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Original article

Functional traits determine formation of mutualism and predation interactions in seed-rodent dispersal system of a subtropical forest

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ABSTRACT

Network structure in plant-animal systems has been widely investigated but the roles of functional traits of plants and animals in formation of mutualism and predation interactions and community structure are still not fully understood. In this study, we quantitatively assessed interaction strength of mutualism and predation between 5 tree species and 7 rodent species by using semi-natural enclosures in a subtropical forest in southwest China. Seeds with high handling-time and nutrition traits (for both rat and mouse species) or high tannin trait (for mouse species) show high mutualism but low predation with rodents; while seeds with low handling-time and low nutrition traits show high predation but low mutualism with rodents. Large-sized rat species are more linked to seeds with high handling-time and high nutrition traits, while small-sized mouse species are more connected with seeds with low handling-time, low nutrition value and high tannin traits. Anti-predation seed traits tend to increase chance of mutualism instead of reducing predation by rodents, suggesting formation of mutualism may be connected with that of predation. Our study demonstrates that seed and animal traits play significant roles in the formation of mutualism and predation and network structure of the seed-rodent dispersal system.

1. Introduction

Mutualism and predation interactions between animals and plants are essential in shaping community structure and the networks in animal–plant systems. Very few plant–animal interactions were found co-evolved between one plant species and one animal species (Herrera, 1985; Reid, 1991). Instead, seed and dispersers have been widely recognized as cases of diffuse co-evolution (Lapchin and Guillemaud, 2005; Vander Wall and Beck, 2012). Nearly all of these interactions appeared to involve combinations of numerous species (Hollander and Vander Wall, 2004). The feeding or hoarding behaviors of one animal species could affect formation of mutualism or predation with two or more plant species; meanwhile, seed trait of one plant species could also affect formation of interaction with many animal species (Smith, 1970; Benkman, 1995; Ben-Moshe et al., 2001; Forget and Vander Wall, 2001; Dunn et al., 2007; Lomascolo and Schaeferh, 2010). Unfortunately, studies based on multiple tree and rodent species are still lacking, and thus the roles of functional traits of plants and animals in formation of mutualism and predation interactions and community structure.

By acting as seed dispersal vectors, seed-eating animals (e.g., rodents) play an essential role in the reproductive cycle of their food plants (Smith and Reichman, 1984; Vander Wall, 1990; Herrera, 1995). Although rodents consume large proportions of seed crops of many plants, they also have important positive impacts on seedling establishment and plant regeneration by dispersing and caching seeds (Zhang et al., 2008; Cao et al., 2011; Carlo et al., 2011; Gutiérrez-Granados, 2011; Meng et al., 2012). Different hoarding behavior of rodents can often result in different outcomes in terms of seed dispersal and seedling success. Seed hoarders can consume many of the seeds they disperse whereby harvesting is largely equivalent to predation and detrimental to the plant species (Hulme, 2002; Mendoza and Dirzo, 2007; Gomez et al., 2008). At the same time, seed hoarder (especially scatter-hoarding animals) can provide effective dispersal because the behavior can reduce predation, desiccation and improve hydration, germination (Vander Wall, 2001; Schupp et al., 2010).

The seed items that animals hoard or eat are not randomly selected, and how an animal treats a particular type of seed

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Table 1
Seed traits of the 5 tree species used in experiments. Bold numbers show the largest or second largest values of the seed traits.

Seed species	Fresh weight[a]	Coat hardness[b]	Crude protein[c]	Crude fat[c]	Crude starch[c]	Tannin[c]	Caloric[c]
Lithocarpus harlandii	**4.56 ± 0.22**	**1.45 ± 0.04**	5.80	0.91	37.66	1.34	17.11
Quercus variabilis	**2.42 ± 0.11**	**0.61 ± 0.01**	5.92	3.94	54.17	**11.68**	17.63
Quercus serrata	0.97 ± 0.06	0.44 ± 0.01	6.07	3.02	54.01	**10.62**	17.29
Camellia oleifera	0.87 ± 0.07	0.39 ± 0.01	**10.91**	**51.79**	**11.74**	0.10	**29.56**
Castanopsis fargesii	0.46 ± 0.03	0.29 ± 0.01	4.90	1.22	67.65	0.24	17.03

[a] Mean ± S.E. g, $N = 60$.
[b] Mean ± S.E. mm, $N = 60$.
[c] Data of chemical compositions (i.e. crude protein, crude fat, crude starch and tannin (%)) of dry nutmeat were provided by the Center of Grain Quality of Ministry of Agriculture, China, and caloric value (J/g) of dry nutmeat was measured by Bomb Calorimetre (PARR 1281) in the Institute of Zoology, CAS.

