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

Yang, Xifu ; Yan, Chuan ; Zhao, Qingjian ; Holyoak, Marcel ; Fortuna, Miguel A ; Bascompte, Jordi ; Jansen, Patrick A ; Zhang, Zhibin

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 incursive ones from farmlands and human residences at early succession stage.

1   Running head: Succession and seed-rodent interactions

2   Title: Ecological succession drives the structure of seed-rodent interaction networks

3   Xifu Yang[1,2], Chuan Yan[1,*], Qingjian Zhao[1], Marcel Holyoak[3], Miguel A. Fortuna[4],

4   Jordi Bascompte[4], Patrick A. Jansen[5], Zhibin Zhang[1,*]

5   [1] State Key Laboratory of Integrated Management of Pest Insects and Rodents in

6   Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101,

7   China.

8   [2] University of Chinese Academy of Sciences, Beijing 100049, China.

9   [3] Department of Environmental Science and Policy, University of California, 1 Shields

10   Avenue, Davis, CA 95616, USA.

11   [4] Department of Evolutionary Biology and Environmental Studies, University of

12   Zurich, Zurich, Switzerland.

13   [5] Department of Environmental Sciences, Wageningen University, PO Box 47, 6700

14   AA Wageningen, The Netherlands

15   [*]Corresponding author, Email: zhangzb@ioz.ac.cn (+86-01064807069),
16   yanchuan@ioz.ac.cn
17

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22

Abstract

Deforestation and fragmentation have been shown to trigger massive species loss in forest ecosystems. Although changes of species composition are expected to alter species interactions, existing studies have rarely investigated such changes in the context of plant-animal networks. In this study, we investigated the association of forest deforestation and fragmentation with interaction networks of assemblages of rodents and trees seeds in a subtropical forest region. We compared seed-rodent interactions between forest patches that ranged from 10 to at least 100 years old. We expected that deforestation and fragmentation would reduce seed production and diversify rodent communities, resulting in higher interaction strengths and connectivity, but weak nestedness. We tested these ideas by using seed tagging and infrared camera trapping to measure the frequency of rodents removing seeds (interaction strength) in 14 regrowth forest patches which formed a successional gradient during 3 successive years. We found that the relative abundances of seeds and rodents changed with stand age not patch size, as did their interactions: older patches produced more seeds, but contained fewer individuals and species of rodents. Consequently, seed-rodent networks in older patches had lower connectance and interaction strength, but higher nestedness. While connectance and interaction strength increased with rodent abundance, nestedness decreased; conversely, seed richness increased nestedness. Our results suggest that an early successional state dominated by seed production and removal was replaced by a more mature state with fewer seeds produced in less connected networks. Future studies should test whether it is a general finding that post-deforestation forest succession and community assembly restore network structure towards that found in old stands with weakened seed-rodent interactions.

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INTRODUCTION

Many studies have demonstrated that habitat loss and fragmentation has huge negative

effects on biodiversity (Aguilar *et al.*, 2006). One negative effect of fragmentation

that has been reported concerns the breakdown of species interactions by habitat

degradation, edge effects and fragment isolation and area (Magrach *et al.*, 2014).

Recent studies have shown that mutualisms, such as pollination and seed dispersal,

are sensitive to the negative effects of forest fragmentation (Aguilar *et al.*, 2006,

Fortuna & Bascompte, 2006, Magrach *et al.*, 2014, Uriarte *et al.*, 2010). Although

effects of anthropogenic disturbance on forest species richness and abundance have

been widely explored, its consequences for species interactions have rarely been

investigated.

Various ecological interaction networks have been investigated in literature, 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) (CaraDonna *et al.*, 2017, Dattilo *et al.*, 2014, Neuhauser & Fargione,

2004, Schleuning *et al.*, 2011). The interests of many studies have largely lied in

linking specific network measures to structure and stability of ecological communities

or ecosystems. Two basic metrics for ecological networks are connectance (probability

of realized interaction) and interaction strength (May, 1972). Strong interaction

strength and high connectance in more diverse networks often decrease local stability

of random ecological networks (May, 1972), while Thebault and Fontaine (2010)

demonstrated that a highly connected architecture promoted community stability in

mutualistic networks with empirical structure. Weak interaction strength has been

widely accepted as a potential mechanism for maintaining diversity and stability

(Berlow, 1999, Neutel *et al.*, 2002). In recent decades, nestedness (i.e., specialists

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75   interact with proper subsets of the species interaction of generalists) and modularity

76   (i.e., compartmentation of species interactions) have been identified as common

77   architectures in ecological networks and could promote stability (Bascompte &

78   Jordano, 2007, Bascompte *et al.*, 2003, Bascompte *et al.*, 2006, Gilarranz *et al.*, 2017,

79   Olesen *et al.*, 2007, Rohr *et al.*, 2014). Besides above ones, other metrics have been

80   and may continue to be investigated, such as mixture of interaction types (Allesina &

81   Tang, 2012, Mougi & Kondoh, 2012), omnivory (McCann & Hastings, 1997) and

82   non-monotonicity (Yan & Zhang, 2014). Therefore, network metrics could be used to

83   test how human disturbance affects structure and stability of natural communities.

84   Seed-rodent networks are an important interaction network type in forest

85   ecosystems, and they play an important role in the maintenance of biodiversity and

86   ecosystem services (Thayer & Vander Wall, 2005, Zhang *et al.*, 2016a). In nature, a

87   majority of plant seeds are finally consumed by rodents, but a small proportion of

88   them survive from predation by rodents and develop into seedlings (Vander Wall,

89   2010). Consequently, interactions between tree seeds and rodents vary between being

90   predatory and mutualistic (Garzon-Lopez *et al.*, 2015, Theimer, 2005, Xiao & Zhang,

91   2016, Zhang *et al.*, 2016b). Both the abundance and functional traits of rodents and

92   seed species are key factors in the formation of mutualistic and predatory interactions

93   between seeds and rodents (Garzon-Lopez *et al.*, 2015, Wang *et al.*, 2014, Zhang *et al.*,

94   2015). Previous studies have evaluated specific seed-rodent interactions in

95   semi-natural enclosures (Wang *et al.*, 2014, Zhang *et al.*, 2016b), but never in field

96   conditions because of a lack of methods for measuring seed-rodent interaction

97   strength. Therefore, little is known about the structure of natural seed-rodent

98   interaction networks and how they could be affected by human disturbances such as

99   forest deforestation and fragmentation.

