

Mutualistic and predatory interactions are driven by rodent body size and seed traits in a rodent–seed system in warm-temperate forest in northern China

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Abstract

Context. Mutualistic interactions between animals and plants shape the structure of plant–animal systems and, subsequently, affect plant-community structure and regeneration.

Aims. To assess the effects of plant and rodent functional traits on the formation of mutualistic and predatory interactions regarding seed dispersal and predation in a warm-temperate forest.

Methods. Seed scatter-hoarding and predation by six sympatric rodent species on seeds belonging to five sympatric tree species were tested under enclosure conditions.

Key results. Functional traits (i.e. rodent body size and seed traits) are important to mutualism/predation in this seed–rodent system. The rodent–seed network is highly nested: large-sized rodents have mutualistic or predatory interactions with both large- and small-sized seed species, but small-sized rodents interacted with small-sized seed species only. Large seeds or seeds with hard coats enhanced mutualism and reduced predation.

Conclusion. Body size of rodents and seed traits such as handling time and nutritional value are key factors in the formation of mutualistic and predatory interactions within seed–rodent systems.

Implications. To promote seedling establishment in degenerated forests, introducing or protecting large-sized scatter hoarders and reducing the density of pure seed eaters are needed.

Additional keywords: behavioural difference, plant–animal interactions, plant regeneration, seed dispersal.

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Introduction

Small rodents play an essential seed-dispersal role in the reproductive cycle of plants by scatter-hoarding seeds at safe sites (Howe and Smallwood 1982; Smith and Reichman 1984; Zhang *et al.* 2005, 2013a; Gómez *et al.* 2008; Chimera and Drake 2011; Meng *et al.* 2012). Larder hoarding is less effective seed dispersal than is scatter-hoarding, because larder-hoarded seeds at one site are more easily discovered and consumed by animals (Vander Wall 1990), or competition is intensified between the seedlings (Jansen and Forget 2001; Zhang *et al.* 2005). How sympatric animals differ in seed-hoarding patterns and subsequently affect seed dispersal and plant regeneration remains contentious (Hollander and Vander Wall 2004; Vander Wall and Beck 2012; Chang and Zhang 2014). For example, a few studies have found co-evolved interactions between one plant

species and one animal species (Herrera 1985; Reid 1991); however, dynamics between sympatric seed hoarders and plants are more complicated at the community level. Nearly all plant–animal interactions appear to involve combinations of numerous species (Hollander and Vander Wall 2004; Vander Wall and Beck 2012; Matsuda *et al.* 2013; O’Farrill *et al.* 2013), and should be recognised as cases of diffuse co-evolution in which one species is dependent on multiple species (Smith 1970; Benkman 1995; Forget and Vander Wall 2001; Dunn *et al.* 2007; Lomáscolo and Schaeferh 2010; Vander Wall and Beck 2012). Studies of mutualistic interactions between multiple animal and plant species at the community level remain uncommon.

How a particular type of seed is treated by an animal is dependent on its traits and that of the animal. Many factors

have an important impact on rodent hoarding behaviour, such as seed size (Stapanian and Smith 1978, 1984; Jansen *et al.* 2002; Vander Wall 2003; Theimer 2003; Xiao *et al.* 2005; Zhang *et al.* 2008; Chang *et al.* 2009; Wang and Chen 2009; Lai *et al.* 2014), seed-coat hardness (Jacobs 1992; Izhaki 2002; Xiao *et al.* 2003; Zhang and Zhang 2008; Lai *et al.* 2014), nutrient content (Smallwood and Peters 1986; Izhaki 2002; Chang and Zhang 2014), tannins (Steele *et al.* 1993; Smallwood *et al.* 2001; Xiao *et al.* 2008, 2009), germination schedule (Hadj-Chikh *et al.* 1996; Steele *et al.* 2001, 2006; Chang *et al.* 2009; Xiao *et al.* 2009) and seed odor (Vander Wall 2010; Hollander *et al.* 2012). Rodents prefer to remove and hoard large seeds over small seeds (Jansen *et al.* 2002; Xiao *et al.* 2005; Zhang *et al.* 2008), hard seeds over soft seeds (Zhang and Zhang 2008), seeds of high nutritional value over those of low value (Smallwood and Peters 1986; Izhaki 2002), non-germinating seeds over germinating seeds (Steele *et al.* 2006; Chang *et al.* 2009) and high-tannin seeds over low-tannin seeds (Xiao *et al.* 2008; Wang and Chen 2008; but see Zhang *et al.* 2013b). Rodents tend to eat *in situ* small seeds rather than large seeds (Zhang *et al.* 2008), soft seeds rather than hard seeds (Zhang and Zhang 2008), germinating seeds rather than non-germinating seeds (Xiao *et al.* 2009), infested seeds rather than intact seeds (Cheng and Zhang 2011) and cultivated seeds rather than wildland seeds (Hollander *et al.* 2012). The seed-hoarding strategies of animals are also affected by their own traits (e.g. body size and jaw strength) (Ben-Moshe *et al.* 2001; Zhang and Zhang 2008). For example, large rodents with strong jaws often have a wider diet (Zhang and Zhang 2008; Chang and Zhang 2014), and are more capable of consuming large and/or hard seeds than are smaller rodent species (Zhang and Zhang 2008). Seed and animal traits are very important to the formation of mutualistic–predatory interactions among multiple plant and animal species, but studies of these factors in seed–rodent networks are rare (but see Chang and Zhang 2014; Wang *et al.* 2014).

