Acta Oecologica 55 (2014) 43–50

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

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

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ARTICLE INFO

Article history:
Received 28 May 2013
Accepted 14 November 2013
Available online 12 December 2013

Keywords:
Plant–animal interaction
Network structure
Stability
Functional traits
Hoarding behavior
Mutualism/predation
Rodent
Seed

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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http://dx.doi.org/10.1016/j.actao.2013.11.004

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 fulves*cens) (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 fulves*cens 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 target animals in a non-reproductive state (reproductively active animals were released on site) were then transferred to our laboratory for housing. Prior to experimentation, all animals were housed individually in a large mouse cage (50 cm × 30 cm × 25 cm) containing nesting material. The housing room was maintained at 10–15 °C with a natural light/dark cycle (12L:12D) with food and water provided *ad libitum*. All experimental procedures on use and care of animals complied with regulations of the Institute of Zoology, Chinese Academy of Sciences.

We used four rat species and three mouse species, including 24 adult Edward's long-tailed rats (10 ♂, 14 ♀), 16 adult Chestnut rats (8 ♂, 8 ♀), 12 adult White-bellied rats (5 ♂, 7 ♀), 9 adult Himalayan rats (5 ♂, 4 ♀), 4 adult Sichuan field mice (3 ♂, 1 ♀), 5 adult Chevrier's field mice (4 ♂, 1 ♀) and 8 adult South China field mice (4 ♂, 4 ♀). Each individual of these 7 species was used only once for each experiment. By the end of the experiment (lasting for 2–3 months), all animals were released at the sites of capture. We used the relative dominance index (RDI) to represent the relative abundance of rodents:

$$\mathrm{RDI} = \frac{\text{Individual quantities of one species}}{\text{Total individual quantities of all species}}$$

2.2. Experimental design

We conducted all experiments in four 10 m × 10 m semi-natural enclosures (see Chang and Zhang, 2011 for detail). To habituate animals to the testing environment they were introduced into the enclosure one night prior to experiments. Each animal was presented with 10 seeds from each of the *Q. variabilis*, *Q. serrata*, *L. harlandii*, *C. oleifera* and *C. fargesii* species. Each experiment lasted one night from 17:30 to 07:30 for each subject. The following day, we searched the enclosure and recorded the fate of each seed after removing the animal. We labeled seeds with small coded plastic tags in order to find the seeds hoarded by animals quickly. This tagging has been shown to have a negligible effect on seed removal and hoarding (Xiao and Zhang, 2006).

Five categories of the seed fates were defined for seeds or their fragments with a small modification of the categories defined by Cheng et al. (2005): (1) remained *in situ* (RIS) – the seed remained at the release site untouched; (2) eaten *in situ* (EIS) – the seed was gnawed open with the entire kernel, or majority of, consumed at the release site; (3) eaten after removal (EAR) – the seed was gnawed open with the entire kernel, or majority of, consumed at the sites after removal; (4) scatter-hoarded (SH) – the seed was intact and buried in soil or grass; (5) larder-hoarded (LH) – the seed was intact and stored in the nest. These seed fates (seeds of each category/all released seeds %) were used to represent the quantitative interaction strength between seeds and rodents. Seeds that were removed from the station but left intact on the ground were not included in the analysis because of their low number. Because RIS contains effects of EIS, EAR, SH, and LH, it is not analyzed here for simplification. Scatter hoarding is defined as the mutualistic interaction because scatter-hoarded seeds benefit both rodents and plants, while eaten *in situ*, eaten after removal and Larder hoarding (EIS + EAR + LH) is defined as predation interaction because seeds with seed fates of eaten *in situ*, eaten after removal and Larder hoarding only benefit rodents.

2.3. Statistical analyses

All statistical analyses were performed using R version 2.12.0. To identify combined effects of seed traits, the Principal Components Analysis (PCA) was used to identify the principal seed traits. Spearman Correlations were used to test the relationships between seed traits and rodent species for each seed fate (in proportions). Hierarchical cluster analysis was used to identify potential substructures of the seed-rodent network by using average linkage method. All statistical tests were two tailed, and the alpha level was set at 0.05 and 0.01.

3. Results

3.1. Rodent abundances

In total, we captured 184 target animals during the 3-year experiment. Edward's long-tailed rats were the most abundant species and comprised nearly half of all captures (RDI = 0.467). Chestnut rats were the secondly abundant species (RDI = 0.217). The other 5 species were less abundant species (all RDI < 0.1).