Many studies have found that deforestation significantly affects species composition and abundance (Benchimol *et al.*, 2017, Brook *et al.*, 2003, Fisher & Wilkinson, 2005). Deforestation has been shown to decrease seed species richness and abundance by removing large trees (Benchimol *et al.*, 2017, Laurance, 1999). Deforestation or fragmentation also creates suitable open habitats for small rodents, increasing both species richness and abundance. Correspondingly, several studies found that rodent abundance increases with forest disturbance (Duntan & 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). 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 (Xiao *et al.*, 2013, Yi *et al.*, 2011). Optimal foraging theory and optimal diet selection theory describe potential mechanisms (Bolnick *et al.*, 2010, Emlen, 1966). Based on these theories, one may expect that in more disturbed or younger forest patches, seed-rodent interactions are stronger due to relatively low seed availability for rodents, so that the connectance of seed dispersal networks is higher with lower nestedness.

This study aimed to determine how forest succession and fragmentation affect seed-rodent interaction networks. Specifically we tested the following predictions: (1) Rodent species richness and abundance decrease with the size and age of forest patches; (2) interaction strength and connectance decrease, but nestedness increases with the size and age of forest patches; (3) interaction strength and connectance decrease, and nestedness increases with increase of seed availability. Our approach was to compare seed removal rates across 14 patches of subtropical forest in the

125 Dujiangyan region, Sichuan Province, southwest China, that differed in age and size.

126

127 **MATERIALS AND METHODS**

128 **Study site**

129   The study was performed in the deforested and fragmented subtropical evergreen

130 broad-leaf forest, located in the Dujiangyan region (altitude 600-1,000 m, 31°04′

131 N-31°05′ N, 103°42′ E -103°43′ E) of Sichuan Province, southwest China. It lies in

132 the transition zone between the Qinghai-Tibetan Plateau and the plains of Chengdu,

133 and is part of the mountains west of the Sichuan Basin. The climate is subtropical,

134 with a mean annual temperature of 15.2 °C, and annual precipitation of 1200-l800

135 mm. Peak precipitation occurs at the highest elevations within our site and declines

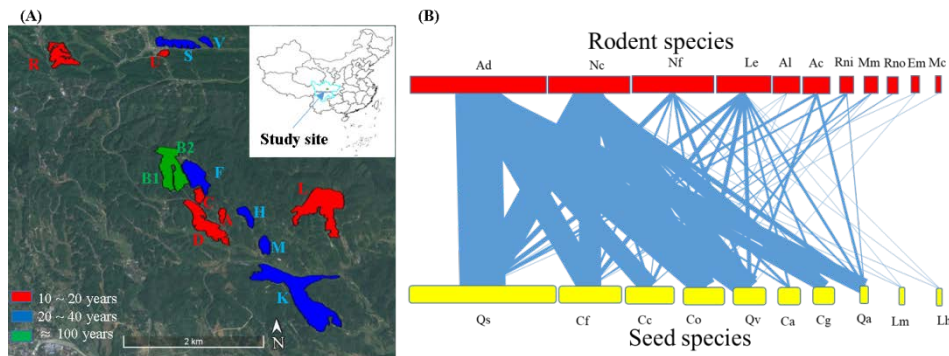136 with elevation. The Dujiangyan region is a hotspot of biodiversity in China.

137   Our study was conducted in 14 forest patches annually from 2014 to 2017. Most

138 of forest was cleared in the 1980s-2000s, and subsequently forest fragments of 2.0 to

139 58.0 ha were allowed to regrow on hilltops while flatter areas were maintained in

140 cultivation or became roads (Zhao *et al.*, 2016). These forest patches were classified

141 into three kinds based on stand ages, and also varied in patch sizes. Experiments were

142 conducted in 14 forest patches (labeled as A, B1, B2, C, D, F, H, K, L, M, R, S, U and

143 V; Fig. 1; Table 1). Forests in patch B1 and patch B2 are at least 100 years old, and we

144 refer to them as primitive, because of their age and protection from the nearby

145 Banruosi Temple. The other forest patches have undergone extensive logging and

146 destruction in the 1980s-2000s and represent early or middle succession stages. The

147 stand age was categorized into early, middle and primitive forests because the

148 accurate year of deforestation was unknown (Table 1).

149

Table 1. The 14 experimental patches in the Banruosi Experiment Forest in the
Dujiangyan region of Sichuan province, China. The capital letters indicate plot codes.

Stand ages (year)	Patch sizes (ha.)					
Early stands (10 ~ 20 years old)	D(22.99)	L(41.89)	R(20.23)	C(4.20)	A(2.68)	U(2.85)
Middle stands (20 ~ 40 years old)	F(17.63)	K(57.51)	S(16.18)	M(5.23)	H(6.05)	V(3.75)
Primitive stands (≈ 100 years old)	B1(40.12)	B2(45.34)				

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 width 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. Abbreviation of rodent species:
Ad-*Apodemus draco*, Nc-*Niviventer confucianus*, Nf-*N. fulvescens*, Le-*Leopoldamys
edwardsi*, Al-*A. latronum*, Ac-*A. chevrieri*, Rni-*Rattus nitidus*, Mm-*Micromys
minutus*, Rno-*R. norvegicus*, Em-*Eothenomys melanogaster* and Mc-*Musmus culus*,
respectively. Abbreviation of seed species: Qs-*Quercus serrata*, Cf- *Castanopsis
fargesii*, Cc-*C. ceratacantha*, Co-*Camellia oleifera*, Qv-*Q. variabilis*,
Ca-*Choerospondias axillaris*, Cg-*Cyclobalanopsis glauca*, Qa-*Q. acutissima*,
Lm-*Lithocarpus megalophyllus* and Lh-*L. hancei*, respectively.