Here, we tested mutualistic–predatory interactions between six rodent species and five seed species within semi-natural enclosures. We tested the hypothesis that functional traits (rodent body size and seed traits) determine interactions in a seed–rodent system (Wang *et al.* 2014; Chang and Zhang 2014). We made the following predictions: (1) large-sized rodents have mutualistic or predatory interactions with both large- and small-sized seed species, whereas small-sized rodents have interactions with small-seed species only; and (2) large seeds or seeds with a hard seed coat facilitate mutualism but reduce predation. We also tested several hypotheses regarding the functional traits of seeds,

including the following: (1) animals tend to hoard large seeds rather than small seeds (seed-size hypothesis, Jansen *et al.* 2002); (2) animals prefer to hoard hard seeds and eat soft seeds (handling-time hypothesis, Jacobs 1992; Zhang and Zhang 2008); (3) animals tend to hoard seeds with high nutritional value and eat those with low nutritional value *in situ* (high-nutrition hypothesis, Lewis 1982; Izhaki 2002); (4) animals like to hoard high-tannin seeds and eat low-tannin seeds (high-tannin hypothesis, Smallwood and Peters 1986; Xiao *et al.* 2008); and (5) large-sized animals can consume and hoard more seed species of variable size than can smaller animals (body size-structured hypothesis, Ben-Moshe *et al.* 2001; Chang and Zhang 2014).

Materials and methods

Study site

The present study was conducted at the Liyuanling field station, a mountainous area in the Donglingshan Mountains, ~120 km north-west of Beijing, China (40°00'N, 115°30'E; 1100 m above sea level). The Donglingshan Mountains are characterised by a temperate continental monsoon climate with 600 mm of annual precipitation and a mean annual temperature of 6.5°C. Major types of land cover are shrublands, secondary forests and abandoned farmlands, and are undergoing natural secondary succession from cultivation and grazing (Zhang *et al.* 2013a). The Chinese white-bellied rat (*Niviventer confucianus*), Korean field mouse (*Apodemus peninsulae*) and David's rock squirrel (*Sciurotamias davidianus*) are common rodent species, and the rat-like hamster (*Tscherskia triton*), striped field mouse (*A. agrarius*) and Siberian chipmunk (*Tamias sibiricus*) are also found in the study area (Li *et al.* 2004; Table 1). These rodent species are mainly responsible for seed predation and dispersal of large-sized seeds (Zhang 2007; Zhang and Zhang 2008). A comprehensive description of the area has been given by Zhang *et al.* (2008).

Plant species and seed-marking

Our focal trees were cultivated walnut (*Juglans regia*), wild walnut (*J. mandshurica*), wild peach (*Amygdalus davidiana*), Liaodong oak (*Quercus wutaishanica*) and wild apricot (*Armeniaca sibirica*) (Table 1). All species are common across the study area. Acorns of *Q. wutaishanica* (dispersal unit, hereafter the seed) mature and fall in September, and become seedlings next spring (April–May; Li and Zhang 2003). Fruits of the other four trees are drupes. Their dispersal units comprise a single seed enclosed in a hard woody endocarp (hereafter the

Table 1. Seed traits for five tree species used in the experiments

The chemical composition (crude protein, crude fat, crude fibre and tannin) of dry kernel was measured by the Centre of Grain Quality of Ministry of Agriculture, China. Dry-kernel caloric values were calculated by the average gross-energy equivalents of protein (17.2 KJ g⁻¹), fat (38.9 KJ g⁻¹) and starch (17.2 KJ g⁻¹) (see also Zhang and Zhang 2008); n.a., not applicable