3.2. Effects of independent seed traits

Eaten *in situ* are negatively correlated to fresh weight and coat hardness (3 rat species); but positively correlated to crude starch (3 rat species), tannin (1 mouse species), suggesting that high handling-time seeds (high fresh weight and coat hardness) are less eaten *in situ* by rat species, while low nutritional seeds (high crude starch) or high toxicant seeds (high tannin) are more likely eaten *in situ* by rat or mouse species (Table 2).

Eaten after removal are positively correlated to crude protein (2 rat species, 1 mouse species), crude fat (3 rat species), caloric (2 rat species), crude starch (1 mouse species) and tannin (2 mouse species); but negatively to fresh weight and coat hardness (1 rat species), crude starch (1 rat species), crude protein (1 mouse species). These results suggest that, for rat species, high nutritional seeds (high crude protein, high crude fat and high crude caloric) are more likely eaten after seed removal, while low nutritional seeds (high crude starch) or high handling-time seeds (high fresh weight, high coat hardness) are less likely eaten after removal. For mouse species, low nutritional seeds (high crude starch) or high toxicant seeds (high tannin) are more likely eaten by mouse species after seed removal (Table 2).

Scatter hoarding (mutualism) are positively correlated to fresh weight and coat hardness (1 rat species, 1 mouse species), crude protein and caloric (1 rat species), and tannin (2 mouse species); but negatively correlated to crude starch (1 rat species), suggesting high nutritional and high handling-time seeds are more likely scatter hoarded by rat species (high mutualism), low nutritional seeds are not favored by rat species for scatter hoarding (low mutualism). High tannin seeds and high handling-time seeds are more likely scatter hoarded by mouse species (high mutualism) (Table 2).

Larder hoarding of rat species is positively correlated to fresh weight and coat hardness (1 species), suggesting high handling-time seeds are more larder hoarded by rat species (Table 2).

EIS + EAR + LH (predation) are positively correlated to crude starch (2 rat species, 1 mouse species), but negatively correlated to fresh weight and coat hardness (1 rat species), crude protein (1 mouse species), caloric (1 mouse species). These results suggest that low nutritional seeds (high crude starch) suffered more predation from both rat and mouse species; high nutritional seeds (high crude protein and high crude caloric) or high handling-time seeds suffered less predation from both rat and mouse species (Table 2).

3.3. Effects of combined seed traits

Using Principal Components Analysis, three principal factors were extracted from these seven seed traits (Table 3). These three

Table 2
Correlations between individual seed traits and seed fates (in proportions) handled by sympatric rodents. Bold numbers show the significant correlations.