In the study site, the common tree species include *Lithocarpus hancei*, *Quercus
acutissima*, *Q. serrata*, *Q. variabilis*, *Cyclobalanopsis glauca*, *L. megalophyllus*,

168   *Choerospondias axillaris*, *Castanopsis fargesii*, *C. ceratacantha* and *Camellia*

169   *oleifera*. We recorded 11 sympatric rodent species in this region, including South

170   China field mice (*Apodemus draco*), Chevrier's field mice (*A. chevrieri*), Sichuan

171   field mice (*A. latronum*), Edward's long-tailed rats (*Leopoldamys edwardsi*), Chestnut

172   rats (*Niviventer fulvescens*), Chinese white-bellied rats (*N. confucianus*), Norway rats

173   (*Rattus norvegicus*), Himalayan rats (*R. nitidus*), Pere David's vole (*Eothenomys*

174   *melanogaster*), Harvest mice (*Micromys minutus*) and House mouse (*Musmus culus*)

175   (Xiao *et al.*, 2013). These rodent species either feed on tree seeds such as nuts and

176   acorns or hoard them. Thus, rodent seed dispersers potentially play a significant role

177   in forest seed regeneration as seed dispersers. All recorded rodent species are

178   nocturnal.

179

180   **Sampling design**

181   *Seeds*

182   Seed fall was measured using seed traps made of Vinylon (New Agricultural Net

183   Factory, Dujiangyan, China, mesh size =2 mm) (Zhang *et al.*, 2016b, Zhao *et al.*,

184   2016). Each trap sampled a square 1×1 m area (Fig. S1A). In late August 2014, we

185   set up 178 traps suspended 0.8-m above the ground using bamboo or trunk posts to

186   prevent access by terrestrial vertebrates. To allow for differences in patch sizes, 3-7

187   seed traps were placed in a plot, in 2 or 4 sampling lines with a spacing of 10 m

188   between adjacent traps. In each year, we collected fallen seeds every 2 weeks from

189   early September to late December when seeds became mature. Seed rain from each

190   seed trap was put separately into an envelope and marked with a unique code. Seeds

191   were transported back to the lab and oven-dried (Xinkangyida Technology

192   Development Co. Ltd, model DH-101-3BS, Beijing, China) at 60°C for 12 hours.

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193   After drying, seeds were weighed, counted, identified to species, and any insect

194   infection noted. During the peak period of seed rain, fresh and intact seeds of each

195   species were collected for use in seed-dispersal experiments.

196   *Rodents*

197   We used wire live traps (30 × 13 × 12 cm), baited with fresh chestnuts to trap

198   small rodents (Zhao *et al.*, 2016). We placed them into 4×10 grids with intervals of 10

199   m in each plot (Fig. S1B) for five consecutive nights during October to November

200   each year. Traps were placed at 15:00 - 17:00 hours in the afternoon and were checked

201   at 7:00 - 9:00 hours the next morning. All captured animals were weighed and

202   identified to species, sex and reproductive status (females pregnant, lactating or not;

203   males with testes descended or not). Individuals were also marked with unique and

204   distinguishable patterns on their back with wine-red human hair dye (Gu *et al.*, 2017)

205   and then released *in situ*. Color labeling was used for mark-recapture analysis of

206   abundance and to identify individuals on infrared cameras and determine if they ate or

207   removed seeds at the seed stations (Gu *et al.*, 2017, Zhao *et al.*, 2016). Procedures for

208   capturing and raising animals were in accordance with the regulations of the Institute

209   of Zoology, Chinese Academy of Sciences.

210

211   **Seed-rodent interactions**

212   Seed removal trials were carried out from August 2014 to April 2017 in the

213   Banruosi Experimental Forest and its periphery (700–1000 m ASL, 31°04′ N, 103°43′

214   E) in the Dujiangyan region. We used infrared (IR) cameras to monitor large and

215   medium-sized rodent species, and measuring seed caching and pilferage(Jansen *et al.*,

216   2002). We applied a modified seed tagging method (Forget, 1990, Xiao *et al.*, 2006,

217   Zhang & Wang, 2001) and IR cameras to track the removal and fate of individual

9

218 seeds by rodents and thus measure the interaction strength between rodents and tree

219 seeds, as follows (also see: Zhao et al. 2016, Gu et al. 2017). We selected seeds of 10

220 common tree species: *L. hancei*, *Q. acutissima*, *Q. serrata*, *Q. variabilis*, *C. glauca*, *L.*

221 *megalophyllus*, *C. axillaris*, *C. fargesii*, *C. ceratacantha*, and *C. oleifera*. The seed

222 rain periods of these tree seeds generally overlapped, with only minor variation in

223 peak time (Zhao *et al.*, 2016). During the time when various seeds were mature, fresh

224 and intact seeds were collected from the ground or trees outside of the experimental

225 patches, and air dried in a cool place.

226 　　We labeled seeds using the tagging methods of Zhao *et al.* (2016). A 0.5-mm

227 diameter hole was drilled through the husk near the germinal disc of each seed.

228 Though the cotyledons were partly damaged (except for *L. hancei* nuts), the embryo

229 remained intact and was capable of germinating. A small, light white plastic tag (3.6

230 × 2.5 cm, < 0.1 g) with different shapes was tied through the hole using a thin steel

231 wire 10 cm long (Figs S1C, D). Each weighed seed was given a unique code by

232 writing on the tag using a fine point metal-pen. When rodents buried the seeds in the

233 soil, the plastic-tags were often left on the surface, making them easy visually

234 relocate.