depends on seed and animal traits. There are several hypotheses based on seed traits to predict behavioral response by rodents. First, the seed size hypothesis (or handling-time hypothesis) predicts that hoarding animals prefer to harvest and then hoard more large seeds over small ones (e.g., Jacobs, 1992; Jansen et al., 2002; Vander Wall, 2003; Theimer, 2003; Xiao et al., 2005a; Zhang et al., 2008; Chang et al., 2009; Wang and Chen, 2009). Beside, endocarp thickness of seeds is found to reduce seed consumption *in situ* and to increase seed hoarding by rodents (Zhang and Zhang, 2008); this observation can be explained by the handling-time hypothesis. Second, the high nutrition hypothesis predicts that hoarding animals prefer to hoard more seeds with high nutritional contents (e.g., Fat, Lewis, 1982; Smallwood and Peters, 1986; Izhaki, 2002). Third, the high tannin hypothesis predicts that hoarding animals prefer to hoard high-tannin seeds but eat low tannin acorns first (e.g., Smallwood and Peters, 1986; Steele et al., 1993; Smallwood et al., 2001; Xiao et al., 2008, 2009; Wang and Chen, 2008). Besides, animal traits (e.g., body size) also affect seed hoarding (e.g., Ben-Moshe et al., 2001). Considering the differences of strength in both body and jaws between large and small animals, large animals, as compared to small ones, should be more capable of consuming large seeds or seeds with hard seed coat when encountering predation risk (e.g., eating more seeds *in situ*); while by considering the energy intake needs, large animals should prefer to hoard high nutritional seeds as predicted by the optimal foraging hypothesis (Pyke, 1984). These seed or animal traits may be very important in formation of mutualism and predation interactions (and thus the network structure) among multiple plant and animal species, but such studies are still rare.

The purpose of this paper is to quantitatively assess interaction strength of mutualism and predation between 5 tree species and 7 rodent species in a subtropical forest of southwest China. We estimated the effects of independent and combined seed traits on hoarding behaviors of rodents by using semi-natural enclosures. The handling time hypothesis, high tannin hypothesis, high nutrition hypothesis and body-size structured hypothesis are tested to reveal the effects of functional traits on formation of mutualism and predation interactions. The interactions between rodents and seeds were reconstructed and analyzed using quantitative interaction strength data, and the roles of functional traits of seeds and rodents in formation of interactions were discussed. We hypothesize that convergent or divergent formation of mutualism and predation interactions should be closely linked to functional traits of plants and animals. We predict that seeds of a group of tree species sharing similar traits should be more closely linked to similar hoarding behaviors of a group of rodent species (convergent formation), while seeds of a group of tree species sharing different traits from other groups should be more closely linked to different hoarding behaviors of a group or other group of rodent species (divergent formation).

2. Materials and methods

2.1. Study site and study species

This study was conducted in an experimental forest in Dujiangyan, Sichuan province, China (700–1000 m a.s.l.; 31° 4′ N, 103° 43′ E) from September to December in 2005, 2006 and 2007. The area is characterized by subtropical evergreen broadleaf forest. In this forest, *Lithocarpus harlandii*, *Quercus variabilis*, *Quercus serrata*, *Castanopsis fargesii* and *Camellia oleifera* were the dominant tree species. The seed traits of these species are shown in Table 1. Correlation analysis indicated that seed fresh weight and seed coat hardness were positively correlated ($r = 0.976$, $n = 5$, $p = 0.04$); seed caloric value was positively associated with seed protein and fat content ($r = 0.986$, $n = 5$, $p = 0.002$, $r = 1.000$, $n = 5$, $p = 0.000$), while protein content was negatively associated with starch content ($r = -0.914$, $n = 5$, $p = 0.03$). Our previous and ongoing studies have shown that all these 5 species are largely dispersed by rodent species (Xiao et al., 2004, 2005a, 2005b, 2006; Xiao and Zhang, 2006; Cheng et al., 2005; Chang and Zhang, 2011). Based on Table 1, we define *Q. variabilis* as “high handling-time and high tannin seed”, *Q. serrata* as “high tannin seed”, *L. harlandii* as “high handling-time seed”, *C. oleifera* as “high nutritional seed”, *C. fargesii* as “low tannin, low nutrition and low handling-time seed”.

Several rodent species are commonly seen in this subtropical evergreen broadleaf forests, including Edward’s long-tailed rats (*Leopoldamys edwardsi*) (mean body weight, 386 ± 17 g), Chestnut rats (*Niviventer fulvescens*) (mean body weight, 70 ± 7 g), White-bellied rats (*N. confucianus*) (mean body weight, 87 ± 11 g), Himalayan rats (*Rattus nitidusa*) (mean body weight, 123 ± 15 g), Sichuan field mice (*Apodemus latronum*) (mean body weight, 44 ± 10 g), Chevrier’s field mice (*Apodemus chevrieri*) (mean body weight, 50 ± 5 g) and South China field mice (*Apodemus draco*) (mean body weight, 23 ± 2 g). *Leopoldamys edwardsi*, *R. nitidusa* are defined as large-sized rodent species; *Niviventer fulvescens* and *N. confucianus* are defined as medium-sized rodent species; *A. latronum*, *A. chevrieri* and *A. draco* are defined as small-sized rodent species. All large- or medium-sized rodents were categorized as rat species while small-sized rodent were categorized as mouse species.

To trap animals, we used large wired cage traps (30 cm × 25 cm × 20 cm) baited with peanuts (for food) and cabbage (for water) and provisioned with local dry leaves as nest material. The traps and nesting material protected rodents from cold weather and predators. From August to September of each study year, trapping was conducted at 10 plots in this study site. Forty traps were set 10 m apart along 2 transect lines in each plot and checked for 3 consecutive days. Traps were deployed at 19:00 to 19:30 and checked after 12 h (dense vegetation and steep landscape prevented us from checking traps during the night). All