Seed fates	Rodent species	Fresh weight	Coat hardness	Crude protein	Crude fat	Crude starch	Tannin	Caloric
Remained *in situ* (RIS)	Edward's long-tailed rats	**0.239**[a]	**0.239**[a]	−0.054	−0.087	−0.021	0.159	−0.002
	Chestnut rats	**0.617**[a]	**0.617**[a]	0.104	−0.077	**−0.370**[a]	0.208	0.204
	White-bellied rats	**0.388**[a]	**0.388**[a]	−0.134	−0.193	**−0.270**[b]	−0.083	0.003
	Himalayan rats	0.227	0.227	0.142	0.006	**−0.494**[a]	**−0.295**[b]	0.190
	Sichuan field mice	−0.047	−0.047	**0.615**[a]	**0.508**[b]	**−0.533**[b]	−0.243	**0.578**[a]
	Chevrier's field mice	−0.339	−0.339	0.311	0.124	−0.469	**−0.644**[a]	0.119
	South China field mice	−0.185	−0.185	−0.181	−0.089	−0.185	**−0.573**[a]	−0.097
Eaten *in situ* (*EIS*)	Edward's long-tailed rats	**−0.559**[a]	**−0.559**[a]	−0.035	0.098	**0.381**[a]	−0.075	−0.169
	Chestnut rats	**−0.582**[a]	**−0.582**[a]	−0.096	0.058	**0.405**[a]	−0.116	−0.220
	White-bellied rats	**−0.385**[a]	**−0.385**[a]	0.142	0.155	0.215	0.032	−0.025
	Himalayan rats	−0.250	−0.250	−0.131	−0.028	**0.456**[a]	0.242	−0.208
	Sichuan field mice	/	/	/	/	/	/	/
	Chevrier's field mice	/	/	/	/	/	/	/
	South China field mice	−0.071	−0.071	0.081	0.013	0.264	**0.358**[b]	−0.071
Eaten after removal (EAR)	Edward's long-tailed rats	0.148	0.148	**0.280**[a]	**0.239**[a]	**−0.329**[a]	−0.069	**0.342**[a]
	Chestnut rats	**−0.250**[b]	**−0.250**[b]	0.147	**0.221**[b]	0.039	−0.083	0.119
	White-bellied rats	−0.064	−0.064	**0.309**[b]	**0.406**[a]	−0.051	0.090	**0.366**[a]
	Himalayan rats	0.107	0.107	0	0.107	0.107	0.213	0.107
	Sichuan field mice	−0.123	−0.123	**−0.526**[b]	−0.286	**0.609**[a]	0.223	−0.442
	Chevrier's field mice	0.006	0.006	−0.068	0.130	0.501	**0.563**[b]	0.006
	South China field mice	0.205	0.205	**0.325**[b]	0.223	0.046	**0.523**[a]	0.258
Scatter hoarded (SH, mutualism)	Edward's long-tailed rats	**0.296**[a]	**0.296**[a]	**0.224**[b]	0.177	**−0.374**[a]	−0.032	**0.341**[a]
	Chestnut rats	/	/	/	/	/	/	/
	White-bellied rats	0.002	0.002	0.129	0.196	−0.062	0.004	0.196
	Himalayan rats	/	/	/	/	/	/	/
	Sichuan field mice	0.319	0.319	0.085	0.044	0.113	**0.516**[b]	0.113
	Chevrier's field mice	**0.603**[b]	**0.603**[b]	−0.182	−0.126	0.056	0.477	0.056
	South China field mice	0.201	0.201	0	0.201	0.201	**0.402**[b]	0.201
Larder hoarded (LH)	Edward's long-tailed rats	**0.214**[b]	**0.214**[b]	−0.025	−0.120	**−0.189**[b]	−0.047	−0.002
	Chestnut rats	0.180	0.180	0.002	0	−0.078	0.067	0.073
	White-bellied rats	0.092	0.092	0	0.092	0.092	0.184	0.092
	Himalayan rats	/	/	/	/	/	/	/
	Sichuan field mice	−0.024	−0.024	−0.359	−0.347	0.135	−0.124	−0.359
	Chevrier's field mice	0.378	0.378	−0.189	−0.378	−0.189	0	−0.189
	South China field mice	0.296	0.296	0.028	0.105	−0.046	0.237	0.116
EIS + EAR + LH (predation)	Edward's long-tailed rats	−0.450	−0.450	−0.008	0.055	0.220	−0.148	−0.138
	Chestnut rats	−0.634	−0.634	−0.096	0.090	0.382	−0.202	−0.201
	White-bellied rats	**−0.415**[b]	**−0.415**[b]	0.131	0.199	**0.291**[b]	0.084	−0.011
	Himalayan rats	−0.231	−0.231	−0.138	−0.009	**0.487**[b]	0.287	−0.191
	Sichuan field mice	−0.102	−0.102	**−0.559**[b]	−0.354	**0.569**[b]	0.172	**−0.489**[b]
	Chevrier's field mice	0.185	0.185	−0.185	−0.095	0.382	0.507	−0.119
	South China field mice	0.149	0.149	0.184	0.076	0.187	0.548	0.073

[a] Correlation is significant at the 0.01 level (2-tailed).
[b] Correlation is significant at the 0.05 level (2-tailed).

factors explained 99.61% variance of seed traits. Factor 1 represents the nutritional with high protein, high fat, low starch and high caloric contents (here it is defined as high nutritional trait). Factor 2 represents physical trait with heavy fresh weight and high coat hardness (here it is defined as high handling-time trait). Factor 3 represents secondary chemical traits with high tannin (here it is defined as high toxicant trait). The factor scores were saved as variables to analyze correlations with seed fates (Table 4).

Eaten *in situ* is negatively correlated to nutritional traits (2 rat species, 1 mouse species) and high handling-time trait (2 rat species, 1 mouse species), suggesting high nutritional seeds or high handling-time seeds are less likely eaten *in situ* by both rats and mice (Table 4).