235 　　In November or December of 2014, 2015 and 2016, three seed stations 30-m apart

236 were haphazardly established in each stand. Depending on the availability of seed

237 species in each patch, 2-8 seed species were placed at a single station, and each

238 species including 10 tagged seeds with unique codes reflected in different tag shapes,

239 spaced evenly on the soil surface within 1-2 m^2 (Fig. S1C, D). IR camera traps (Ltl

240 -5210A, Zhuihai Ltl Acorn Electronics Co., Ltd, Zhuihai, China) were tied to a tree

241 adjacent to each seed station (0.4-0.7 m high) and set on video record mode (Video

242 Size: 640 ×480；PIR sensitivity: High; Video Length: 20 s; Trigger Interval: 0 s) to

243 monitor seeds removed or eaten by small rodents (Fig. S1E, F). The day following

244 seed release, we checked the tagged seeds at each station to record seeds as being

245 removed or eaten. We then replaced the camera memory card, removed all remaining

246 seeds, and released new seeds for another round. This was replicated for three

247 consecutive days. Thus, we released 90 seeds per tree species per forest patch in each

248 of 3 years, and 13,830 seeds in total. We randomly searched a 25-m radius around

249 each station with equal effort (2-3 hours by two people for each plot visit), and record

250 the fate of the tagged seeds or whether seeds were missing with unknown fate. In the

251 lab, we systematically analyzed the video recordings (all capacity 537.3 gigabytes)

252 and identified rodent and seed species for each interaction.

253

254 **Data analysis**

255 *Measures of seeds and rodents*

256 Species richness of seeds (SR) was measured as the number of species observed in

257 each forest patch. Seed density (D) (m^{-2}) was calculates as the Total number of seeds

258 collected (No.) divided by the Total area of seed collector (m^2). Seed abundance (SA)

259 was measured as the total number of seeds produced by a patch. Metabolic seed

260 abundance (estimated by the seed calorific value per seed individual, MSA) was

261 calculated as: $MSA = (\sum_{i=1}^{s} n_i CV_i)/S$, where S = the number of seed species; n_i= the

262 number of a given seed species i; CV_i = the average seed calorific value of a given tree

263 species i.

264 Species richness of rodents (RR) was measured by number of species observed in

265 each forest patch. Rodent abundance (RA) was estimated using the minimum number

266 alive (MNA) by the live trapping method described above for each plot and year.

267 Metabolic rodent abundance (the sum of metabolic-scaling body mass from each

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268   rodent species each year, MRA) was calculated as: $MRA = \sum_{i=1}^{S} n_i BM_i^{0.75}$, where $S =$

269   the number of rodent species; $n_i=$ the population size (here MNA) of a given rodent

270   species i; $BM_i^{0.75}$ = the average metabolic-scaling body mass of a given species i. Per

271   capita seed availability (PCSA): PCSA=SA/RA. Metabolic per capita seed availability

272   (MPCSA): MPCSA= MSA/MRA (Xiao *et al.*, 2013).

273   *Network measures*

274   Among various network measures, we only considered several measures that are

275   mostly related to structure and interaction strength of seed-rodent interactions in this

276   study. Optimal diet theory predicts food availability can induce diet expansion or

277   shifting, thus we chose connectance and links per species as the first set of network

278   metrics to quantify the probability of interactions in each seed-rodent network. Changes

279   in connectance and links per species should reflect the degradation or restoration of

280   seed predation and dispersal function in forests. Connectance was measured by the

281   proportion of realized links in a network, and the number of links per species was

282   measured by the mean number of interaction links per species (Dunne *et al.*, 2002). The

283   second set of network metrics quantifies nested architecture including nestedness and

284   weighted nestedness. The latter takes into account the weight of the interaction strength

285   (Galeano *et al.*, 2009). They were chosen because they are related to network stability

286   (Bascompte *et al.*, 2003, Burgos *et al.*, 2007) and also reflect the structure of

287   seed-rodent interactions as rodents, as generalists, might shift their diets as species

288   composition changes. The last network metric is interaction strength (IS) between seed

289   and rodent species, which is a direct measure of seed dispersal and predation by rodents,

290   calculated as IS = overall number of seeds eaten and removed by rodents divided by the

291   total number of tagged seeds released ×100% (Vazquez *et al.*, 2005). The *bipartite*

292   package was used for calculation of network measures in the R 3.3 program (R

12

293   Development Core Team, 2014).

294   *Statistical analysis*

295   To identify the associations of post-deforestation succession and fragmentation with

296   seed-rodent interactions, we used linear mixed models to test: (1) The degree to which

297   stand age and patch size explained variation in the different species indices of seeds and

298   rodents (SR, SA, MSA, RR, RA, MRA, PCSA or MPCSA) across the 14 patches, with

299   year as a random variable. (2) The degree to which stand age and patch size explained

300   variation in the different network metrics (connectance, links per species, nestedness,

301   weighted nestedness and interaction strength), with year as a random variable. (3) The

302   degree to which species indices explained variation in network metrics, with year as a

303   random variable. The response variables were log-transformed to meet assumptions of

304   the statistical models if necessary. All linear mixed models were performed by *lme4*

305   and *lmerTest* in the R 3.3 program (R Development Core Team, 2014). We were not

306   able to do standard structural equation modeling analysis from stand age to network

307   metrics via abundance/richness of rodents/seeds because stand age of forest patches

308   was not a continuous variable.

309

310   **RESULTS**

311   **Forest stand age, size and species richness/abundance**

312   Rodent species richness ranged from 1 to 6 species, and rodent abundance ranged 3

313   to 19 individuals across the 14 forest patches. Rodent species richness ($F_{2, 33} = 9.97$, *P*

314   < 0.001), and rodent abundance ($F_{2, 33} = 9.77$, *P* < 0.001) or MRA ($F_{2, 33} = 4.59$, *P*

315   =0.017; Fig. 2; Table S1) significantly decreased with stand age. Seed species richness

316   ranged from 1 to 7 species, and seed abundance ranged 0.72 to 63.88 seeds across the

317   14 forests. Stand age had a significant positive association with seed species richness

13

318   ($F_{2, 33}$=18.25, $P < 0.001$), but no significant association with seed abundance ($F_{2, 31}$

319   =0.81, $P = 0.452$) or MSA ($F_{2, 31} = 1.97$, $P =0.157$; Fig. 2; Table S1). Stand age had a

320   significant positive association with PCSA ($F_{2, 31}$=3.91, $P = 0.031$) and MPCSA ($F_{2, 31}$