Seed species	Seed weight (±s.e.) (g)	Kernel weight (±s.e.) (g)	Coat hardness (±s.e.) (m)	Crude starch (g per 100 g)	Crude protein (g per 100 g)	Crude fat (g per 100 g)	Crude fibre (g per 100 g)	Tannin (g per 100 g)	Caloric (KJ g ⁻¹)
<i>Juglans regia</i>	9.09 (0.24)	4.34 (0.12)	1.22 (0.04)	n.a.	15.39	70.68	1.36	0.56	30.14
<i>Juglans mandshurica</i>	6.13 (0.14)	1.32 (0.02)	2.66 (0.07)	n.a.	28.07	62.30	0.98	0.47	29.06
<i>Amygdalus davidiana</i>	3.23 (0.07)	0.52 (0.01)	3.86 (0.09)	n.a.	29.04	52.67	3.01	0.05	25.48
<i>Quercus wutaishanica</i>	1.96 (0.13)	1.68 (0.11)	0.26 (0.01)	34.06	11.46	1.48	4.14	8.56	8.41
<i>Armeniaca sibirica</i>	1.68 (0.04)	0.66 (0.02)	1.09 (0.02)	n.a.	25.12	53.08	2.93	0.04	24.96

seed). After maturation (in July for *A. sibirica* and *A. davidiana*, September for *J. mandshurica* and *J. regia*), fruits fall to the ground directly (*A. davidiana*, *J. mandshurica* and *J. regia*), or the fleshy layer (mesocarp) opens and the seed falls to the ground (*A. sibirica*). Seedlings often emerge during the following spring (April–May). These seeds are favoured for eating and hoarding by rodents (Zhang and Zhang 2008) and are dispersed strictly by rodents (Zhang 2007). Small rodents gather seeds from the ground surface or from trees directly (*S. davidianus* and *T. sibiricus*), and then eat, scatter-hoard in soil and litter and/or larder hoard in burrows and caves.

Experimental seeds were collected in forests around the field station during seed fall in 2006 and 2008, and maintained in a dry and ventilated environment to prevent rotting and mildew growth. So as to facilitate relocation, each experimental seed was marked with a tin-tag: a small tin-tag (3.0 cm × 1.0 cm, 0.1 g) was tied to a seed with a 3-cm piece of fine steel wire (Zhang and Wang 2001). This method does not appear to affect seed removal and hoarding by rodents (Xiao *et al.* 2006).

Animal trapping and handling

The focal animals were *S. davidianus*, *T. triton*, *T. sibiricus*, *N. confucianus*, *A. agrarius* and *A. peninsulae* (Table 2). Individuals used in experiments were trapped in 8–10 plots (2.5 ha, 50–100 m apart) during July–September in 2006 and 2008 (also see Zhang *et al.* 2011). Large wire live traps (30 cm × 25 cm × 20 cm) with peanuts (5–10 g) as bait and extraneous food supply, cabbage as water supply, and local dry leaves as nest material were used in animal trapping. The traps were covered to protect animals from bad weather and predators. In all, 20–30 traps were placed 5–7 m apart along two or three transects (~100 m long, 20–30 m apart) within each plot between 1800 hours and 1900 hours, and checked between 0600 hours and 0700 hours, between 1200 hours and 1300 hours and between 1900 hours and 2000 hours for three consecutive days. No animals died during the trapping season. Each captured individual was carefully transferred to the laboratory by using a cloth bag, except for young animals that were released immediately on site. Each individual was sexed, weighed, numbered, and subsequently housed separately in a PVC box (37 cm × 26 cm × 17 cm) or in a wheel cage (100 cm × 100 cm × 120 cm) (*S. davidianus* and *T. sibiricus*) in a well ventilated room at ambient temperature (18–25°C) and a late summer photoperiod (10/14 h cycle of dark/light). Ample commercial mouse chow (Keao Feed Ltd, Beijing, China), water and nest

material (wood chips or cotton) were provided *ad libitum*. Seeds and nuts of local plants (e.g. *Q. wutaishanica*, *A. sibirica*, *J. mandshurica* and *J. regia*) were provided *ad libitum* to maintain a natural diet, and 5–10 g of peanuts per animal were provided every 1 or 2 days as a nutritional supplement. Animals were acclimatised to laboratory conditions at least a full week before experiments. All animals maintained health and weight during captivity and experimentation, and were released back to their capture site or kept in the laboratory for other experiments. In addition, four connective days of animal trapping (using 40 traps) were conducted in three plots (2.5 ha, >1000 m apart) in secondary forest, shrubland and abandoned farmland around the field station for surveying small-mammal abundance in September 2006 and September 2008 (480 trap-days per year; Table 2). All captured animals were released immediately after species identification. Animal trapping and our research protocols were approved by the Institute of Zoology, The Chinese Academy of Sciences and the local government.