Eaten after removal is positively correlated to nutritional trait (2 rat species), high handling-time trait (1 rat species) and toxicant trait (1 rat species and 1 mouse species), suggesting high nutritional, high handling-time or toxicant seeds are more likely eaten after seed removal. High toxicant seeds are also more likely eaten after removal by mice (Table 4).

Scatter hoarding (mutualism) is positively correlated to nutritional trait (1 rat species) and high handling-time trait (1 rat species, 1 mouse species), and toxicant trait (2 mouse species), suggesting high nutritional seeds or high handling-time seeds are more likely scatter-hoarded by both rats and mice (high mutualism), while high toxicant seeds are more likely scatter-hoarded by mice (high mutualism) (Table 4).

Larder hoarding is positively correlated to high handling-time trait (1 rat species), suggesting high handling-time seeds are more likely larder hoarded by rats (Table 4).

EIS + EAR + LH (predation) is negatively correlated to nutritional traits (2 rat species, 1 mouse species) and high handling-time trait (2 rat species) but positively correlated to toxicant trait (1 mouse species), suggesting high nutritional seeds or high handling-

Table 3
Principal seed traits as revealed by using PCA. Bold numbers show the principal seed traits.

Seed trait	Nutrition trait (Factor 1)	Handling time trait (Factor 2)	Toxicant trait (Factor 3)
Protein	**0.986**	−0.143	−0.085
Starch	**−0.951**	−0.261	0.147
Caloric	**0.950**	−0.230	−0.204
Fat	**0.950**	−0.245	−0.188
Coat hardness	−0.093	**0.989**	−0.100
Fresh weight	−0.100	**0.989**	0.041
Tannin	−0.244	−0.054	**0.968**

Table 4
Correlations between the combined seed traits and seed fates handled by sympatric rodent species. Bold numbers show the significant correlations.

Seed fates	Rodent species	Nutrition trait	Handling time trait	Toxicant trait
Remained *in situ* (RIS)	Edward's long-tailed rats	0.061	**0.222**^{b}	0.084
	Chestnut rats	0.387	0.662	0.214
	White-bellied rats	**0.274**^{b}	**0.530**^{b}	−0.143
	Himalayan rats	0.389	0.414	−0.137
	Sichuan field mice	**0.518**^{b}	0.101	0.243
	Chevrier's field mice	0.102	−0.203	−0.345
	South China field mice	0.129	0.070	−**0.521**^{b}
Eaten *in situ* (EIS)	Edward's long-tailed rats	−**0.409**^{b}	−**0.669**^{b}	−0.083
	Chestnut rats	−0.437	−0.678	−0.151
	White-bellied rats	−**0.287**^{b}	−**0.527**^{b}	0.092
	Himalayan rats	−0.409	−0.437	0.089
	Sichuan field mice	/	/	/
	Chevrier's field mice	/	/	/
	South China field mice	**−0.320**^{b}	**−0.320**^{b}	0.274
Eaten after removal (EAR)	Edward's long-tailed rats	**0.398**^{b}	**0.268**^{b}	0.164
	Chestnut rats	0.011	−0.234	0.060
	White-bellied rats	**0.266**^{b}	−0.022	**0.338**^{b}
	Himalayan rats	0.107	0.107	0.213
	Sichuan field mice	−0.442	−0.229	−0.146
	Chevrier's field mice	−0.173	−0.173	0.439
	South China field mice	0.039	0.004	**0.593**^{b}
Scatter hoarded (SH, mutualism)	Edward's long-tailed rats	**0.474**^{b}	**0.445**^{b}	0.162
	Chestnut rats	/	/	/
	White-bellied rats	0.196	0.167	0.133
	Himalayan rats	/	/	/
	Sichuan field mice	0.028	0.165	**0.448**^{b}
	Chevrier's field mice	0.238	**0.603**^{b}	0.294
	South China field mice	0.201	0.201	**0.402**^{b}
Larder hoarded (LH)	Edward's long-tailed rats	0.117	**0.261**^{b}	−0.072
	Chestnut rats	0.147	0.218	0.069
	White-bellied rats	0.092	0.092	0.184
	Himalayan rats	/	/	/
	Sichuan field mice	−0.247	−0.024	−0.359
	Chevrier's field mice	0	0.378	−0.189
	South China field mice	0.169	0.289	0.218
EIS + EAR + LH (predation)	Edward's long-tailed rats	**−0.310**^{b}	**−0.518**^{b}	−0.133
	Chestnut rats	−0.396	−0.685	−0.203
	White-bellied rats	−0.293	−0.562	0.143
	Himalayan rats	**−0.392**^{b}	**−0.419**^{b}	0.131
	Sichuan field mice	**−0.459**^{b}	−0.202	−0.221
	Chevrier's field mice	−0.185	0.018	0.280
	South China field mice	−0.168	−0.118	**0.495**^{b}