321   =7.33, $P =0.002$; Table S1). Patch size had no significant association with species

322   richness or abundance of either rodent or seed species (all $P >0.05$).
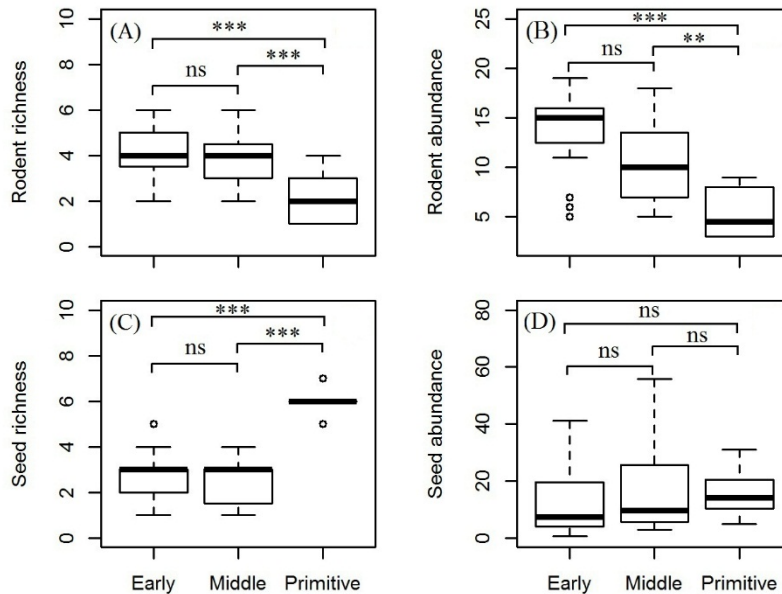
323

324   Fig. 2. Relationship between stand age and species richness and abundance of rodents

325   (A, B) and seed richness and abundance (C, D). *, **, *** indicate $P < 0.05$, 0.01,

326   0.001, respectively, and ns indicates non-significant effect ($P > 0.05$). The bottom and

327   top limits of each box are the lower and upper quartiles, respectively; the horizontal

328   black band within each box is the median; and error bars equal ± 1.5 times the

329   interquartile range.

330

331   **Forest stand age, size and network metrics**

332   Connectedness ranged from 0.44 to 1, interaction strength ranged 0.07 to 1, and

333   nestedness ranged 0 to 35.32 across the 14 forest patches. Stand age had significant

334   negative associations with connectance ($F_{2, 31}$=3.93, $P = 0.030$) and interaction

14

335 strength ($F_{2, 31}$=3.82, P = 0.033; Fig. 3 and 4; Table S1). Stand age had a significant

336 positive associations with nestedness ($F_{2, 22}$=8.05, P = 0.002; Fig. 3C and 4; Table S1).

337 There were no significant associations of stand age on links per species or weighted

338 nestedness (all P > 0.05; Table S1). Patch size had no significant associations with

339 any network metric examined (all P >0.05; Table S1).
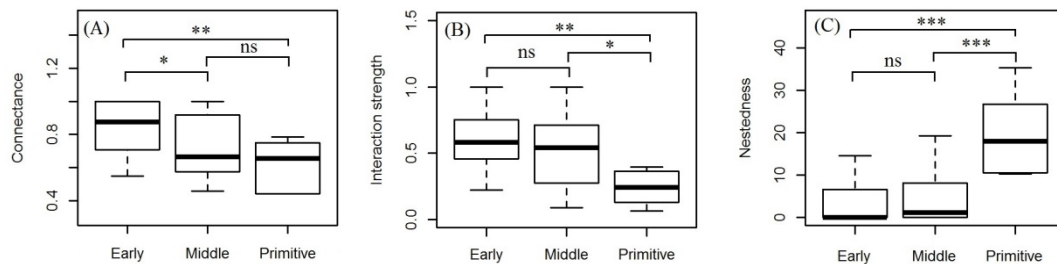
340

341 Fig. 3. Relationship between stand age and network metrics. *, **, *** indicate $P <$

342 0.05, 0.01, 0.001, respectively, and ns indicates non-significant effect (P > 0.05). The

343 bottom and top limits of each box are the lower and upper quartiles, respectively; the

344 horizontal black band within each box is the median; and error bars equal ±1.5 times

345 the interquartile range.

346

347 **Species abundance/richness and network metrics**

348 Rodent abundance showed significant positive associations with connectance

349 (t=2.158, P =0.039) and interaction strength (t=2.430, P =0.021), and a significant

350 negative association with nestedness (t= -2.251, P =0.035; Fig. 4; Table S2). MRA

351 had a significant positive association with interaction strength (t=2.403, P =0.022; Fig.

352 4; Table S2).

353 Seed richness had a significant positive association with nestedness (t=3.033, P

354 =0.006) (Fig. 4; Table S2). MSA showed significant positive associations with

355 weighted nestedness (t=4.408, P <0.001) and a significant negative association with

356 connectance (t= -3.274, P =0.002; Fig. 4; Table S2). PCSA had no significant

15

357   associations on network metrics examined (all P >0.05; Fig. 4; Table S2). MPCSA

358   had significant negative associations with connectance (t=-2.282, P =0.039) and

359   interaction strength (t= -2.361, P =0.024; Fig. 4; Table S2).
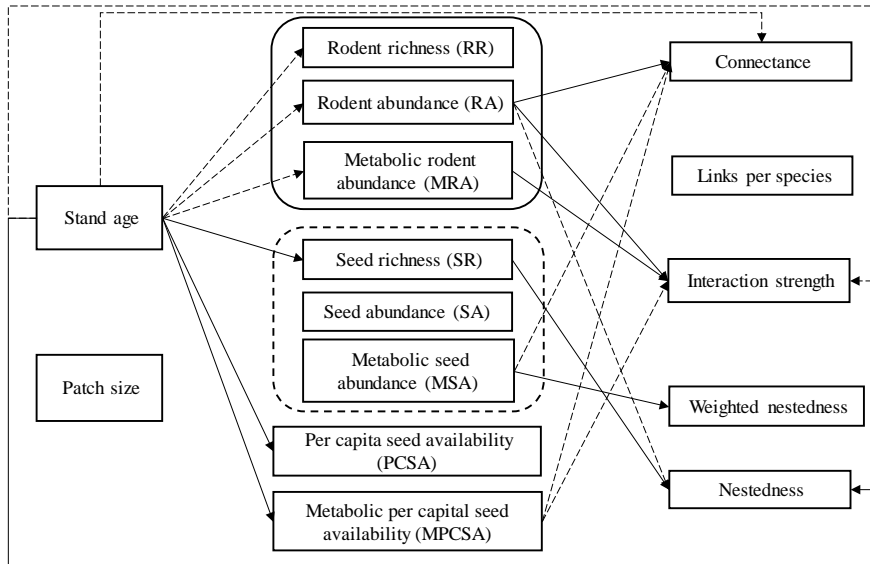
360