Enclosure design

Four 10 m × 10 m × 1 m semi-natural enclosures were constructed using bricks in an open area at the field station (see Lu and Zhang 2008). So as to prevent animals from entering and escaping the enclosures, each enclosure was covered with wire mesh (1.2 cm × 1.2 cm grid) and its walls were buried 30 cm below ground. Sandy soil (5–10 cm) was spread on the ground surface within each enclosure to facilitate animal hoarding. A wooden nest box (40 cm × 20 cm × 20 cm) and a water plate were placed in one corner, and a feeding station (0.5 m²), where tagged seeds were presented, was established at the centre of each enclosure. Vegetation in and around the enclosures is dominated by *Artemisia* spp., *Elymus excelsus*, and *Poa* spp. 30–80 cm tall and with 30–60% cover in different years. Vegetation and branches were placed on the mesh to simulate the ~30% canopy cover around enclosures.

Experimental procedures

Experiments were conducted from September to October, the peak time for food hoarding (Zhang 2007). *Niviventer confucianus* (7 ♂, 9 ♀), *A. peninsulae* (9 ♂, 7 ♀) and *S. davidianus* (8 ♂, 7 ♀) were tested in 2006, and *T. triton* (5 ♂, 5 ♀), *A. agrarius* (6 ♂, 5 ♀) and *T. sibiricus* (6 ♂, 3 ♀) were tested in 2008 (Table 2).

Table 2. Species of rodents involved in seed-selection experiments conducted within semi-natural enclosures and the number trapped in the study area

480 trap-days per year. AF, abandoned farmland; LH, larder hoarding; SF, secondary forest; SH, scatter hoarding; SL, shrubland

Rodent species	No. of samples	Bodyweight (±s.e.) g	Body length (±s.e.) mm	Hoarding pattern	Habit	Habitat	Number trapped (%)	
							2006	2008
<i>Sciurotamias davidianus</i>	8 ♂, 7 ♀	225.2 (6.3)	211.2 (5.3)	LH, SH	Diurnal	SF, SL, AF	9 (11.1)	4 (11.8)
<i>Tscherskia triton</i>	5 ♂, 5 ♀	131.0 (2.0)	134.7 (6.9)	LH	Nocturnal	SL, AF	5 (11.1)	3 (8.8)
<i>Tamias sibiricus</i>	6 ♂, 3 ♀	82.3 (6.7)	130.6 (4.6)	LH, SH	Diurnal	SF, SL, AF	1 (2.2)	0
<i>Niviventer confucianus</i>	7 ♂, 9 ♀	67.3 (1.8)	127.4 (5.2)	LH	Nocturnal	SF, SL, AF	17 (37.8)	14 (41.2)
<i>Apodemus agrarius</i>	6 ♂, 5 ♀	23.3 (0.7)	97.5 (5.1)	LH, SH	Nocturnal	AF	2 (4.4)	1 (4.4)
<i>Apodemus peninsulae</i>	9 ♂, 7 ♀	23.3 (1.1)	92.4 (5.3)	LH, SH	Nocturnal	SF, SL, AF	15 (33.3)	12 (33.3)

Each animal was kept in the enclosure for 3 days during each experimental trial. Day 1 was designated for acclimation and the remaining 2 days for observation. A subject was introduced into the enclosure at 1200 hours on Day 1 and 10 untagged seeds (two per species) were provided. Fifty tagged seeds (10 per species) were provided on Day 2 and their fates were recorded after 48 h (between 1200 hours and 1400 hours). Water and five peanuts (~5 g, extraneous nutrition) were provided daily. Enclosures were refreshed by removing all seeds and their fragments and replacing the nest box and water plate at the completion of a trial. A 24-h break was allowed between enclosure use so as to limit possible interactions.

Seed fates were recorded as scatter-hoarded (SH) if a seed was buried in the soil, or predated (PRE) if a seed was eaten or moved into the nest. SH represents a mutualistic interaction (positive effect), and PRE represents a predatory interaction (negative effect) between rodents and trees (also see Wang *et al.* 2014).

Kernel eating

Kernel eating of the five seed species by rodents was used as a test of the handling-time hypothesis that endocarp thickness promotes seed hoarding but reduces seed eating (Zhang and Zhang 2008). This experiment was conducted in 12 *S. davidianus* (6 ♂, 6 ♀), six *T. triton* (3 ♂, 3 ♀), six *T. sibiricus* (3 ♂, 3 ♀), 10 *N. confucianus* (5 ♂, 5 ♀), six *A. agrarius* (4 ♂, 2 ♀) and eight *A. peninsulae* (4 ♂, 4 ♀) individuals in October 2008. Animal trapping and handling are as detailed in the previous section. *S. davidianus* and *T. sibiricus* were tested in a wheel cage (100 cm × 100 cm × 120 cm), and the other four species were tested in a PVC nest box (37 cm × 26 cm × 17 cm). Each subject was food deprived for 6 h before testing, to increase its motivation for food. Individual *S. davidianus* and *T. triton* animals were provided 50 g of kernel (10 g per seed species), and individuals of the other four species were provided 25 g of kernel (5 g per seed species) between 1200 hours and 1300 hours to consume freely in 48 h. All experimental kernels were cut into 0.5-g pieces and mixed together. Remaining kernels and fragments were collected and weighed separately for each species at the completion of the test, to determine the preferences of rodents.