time seeds suffer less predation from both rat and mouse species; high toxicant seeds suffered more predation from mouse species (Table 4).

3.4. Seed-rodent interactions

3.4.1. Eaten in situ

Small-sized rodent species showed no (*A. latronum*, *A. chevrieri*) or less (*A. draco*) EIS, while the other large-sized or medium-sized species showed more EIS interactions (Fig. 1a); *Q. serrata* (high tannin seed) and *C. fargesii* (low tannin, low nutrition and low handling-time seed) showed more EIS interactions, while the other three seed species showed less EIS (Fig. 1a).

There are two clusters of rodents in EIS: the first cluster is composed of *L. edwardsi* and *R. nitidusa* (large-sized rodent species) which ate more *Q. serrata* and *C. fargesii*; while the second cluster is composed of the other four rodent species which ate little seed *in situ* (especially for three small-sized mouse species: *A. latronum*, *A. chevrieri*, *A. draco*). There are two obvious clusters of seeds in EIS: the first one is composed of *Q. variabilis* (high handling-time and high tannin seed), *L. harlandii* (high handling-time seed) and *C. oleifera* (high nutritional seed) which were less eaten *in situ*; while the second cluster is composed of *Q. serrata* (high tannin seed) and *C. fargesii* (low tannin, low nutrition and low handling-time seed) which were more eaten *in situ*.

3.4.2. Eaten after removal

Except for R. *nitidusa*, all rodent species showed high EAR interactions; and all seed species showed high EAR interactions (Fig. 1b). There is no clear cluster of rodents in EAR. There is no clear cluster of seeds in EAR, but *Q. variabilis*, *L. harlandii* and *C. oleifera* are closely clustered together as they were less eaten after removal.

3.4.3. Scatter hoarding (mutualism)

L. edwardsi and *A. latronu* showed high SH, *A. chevrieri*, *N. confucianus* and *A. draco* showed medium SH, while *R. nitidusa* and *N. fulvescens* showed no SH; *Q. variabilis* and *L. harlandii* showed high SH; *Q. serrata* and *C. oleifera* showed medium SH, while *C. fargesii* show no SH (Fig. 1c).

There is no clear cluster of rodents in SH. There are two obvious clusters of seeds in SH: the first one includes *Q. serrata* and *C. oleifera* which were less scatter hoarded; while the second one includes *Q. variabilis*, *C. oleifera* and *L. harlandii* which were more scatter hoarded.

3.4.4. Larder hoarding

A. draco, *L. edwardsi* and *N. fulvescens* showed high LH, *A. latronum showed medium LH, while A. chevrieri*, *N. confucianus* and *R. nitidusa* showed small or none LH (Fig. 1d). *Q. variabilis* and *L. harlandii* showed high LH; *C. oleifera* showed medium LH; *Q. serrata* and *C. fargesii* showed low LH (Fig. 1d).

There is no clear cluster of rodents in LH. There is no clear clusters of seeds in LH, but *Q. serrata*, *Q. variabilis* and *C. oleifera* are closely clustered together.

EIS + EAR + LH(predation)

Small-sized rodent species (*A. latronum*, *A. chevrieri* and *A. draco*) showed less predation interaction on *L. harlandii* and *C. oleifera*. Large-sized species (*L. edwardsi*) showed more predation interaction on all five seeds, while the other large-sized or medium-sized species showed more predation interaction on four seeds except for *L. harlandii* (Fig. 1e).

There is no clear cluster of rodents in predation interactions. There is no clear cluster of seeds in predation interactions, but *Q. variabilis*, *L. harlandii* and *C. oleifera* are closely clustered together which showed low predation.