361   Fig. 4. Relationship of stand age and patch size with network metrics via species

362   indices of rodents and seeds. Solid black lines represent significant positive

363   associations, and dotted black lines represent significant negative associations. Solid

364   line box represent rodent species indices, and dotted line box represent seed species

365   indices. PCSA= SA/ RA; MPCSA= MSA/ MRA.

366

367   **DISCUSSION**

368   Deforestation or fragmentation can cause substantial change in species composition

369   and abundance of forests (Brook *et al.*, 2003, Duntan & Fox, 1996, Fahrig, 2003).

370   However, the consequences of such changes for interaction networks in ecosystems

371   and communities are largely unknown. By using a combination of seed tagging and

372   IR camera tracking, we were able to measure the interaction strength between seeds

373   and rodents, and therefore, to quantify the impacts of human deforestation on the

374   mutualistic relationship between plants and their seed dispersers.

16

375   We found that tree seed-rodent network metrics changed significantly with stand

376   age (regrowth time since deforestation), but not with fragment patch size. In younger

377   forest patches, interaction strength was stronger and nestedness was lower than in

378   either older patches or primitive stands. These results suggest changes in network

379   structure were mediated by changes in seed and rodent species richness and

380   abundance, generally supporting the idea that seed availability to rodents changes the

381   structure of seed-rodent networks. Because network metrics are important indicators

382   for diversity and stability of ecosystems, the network architecture favoring stability

383   fundamentally differs between trophic and mutualistic networks (Thebault & Fontaine,

384   2010). Our results provide new insights into the relationship between diversity and

385   stability in forest ecosystems, and have implications for restoring degraded

386   ecosystems.

387   Several previous studies indicated that species richness and diversity of small

388   mammals were higher in young stands than old growth areas (Duntan & Fox, 1996,

389   Sullivan *et al.*, 2000). This might be because deforestation creates open habitats with

390   more grass seeds that benefit small rodents (Fisher & Wilkinson, 2005). Our results

391   are generally consistent with these observations. We found in younger stands, rodent

392   species richness and abundance (or metabolic rodent abundance) were higher, but

393   seed species (or tree species) richness and abundance were lower (Fig. 2, 4; Table S3),

394   supporting our Prediction 1. In our study region, deforestation mainly happened in

395   1980s-1990s, and many large trees like *Q. variabilis*, *C. fargesii* and *Cerasus*

396   *pseudocerasus* were cut. In young stands, *Q.serrata* was the dominant tree species.

397   With forest protection during the last three decades, the forest composition has begun

398   to recover. Bird species are also an important component of the plant-animal

399   interaction network (Gleditsch & Carlo, 2011). In our study site, few bird species (e.g.

17

400 *Garrulus glandarius*) were found to disperse seeds, and only in some patches (Zhao *et*

401 *al.*, 2016). Because of the sparsity of bird-seed interactions, we did not analyze them

402 further.

403   Human disturbance may impact species interactions involved in seed dispersal in a

404 variety of ways. For example, Wright and Duber (2001) reported that poachers and

405 habitat fragmentation indirectly altered the spatial pattern of seed dispersal, seed

406 predation, and seedling recruitment in the palm *Attalea butyraceae* in central Panama

407 when humans disrupted mammal communities. Aguilar *et al.* (2006) found a large and

408 negative effect of fragmentation on pollination and plant reproduction. Spotswood *et*

409 *al.* (2012) demonstrated that the presence of invasive fruit-bearing plants and

410 introduced frugivores altered seed dispersal networks, and found that the patterns of

411 alteration depended on both the frugivore community and the relative abundance of

412 available fruit. In plant-herbivore and host-parasitoid food webs, network structure

413 was altered by habitat fragmentation, with different metrics such as connectance,

414 vulunerablity and generality being affected depending on interaction type (Valladares

415 *et al.*, 2012). However, the effects of human activities such as deforestation on

416 seed-rodent interaction networks are poorly understood (Zhao *et al.*, 2016). We found

417 that the interaction strength and connectance were larger but nestedness was smaller

418 in younger stands, as compared older stands, supporting our Prediction 2. Our results

419 suggest that forest succession after deforestation would increase ecosystem stability

420 according to the previous studies that nestedness (Bascompte *et al.*, 2003, Bascompte

421 *et al.*, 2006, Pawar, 2014, Rohr *et al.*, 2014) and weak interactions (Berlow, 1999,

422 Neutel *et al.*, 2002) enhanced the stability of networks.

423   Habitat fragmentation has been reported to affect species interactions and then

424 network structure (Fahrig, 2003). The components of fragmentation generally include

18

425   changes in fragment size, isolation, edge effects and habitat degradation (Fahrig, 2003,

426   Magrach *et al.*, 2014). Recent studies suggest that mutualisms, such as pollination and

427   seed dispersal, were more sensitive to the negative effects of forest fragmentation than

428   antagonisms, such as predation or herbivory (Aguilar *et al.*, 2006). Applying

429   meta-analytical techniques, Magrach *et al.* (2014) demonstrated that the effects of

430   fragmentation on mutualisms were primarily driven by habitat degradation, edge

431   effects, and fragment isolation, with little effect of fragment size. Dattilo *et al.* (2015)

432   found that fragment size did not affect the topological structure of the

433   individual-based palm-pollinator network. However, Aguirre and Dirzo (2008)

434   reported pollinator abundance was negatively affected by fragment size. In our study,

435   we did not find significant effects of fragment size on the species richness and

436   abundance or network metrics. This was likely because isolation had little effect for

437   rodents and seeds. In our study area, the fragmented forests were isolated by the small

438   and narrow farmlands or roads in the valleys. Small rodents can easily move across

439   these farmlands, and dispersing seeds among patches.