Statistical analyses

Statistical analyses were conducted using SPSS version 18.0 (Carver and Nash 2011). One-way ANOVA, including least significant difference (l.s.d.) for pairwise comparisons, was used to test difference in seed fate (SH, PRE) and kernel eating of the five seed species handled by each rodent species. Spearman's rank correlation was used to test relationships between seed traits and seed fates, kernel traits and kernel eating by each species. Seed species were excluded from the analysis if they were totally rejected by a rodent. All statistical tests are two tailed, and the α level was set at 0.05.

Results

Seed hoarding and predation

Sciurotamias davidianus interacted with different seed species in different ways (SH: $F_{4,70}=28.567$, $P<0.001$; PRE:

$F_{4,70}=80.800$, $P<0.001$). The squirrel tended to scatter-hoard large seeds and hard seeds (*J. regia* and *J. mandshurica*) and eat small seeds and soft seeds (*A. sibirica* and *Q. wutaishanica*) ($P<0.05$ for all; Fig. 1a). Mutualistic interactions were positively correlated with seed weight, kernel weight, crude fat and caloric value; seed predation was positively correlated with tannin content, and negatively correlated with seed-coat hardness, crude fat and caloric value ($P<0.05$ for all; Table 3).

Tscherskia triton predated the seeds of the five species similarly ($F_{4,45}=1.678$, $P=0.172$) and did not scatter-hoard seeds under enclosure conditions (Fig. 1b). The hamster either ate the seeds or transferred all seed species to its nest ($P>0.05$ for all).

Tamias sibiricus predated on seeds of different species differently ($F_{4,40}=124.633$, $P<0.001$), but interacted mutualistically with all species in a similar way ($F_{4,40}=1.746$, $P=0.159$). The chipmunk scatter-hoarded more small seeds (*A. sibirica*), ate more small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*), and did not eat very large and hard seeds (*J. regia* and *J. mandshurica*) ($P<0.05$ for all; Fig. 1c). Seed predation was negatively correlated with seed-coat hardness.

Niviventer confucianus predated on seeds of different species differently ($F_{4,75}=167.036$, $P<0.001$), but did not scatter-hoard seeds. The rat tended to eat more small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*), and rejected or ate only a few large and hard seeds (*A. davidiana*, *J. regia* and *J. mandshurica*) ($P<0.05$ for all; Fig. 1d). Seed predation was negatively correlated with seed weight and seed-coat hardness ($P<0.05$; Table 3).

Apodemus agrarius engaged in different mutualistic and predatory behaviour across the seed species (SH: $F_{4,50}=9.944$, $P<0.001$; PRE: $F_{4,50}=367.267$, $P<0.001$). The mouse scatter-hoarded and ate more small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*) than hard seeds (*A. davidiana*), and rejected very large and hard seeds (*J. regia* and *J. mandshurica*) ($P<0.05$ for all; Fig. 1e). No correlations between seed fate and seed traits were found for this rodent ($P>0.05$ for all; Table 3).

Apodemus peninsulae engaged in different mutualistic and predatory behaviour across seed species (SH: $F_{4,75}=15.441$, $P<0.001$; PRE: $F_{4,50}=104.887$, $P<0.001$). The mouse scatter-hoarded and ate small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*) and rejected large and hard seeds (*A. davidiana*, *J. regia* and *J. mandshurica*) (all $P<0.05$; Fig. 1f). Seed predation was negatively correlated with seed-coat hardness ($P<0.05$; Table 3).

In summary, large rodents (*S. davidianus* and *T. triton*) had mutualistic and predatory interactions with both large and small seeds, whereas small and medium-sized rodents (*T. sibiricus*, *N. confucianus*, *A. agrarius* and *A. peninsulae*) interacted with small or soft seeds only. Seed size, seed-coat hardness and nutritional content determined the mutualistic and predatory interaction.