4. Discussion

Seed and animal traits are important forces in shaping the network structure in plant-animal systems, but quantitative analysis is rare. Ben-Moshe et al. (2001) demonstrated a size-structured convergence in hoarding seeds between old and new world rodent guilds; the larger species took significantly larger seeds than the smaller one. Chen and Chen (2011) found that in nutcracker-dominated sites, pines were characterized by smaller cones, smaller seeds, and thinner seed coats; while in sites where nutcrackers were not abundant, pines had relatively larger cones with larger seeds, which could enhance caching activities by scatter-hoarding rodents. These studies are restricted to limited seed or animal traits. In this study, the impacts of the seed traits seed mass, endocarp thickness, nutrition, toxicant and the animal trait body size on formation of mutualism/predation interactions were quantitatively assessed for different seed fates or hoarding behaviors. We found seed traits (handling time, nutritional value, toxicants) and animal trait (body size) play significant role in shaping the network structure in a seed-rodent system. In general, high

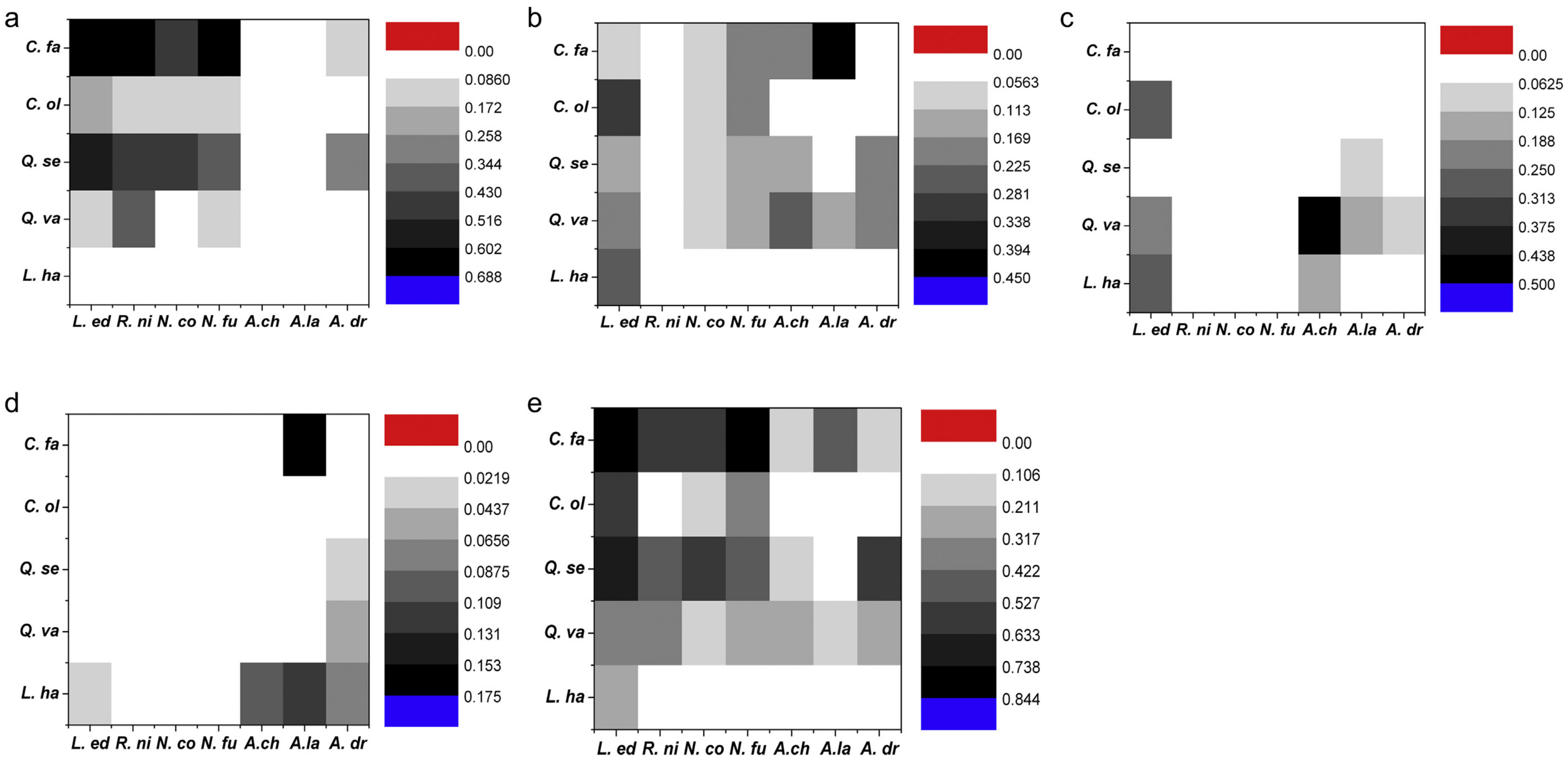

Fig. 1. Interaction strength between seeds and rodents for each seed fate (darkness indicates the interaction strength in proportions). a, EIS; b, EAR; c, SH (mutualism); d, LH; e, EIS + EAR + LH (predation).

