, Cambridge, pp. 283–295.
- Uriarte, M., Bruna, E.M., Rubim, P., ANCIaes, M.A.R.I.N.A., Jonckheere, I., 2010. Effects of forest fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site limitation. *Ecology* 91, 1317–1328.
- Valladares, G., Cagnolo, L., Salvo, A., 2012. Forest fragmentation leads to food web

- contraction. *Oikos* 121, 299–305.
- Vander Wall, S.B., 2010. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philos. Trans. Royal Soc. B* 365, 989–997.
- Vazquez, D.P., Morris, W.F., Jordano, P., 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* 8, 1088–1094.
- Verdu, M., Valiente-Banuet, A., 2011. The relative contribution of abundance and phylogeny to the structure of plant facilitation networks. *Oikos* 120, 1351–1356.
- 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. *Integr. Zool.* 9, 309–319.
- Whitehead, T., Goosem, M., Preece, N.D., 2014. Use by small mammals of a chronosequence of tropical rainforest revegetation. *Wildl. Res.* 41, 233–242.
- Wright, S.J., Duber, H.C., 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33, 583–595.
- Xiao, Z., Jansen, P.A., Zhang, Z., 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *For. Ecol. Manage.* 223, 18–23.
- Xiao, Z., Zhang, Z., 2016. Contrasting patterns of short-term indirect seed-seed interactions mediated by scatter-hoarding rodents. *J. Anim. Ecol.* 85, 1370–1377.
- Xiao, Z., Zhang, Z., Krebs, C.J., 2013. Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. *J. Ecol.* 101, 1256–1264.
- Yi, X., Yang, Y., Zhang, Z., 2011. Effect of seed availability on hoarding behaviors of Siberian chipmunk (*Tamias sibiricus*) in semi-natural enclosures. *Mammalia* 75, 321–326.
- Zhang, H., Wang, Z., Zeng, Q., Chang, G., Wang, Z., Zhang, Z., 2015. Mutualistic and predatory interactions are driven by rodent body size and seed traits in a rodent-seed system in warm-temperate forest in northern China. *Wildl. Res.* 42, 149–157.
- Zhang, H., Yan, C., Chang, G., Zhang, Z., 2016a. Seed trait-mediated selection by rodents affects mutualistic interactions and seedling recruitment of co-occurring tree species. *Oecologia* 180, 475–484.
- Zhang, H., Zhang, Z., 2008. Endocarp thickness affects seed removal speed by small rodents in a warm-temperate broad-leaved deciduous forest, China. *Acta Oecol.* 34, 285–293.
- Zhang, Z., Wang, F., 2001. Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). *Acta Ecol. Sin.* 21, 839–845.
- Zhang, Z., Wang, Z., Chang, G., Yi, X., Lu, J., Xiao, Z., Zhang, H., Cao, L., Wang, F., Li, H., Yan, C., 2016b. Trade-off between seed defensive traits and impacts on interaction patterns between seeds and rodents in forest ecosystems. *Plant Ecol.* 217, 253–265.
- Zhao, Q., Gu, H., Yan, C., Chao, K., Zhang, Z., 2016. Impact of forest fragmentation on rodent-seed network (in Chinese with English summary). *Acta Theriol. Sin.* 36, 15–23.