Kernel eating

All rodent species preferred to eat kernels of *J. mandshurica* and *J. regia* over those of other species. *S. davidianus* preferred to eat kernels of *A. davidiana* and *Q. wutaishanica*, and *T. triton* preferred to eat kernels of *A. davidiana* also (Fig. 2). The kernel-eating preferences of rodents were different ($P<0.001$

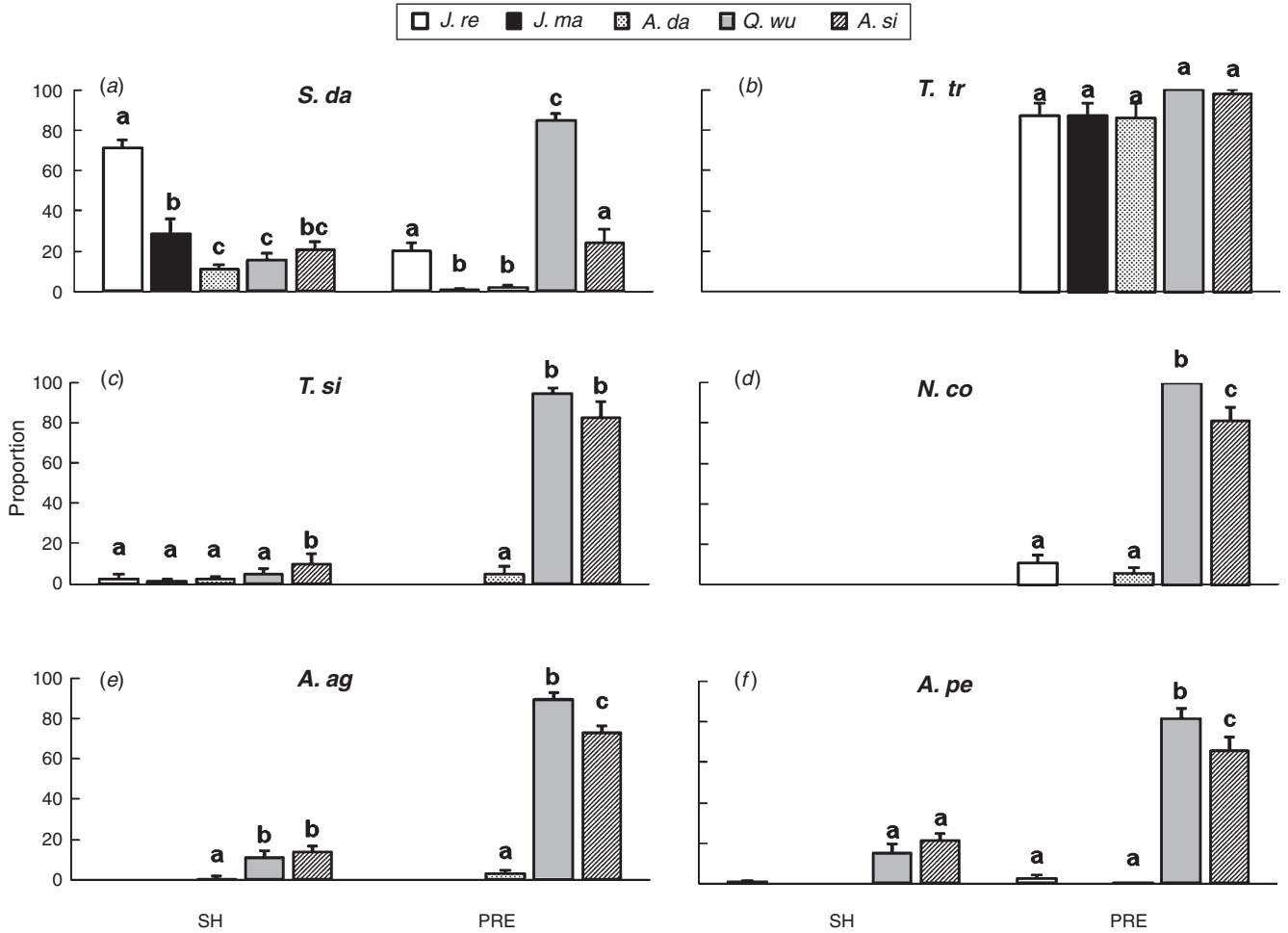


Fig. 1. Proportion of scatter-hoarding and predation of seeds of five tree species by six rodent species under enclosure conditions. Tree species in a descending order of seed size are as follows: *Juglans regia* (*J. re*), *Juglans mandshurica* (*J. ma*), *Amygdalus davidiana* (*A. da*), *Quercus wutaishanica* (*Q. wu*) and *Armeniaca sibirica* (*A. si*). Rodent species in a descending order of bodyweight are as follows: (a) *Sciurotamias davidianus* (*S. da*, $n = 15$), (b) *Tscherskia triton* (*T. tr*, $n = 10$), (c) *Tamias sibiricus* (*T. si*, $n = 9$), (d) *Niviventer confucianus* (*N. co*, $n = 16$), (e) *Apodemus agrarius* (*A. ag*, $n = 11$) and (f) *Apodemus peninsulae* (*A. pe*, $n = 16$). SH, scatter-hoarding (mutualism); and PRE, predation (eating and moving into nest). Data are proportion of seed number (mean \pm se). Bars with the same letters indicate an insignificant ($P > 0.05$) difference.

