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

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A R T I C L E I N F O

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A B S T R A C T

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. 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 regrowth it is not clear which process will dominate in changing species composition. Fragmentation has also been reported to modify species interactions (Magrach 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; Magrach 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–l800 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. ceratacantha* 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