handling-time seeds (high fresh weight and coat hardness) or/and high nutritional seeds are less eaten *in situ*, more likely scatter hoarded and larder hoarded by rodents, particularly by large-sized rat species. While, low nutritional seeds (high crude starch) or high toxicant seeds (high tannin) are more likely eaten *in situ* by rodents, particularly by mouse species; high tannin seeds are more likely scatter hoarded by mouse species. Some seed traits contribute to convergent formations of seed predation by multiple rodent species. For example, heavy seeds with hard seed coat had low seed consumption *in situ* by three rat species (convergent response). Animal trait (i.e., body size) also contributes to the divergent formation of mutualism between seed and rodent species. For example, large-sized rats prefer to scatter hoard heavy, high nutritional seeds with hard seed coat; while small-sized mouse species prefer to scatter hoard low nutritional and high tannin seeds with soft seed coat. Our results demonstrate that the functional traits of seeds and rodents are important in the formations of mutualism and predation in the seed-rodent dispersal system.

Recently, networks in plant-animal mutualism have been described (see review by Bascompte and Jordano, 2007; Bascompte, 2009). Previous studies indicate that mutualistic networks are not evenly or randomly structured. They often present a modular structure (Bascompte, 2009). Alternatively mutualisitc networks may be nested (Bascompte, 2009). In our study, we found significant role of seed and animal traits in formation of mutualism and predation interactions. Large-sized rats prefer to scatter hoard large and nutritional seeds with hard seed coat; while small-sized mice prefer to hoard small and low nutritional seeds with soft seed coat. Our results also showed that the seed-rodent mutualistic network is highly nested (Fig. 1). For example, *L. edwardsi* showed mutualistic interactions with four seed species; the other rodent species showed mutualistic interactions with some of the seed species *L. edwardsi* interacted. *Q. variabilis* showed mutualistic interactions with five rodent species; the other seeds species interacted with some species *Q. variabilis* interacted. Using quantitative interaction strength data, we found some substructures or clusters for interactions between seeds and rodents. In general, seeds of *Q. variabilis*, *L. harlandii* and *C. oleifera* are often clustered together. Seeds of these three species own heavy weight, hard seed coat or high nutrition, which resulted in high mutualism but low predation interactions with rodents. In contrary, the other two species (*Q. serrata* and *C. fargesii*) own low weight, low nutrition and soft seed coat, which resulted in low mutualism but high predation interactions with rodents. As compared with tree species, rodent species showed no clear substructures in the networks, but their interactions are not evenly or randomly connected. There are still small substructures, e.g. the three mouse species were more closely clustered together and rodent species show large differences in their interaction with seeds.

The predation networks in plant–animal dispersal system are hardly studied together with the mutualistic networks. In our study, the predation interactions as measured by EIS + EAR + LH are highly overlapped, but with some obvious clusters. We found high nutritional seeds or high handling-time seeds suffer less predation from both rat and mouse species; high toxicant seeds suffered more predation from mouse species. It is notable that anti-predation seed traits (heavy seed weight, hard seed coat, high tannin) increase chance of mutualism at the same time as reducing predation by rodents, suggesting formation of mutualisms may be closely related to that of predations.

Different seeds have different seed traits (e.g., size, coat hardness, nutrition contents, secondary contents, etc.) and these traits can affect the behavioral decision of animals (e.g., eat, scatter-hoard or larder-hoard) (Chang et al., 2009), and thus further affect interactions between seeds and animals. With the increase of seed size or seed endocarp, the handling time by rodents would increase (Jacobs, 1992). This would bring high predation risk and then may benefit seed dispersal or mutualism (Chang et al., 2010). In this study, we found seed high handling-time trait (i.e., heavy seed and coat hardness) showed negative effects on proportion of seeds eaten *in situ* to most rodent species and positive effect on proportion of seeds scatter-hoarded by 2 rat species, supporting the handling time hypothesis. However, the handling time hypothesis was less supported in mouse species. It is notable that large- or medium-sized rats showed more EIS (Fig. 1a) than small-sized mouse species. This is probably because large animals are more capable of encountering predation risk.