Table 3. Correlations between seed traits and seed fates handled by six rodent species
 PRE, predation (eating and moving into nest); SH, scatter hoarding (mutualism); n.a., not applicable. * $P < 0.05$ (2-tailed)

Rodent species	Seed fate	Seed weight	Kernel weight	Coat hardness	Crude protein	Crude fat	Crude fibre	Tannin	Caloric value
<i>Sciurotamias davidianus</i>	SH	0.916*	0.930*	-0.212	-0.378	0.921*	-0.649	-0.266	0.898*
	PRE	-0.364	0.164	-0.878*	-0.836	-0.903*	0.723	0.949*	-0.930*
<i>Tscherskia triton</i>	SH	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	PRE	-0.638	-0.181	-0.803	-0.490	-0.753	0.729	0.663	-0.767
<i>Tamias sibiricus</i>	SH	-0.588	-0.280	-0.511	-0.039	-0.207	0.471	0.028	-0.219
	PRE	-0.704	-0.243	-0.887*	-0.446	-0.766	0.783	0.648	-0.777
<i>Niviventer confucianus</i>	SH	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	PRE	-0.868*	-0.151	-0.871*	-0.531	-0.777	0.782	0.686	-0.795
<i>Apodemus agrarius</i>	SH	-0.718	-0.305	-0.688	-0.293	-0.605	0.709	0.451	-0.615
	PRE	-0.691	-0.226	-0.769	-0.473	-0.787	0.786	0.679	-0.799
<i>Apodemus peninsulae</i>	SH	-0.659	-0.261	-0.701	-0.280	-0.530	0.638	0.387	-0.542
	PRE	-0.667	-0.192	-0.890*	-0.500	-0.784	0.776	0.686	-0.798

for all), and were negatively correlated with crude fibre ($P < 0.05$) and positively correlated with caloric value ($P < 0.05$ for all; Table 4). These results indicated that without the protection of the seed coat, all rodent species prefer to eat high-nutrition seeds.

Seed–rodent interactions

Small seeds of medium seed-coat hardness (*A. sibirica*) were involved in more mutualistic interactions with rodents than were soft seeds (*Q. wutaishanica*) and large and/or hard seeds (*A. davidiana*, *J. regia* and *J. mandshurica*) because they were preferred for scatter-hoarding (Fig. 3a). Large rodents (*S. davidianus*) had more mutualistic interactions with large and small seeds and were largely responsible for the dispersal of very large and/or hard seeds (*A. davidiana*, *J. regia* and *J. mandshurica*). Small and medium-sized rodents (*A. peninsulae*, *A. agrarius* and *T. sibiricus*) had mutualistic interactions with small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*) only. *T. triton* and *N. confucianus* did not engage in mutualism with these seed species because they did not scatter-hoard seeds (Fig. 3a).

Small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*) suffered high predation by all rodents, whereas hard and/or large seeds (*A. davidiana*, *J. regia* and *J. mandshurica*) were largely eaten by *T. triton* only (Fig. 3b). From the perspective of rodents, *T. triton* and *N. confucianus* had predatory interactions with all seed species, whereas other rodent species predated small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*) only (Fig. 3b). *A. peninsulae* and *S. davidianus* contributed more to rodent–plant mutualism than did the other species; *N. confucianus*, *A. peninsulae*, *S. davidianus* and *T. triton* tended to predate on seeds because of their high abundance in the study area, and *T. triton* and *N. confucianus* are solely seed predators without benefiting trees via seed dispersal and regeneration (Table 2).

Discussion

The six sympatric rodent species have different scatter-hoarding and predation preferences for seeds of the five tree species,

indicating that they each have different impacts on seed fate, seedling regeneration and the mutualism–predation network. All rodent species negatively affected all tree species by acting as seed predators, but only *S. davidianus*, *T. sibiricus*, *A. peninsulae* and *A. agrarius* engaged in mutualism as seed dispersers. Within the plant–rodent network, diffuse mutualism may occur when one species is dependent on multiple species (Hollander and Vander Wall 2004; Vander Wall and Beck 2012; Chang and Zhang 2014). In a subtropical forest in south-western China, diffuse interactions have been reported between five tree and seven rodent species, and the network is driven by seed and animal traits (Chang and Zhang 2014). Here, we found that seed–rodent mutualism followed a nested structure, as has been reported in several other mutualistic networks (Bascompte 2009). *A. peninsulae* formed mutualistic interactions with seeds of the following four tree species: *A. agrarius* had mutualistic interactions with the seeds of *A. sibirica*, *Q. wutaishanica* and *A. davidiana*; *S. davidianus* and *T. sibiricus* had stronger mutualistic interactions with seeds of all tree species; and *N. confucianus* and *T. triton* (pure granivores) appear to have no positive effect on plant regeneration (Figs 1, 3).