440   Most mutualistic networks may be shaped by differences in species abundance

441   among interacting species (Vazquez *et al.*, 2005, Verdu & Valiente-Banuet, 2011). For

442   example, Dattilo *et al.* (2014) showed that the difference in abundance among ants on

443   vegetation partially explained the network structure of mutualistic interactions and

444   that the difference was independent of ant species compositions: abundant ant species

445   generally interacted with more plant species. Gleditsch and Carlo (2011) suggested

446   that bird abundance showed a strong positive association with *Lonicera* fruits.

447   Consequently, the changes of animal and plant abundance were important factors in

448   determining the plant-animal interaction network structure. For seeds and rodents,

449   interaction strength may be affected by many factors, such as seed abundance, rodent

19

450 abundance, or seed availability (Schleuning *et al.*, 2011, Xiao *et al.*, 2013). Our study

451 demonstrated that rodent abundance had significant positive associations with both

452 connectance and interaction strength, but a significant negative association with

453 nestedness. Our study also showed that metabolic rodent abundance (MRA) had a

454 significant positive association with interaction strength, metabolic seed abundance

455 (MSA) had a significant negative association with connectance, and metabolic per

456 capita seed availability (MPCSA) had significant negative association with

457 connectance and interaction strength (Fig. 4; Table S2). These observations also

458 supported the predictions of optimal foraging theory and optimal diet selection theory

459 that interaction degree or diet breadth would increase because of stronger competition

460 for food resources with fewer seed resources or more predators (Araujo *et al.*, 2008,

461 Bolnick *et al.*, 2010, Emlen, 1966).

462   Several studies quantitatively assessed interaction strength between tree seed

463 species and rodent species by using semi-natural enclosures, and found functional

464 traits of seeds and rodents played a significant role in the formation of mutualism and

465 predation of the seed-rodent dispersal system (Wang *et al.*, 2014, Zhang *et al.*, 2015).

466 Zhang *et al.* (2015) found under enclosure conditions, large-sized rodents have

467 mutualistic or predatory interactions with both large- and small-sized seed species, but

468 small-sized rodents interacted with only small seed species. Zhang *et al.* (2016b)

469 provided evidence that the seed fates caused by hoarding behavior of rodents were

470 largely determined by trade-off-related seed traits (nutritional traits, coat thickness

471 and tannin content) and rodent body mass, and not by the phylogenetic relations of

472 species. In this study, we did not focus on the effects of functional traits, but we did

473 find similar results. For example, we showed that *A. draco* (abundant, small-sized

474 rodents) had more links with tree species such as *Q. serrata* (abundant, thin-coated

seeds), *C. fargesii* (small seeds with thin seed coat, low tannin content), but less links

with trees like *C. axillaris* (thick seed coat). *N. fulvescens* and *N. confucianus* (large

rodents) had more links with *Q. serrata*, *Q. serrata* (large seeds, high caloric value

per seed but high tannin content) and *C. oleifera* (small seeds, high caloric value per

seed and low tannin content) (X. F. Yang. unpubl. data). Rodents usually have

generalized diet, and could establish links with dozens of plant seed species. On the

other hand, a seed could also have links with various rodent species.

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 (Gu *et al.*, 2017, Jansen *et

al.*, 2012, Zhao *et al.*, 2016). One reason is that it is difficult to identify the

seed-rodent interactions at an individual or 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 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

small rodents.

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705 SUPPORTING INFORMATION

706 Additional Supporting Information may be found in the online version of this article:

707

708 **Table S1**. Statistical results from linear mixed models for species richness and

709 abundance and network metrics.

710

711 **Table S2**. Statistical results from linear mixed models for species indices of seeds and

712 rodents and network metrics.

713

714 **Table S3.** Relationships between species richness and abundance of seed and tree.

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716 Fig. S1. Illustrations of seed traps, infrared (IR) camera and seed tagging method for

717 measuring seed-rodent interaction strength.

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SUPPORTING INFORMATION

727 Table S1. Statistical results from linear mixed models for species richness and

728 abundance and network metrics: the model used stand age and patch size as fixed

729 factors, and year as a random factor. MRA, metabolic rodent abundance; MSA,

730 metabolic seed abundance; PCSA, per capita seed availability (PCSA= seed

731 abundance/ rodent abundance); MPCSA, metabolic per capita seed availability

732 (MPCSA= MSA/MRA). Fixed factors in bold indicate significant differences ($P <$

733 0.05).The datum of tree richness and abundance come from Zhao *et al*. (2016).

Items	Stand age			Patch size		
	d.f	*F*	*P*	d.f.	*F*	*P*
Species indices						
Rodent richness	**2, 33**	**9.97**	**<0.001**	1, 33	3.54	0.069
Rodent abundance	**2, 33**	**9.77**	**<0.001**	1, 33	1.92	0.175
MRA	**2, 33**	**4.59**	**0.017**	1, 33	1.74	0.196
Seed richness	**2, 33**	**18.25**	**<0.001**	1, 33	0.25	0.619
Seed abundance	2, 31	0.81	0.452	1, 31	2.25	0.144
MSA	2, 31	1.97	0.157	1, 31	1.56	0.221
PCSA	**2, 31**	**3.91**	**0.031**	1, 31	2.41	0.130
MPCSA	**2, 31**	**7.33**	**0.002**	1, 31	0.84	0.367
Tree richness	**2, 33**	**11.4**	**<0.001**	1, 33	0.63	0.432
Tree abundance	**2, 33**	**46.44**	**<0.001**	1, 33	3.04	0.090
Network metrics						
Connectance	**2, 31**	**3.93**	**0.030**	1, 31	0.66	0.424
Links per species	2, 31	0.03	0.974	1, 31	2.88	0.099
Nestedness	**2, 22**	**8.05**	**0.002**	1, 22	0.11	0.747
Weighted nestedness	2, 31	0.13	0.874	1, 31	0.74	0.393
Interaction strength	**2, 31**	**3.82**	**0.033**	1, 31	0.41	0.529