Some previous studies indicate the consuming high tannin levels results in poor digestion in rodents (Smallwood and Peters, 1986), thus forcing rodents to disperse high tannin seeds, and subsequently enhancing mutualism (Steele et al., 1993; Xiao et al., 2008; Wang and Chen, 2008). In this study, the high tannin hypothesis was supported by the observed positive association between scatter-hoarding behavior and high toxicant (i.e., high tannin content) in 3 mouse species but not in the 4 rat species. High nutritional seeds were also more likely dispersed by rodents because they may be more important in securing food supply in varying environments (Lewis, 1982; Izhaki, 2002). In this study, we found high nutritional trait (i.e., high protein, high fat, high caloric, and low starch) were positively related to scatter-hoarding behavior in Edward's long-tailed rat species. These observations support the high nutritional hypothesis. Thus, the handling time hypothesis, high tannin hypothesis, and high nutritional hypothesis were all supported in some, but not all, seed-rodent partners, which is consistent with the observation of divergent formation of seed-rodent interactions.

Recently, some studies have suggested that seed size, more than nutrition or tannin content, primarily affected hoarding behavior of rodents (e.g., Wang and Chen, 2009). In this study, we also found large seed size (or heavy seeds) tend to increase hoarding behavior of rat species, while high tannin seeds tend to increase hoarding behavior of 3 mice species, suggesting the effects of seed traits on hoarding behaviors of rodents may be species-dependent. Seed traits often co-vary with each other. In nature, seed traits affect rodent seed hoarding behavior not independently, but as a whole. In most cases, seed dispersal occurs by the combined effect of a seed-eating guild (Hollander and Vander Wall, 2004). Our PCA analysis identified three principle factors: handling time, nutrition value and tannin level which showed different links with rats and mice. Large seed size is highly co-varied with seed coat hardness or nutrition value; its isolated effect may be different from that of its combined traits.

Animal traits (e.g., body size) also affect seed hoarding (e.g., Ben-Moshe et al., 2001). In our study, we found large-sized rats prefer to hoard large and nutritional seeds with hard seed coat, while small-sized mice prefer to hoard small and low nutritional seeds with high tannin but soft seed coat, supporting the body-size structured hypothesis. Large animals own high capacity of anti-predation and anti-competition, this explains why large-sized rats tended to eat more seeds *in situ* (Fig. 1a), and hoarding heavy seeds. Large animals also need high energy intake, this explains why they prefer high nutritional seeds or large seeds (with high caloric). Thus, animal traits, together with seed traits, play significant roles in the observed convergent/divergent formation of seed-animal species interactions.

The study of seed-rodent interactions would be beneficial in forest management. In this study, we found *C. fargesii* (low tannin, low nutrition and low handling-time seed) show no mutual interactions with any rodent species but suffered high predation. Indeed, the abundance of *C. fargesii* trees is quite low in the study region, probably due to poor mutualism but high predation from rodents. It is necessary to provide help to facilitate seed regeneration of this tree species by controlling rodent predation. We also found Chestnut rats and Himalayan rats did not scatter-hoard seeds of any tree species. They are pure seed-eaters which need to be managed in conditions of their high density so as to promote seedling establishment of forestry.

It is notable that our results are achieved in semi-natural enclosures which are different from the natural conditions where rodents may face competition from the other species in hoarding seeds. Future studies should be directed to assessments of interactions between seeds and rodents in natural condition using novel methods.

Acknowledgments

We are very grateful to Laura Johnson-Hill for valuable comments and language editing on this manuscript. We also thank the Subalpine Mountain Plant Garden of West China, the Chinese Academy of Sciences, and the Forest Bureau of Dujiangyan City of Sichuan Province for their support. Dr. Zhishu Xiao provided help and assistance with this study. This study was supported by the National Natural Science Foundation of China (grants 30930016) and the State Basic Research Program of the Ministry of Science and Technology (grants 2007CB109100). The experiments comply with the current laws of the country in which they were performed.

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