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737 Table S2. Statistical results from linear mixed models for species indices of seeds and

738 rodents and network metrics. First models used species indices of rodent richness,

739 rodent abundance, seed richness and seed abundance as fixed factors and year as a

740 random factor; second model used per capita seed availability (PCSA= seed

741 abundance/ rodent abundance) as a fixed factor and year as a random factor; third

742 model used metabolic rodent abundance (MRA) and metabolic seed abundance (MSA)

743 as fixed factors and year as a random factor; and the last model used metabolic per

744 capita seed availability (MPCSA= MSA/MRA) as a fixed factor and year as a random

745 factor. Fixed factors in bold indicate significant differences ($P < 0.05$).

Fixed factors	Estimate± SD	df	t	P
Connectance				
Rodent richness	-0.204±0.112	32	-1.814	0.079
Rodent abundance	**0.189±0.087**	**31**	**2.158**	**0.039**
Seed richness	-0.054±0.057	30	-0.950	0.350
Seed abundance	-0.058±0.030	32	-1.966	0.058
PCSA	-0.018±0.012	35	-1.467	0.151
MRA	0.076±0.043	33	1.781	0.084
MSA	**-0.271±0.083**	**33**	**-3.274**	**0.002**
MPCSA	**-0.101±0.044**	**35**	**-2.282**	**0.039**
Links per species				
Rodent richness	-0.163±0.227	31	-0.717	0.479
Rodent abundance	0.049±0.176	30	0.277	0.784
Seed richness	0.008±0.114	30	0.071	0.944
Seed abundance	0.099±0.061	31	1.629	0.113

PCSA	0.041±0.023	34	1.789	0.083
MRA	-0.078±0.094	32	-0.829	0.413
MSA	0.132±0.186	33	0.708	0.484
MPCSA	0.083±0.090	34	0.917	0.366
Nestedness				
Rodent richness	7.381±6.651	21	1.110	0.280
Rodent abundance	**-1.135±0.504**	**21**	**-2.251**	**0.035**
Seed richness	**3.157±1.041**	**21**	**3.033**	**0.006**
Seed abundance	1.515±1.816	21	0.835	0.413
PCSA	0.368±0.678	24	0.543	0.592
MRA	-5.238±2.614	23	-2.003	0.057
MSA	-1.731±7.272	23	-0.238	0.814
MPCSA	5.007±2.603	24	1.924	0.066
Interaction strength				
Rodent richness	-0.182±0.151	31	-1.207	0.237
Rodent abundance	**0.284±0.117**	**31**	**2.430**	**0.021**
Seed richness	-0.108±0.076	30	-1.421	0.166
Seed abundance	-0.015±0.040	31	-0.384	0.704
PCSA	-0.017±0.017	34	-1.007	0.321
MRA	**0.151±0.163**	**33**	**2.403**	**0.022**
MSA	-0.082±0.124	33	-0.655	0.517
MPCSA	**-0.144±0.061**	**34**	**-2.361**	**0.024**

Weighted nestedness				
Rodent richness	0.139±0.402	31	0.346	0.731
Rodent abundance	0.111±0.312	31	0.357	0.724
Seed richness	0.173±0.204	30	0.847	0.404
Seed abundance	0.115±0.107	32	1.080	0.288
PCSA	0.030±0.041	34	0.727	0.472
MRA	-0.022±0.130	33	-0.169	0.867
MSA	**1.123±0.255**	**34**	**4.408**	**<0.001**
MPCSA	0.143±0.156	34	0.915	0.367

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750 Table S3. Relationships between species richness (log-10 scale) and abundance

751 (log-10 scale) of seed and tree. *, **, *** indicate $P < 0.05, 0.01, 0.001$, respectively.

752 The data of tree richness and abundance was obtained from Zhao *et al*. (2016).
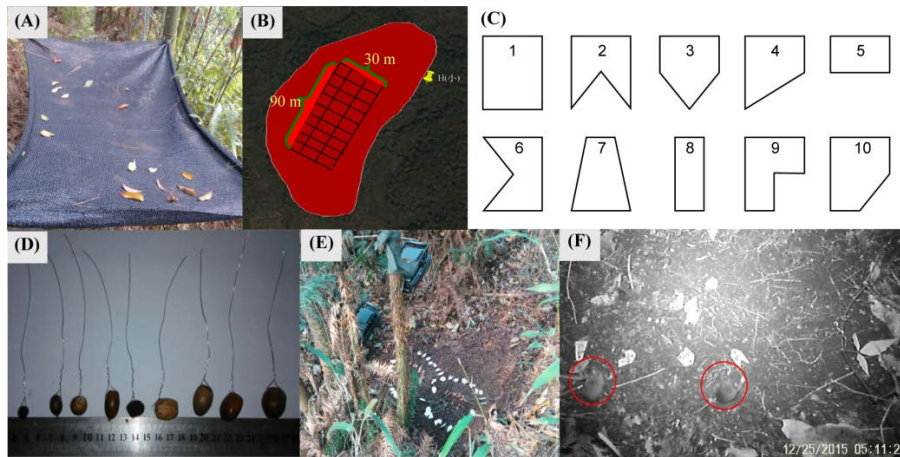
Items	Seed abundance	Tree richness	Tree abundance
Seed richness	-0.042	0.71***	0.42**
Seed abundance		0.13	0.36*
Tree richness			0.55***

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Fig. S1. 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.

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764 **Reference**

765 Zhao, Q., Gu, H., Yan, C., Cao, K. & Zhang, Z. (2016). Impact of forest fragmentation

766   on rodent-seed network. *Acta Theriologica Sinica*, 36, 15-23. (in Chinese with

767   English summary)

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