Seed characteristics are variable (Xiao *et al.* 2005) and seed traits (e.g. size, coat hardness, nutrition content and tannin) affect the behavioural decisions of animals (e.g. eat, scatter-hoard or larder-hoard) (Chang *et al.* 2009; Wang *et al.* 2014) and lead to different patterns of seed dispersal and plant regeneration (Lai *et al.* 2014). In addition, rodent traits determine what behaviour (e.g. eat, hoard or reject) is adopted by rodents and affect the fates of plant seeds. We found that both seed and rodent traits significantly shape the structure of the seed–rodent network, supporting previous hypotheses (Chang and Zhang 2014; Wang *et al.* 2014). Large rodents (*S. davidianus* and *T. triton*) selected more large and/or hard seeds (*J. regia*, *J. mandshurica* and *A. davidiana*), whereas smaller (*A. peninsulae* and *A. agrarius*) and medium-sized (*N. confucianus* and *T. sibiricus*) rodents selected small and/or soft seeds (*A. sibirica* and *Q. wutaishanica*) for eating and hoarding, consistent with the seed-size hypothesis (Jansen

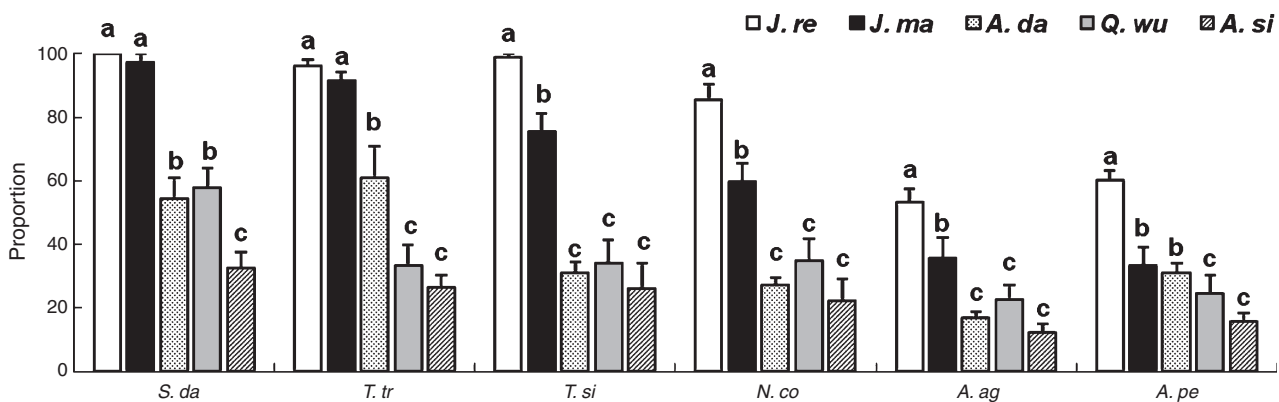


Fig. 2. Kernel eating by six rodent species on five seed species under captive conditions. Seed species in a descending order of seed size are as follows: *Juglans regia* (*J. re*), *Juglans mandshurica* (*J. ma*), *Amygdalus davidiana* (*A. da*), *Quercus wutaishanica* (*Q. wu*) and *Armeniaca sibirica* (*A. si*). Rodent species in a descending order of bodyweight are as follows: *Sciurotamias davidianus* (*S. da*, $n = 12$), *Tscherskia triton* (*T. tr*, $n = 6$), *Tamias sibiricus* (*T. si*, $n = 6$), *Niviventer confucianus* (*N. co*, $n = 10$), *Apodemus agrarius* (*A. ag*, $n = 6$) and *Apodemus peninsulae* (*A. pe*, $n = 8$). Data are proportion of kernel weight (g, mean \pm se). Bars with the same letters indicate an insignificant ($P > 0.05$) difference.

Table 4. Correlations between kernel eating and kernel traits for six rodent species
* $P < 0.05$ (2-tailed)

Rodent species	Crude protein	Crude fat	Crude fibre	Tannin	Caloric value
<i>Sciurotamias davidianus</i>	-0.293	0.251	-0.933*	0.054	0.879*
<i>Tscherskia triton</i>	0.135	0.674	-0.898*	-0.442	0.901*
<i>Tamias sibiricus</i>	-0.405	0.351	-0.894*	-0.021	0.904*
<i>Niviventer confucianus</i>	-0.709	-0.102	-0.887*	0.023	0.884*
<i>Apodemus agrarius</i>	-0.448	0.332	-0.897*	-0.003	0.911*
<i>Apodemus peninsulae</i>	-0.587	0.234	-0.902*	0.091	0.879*

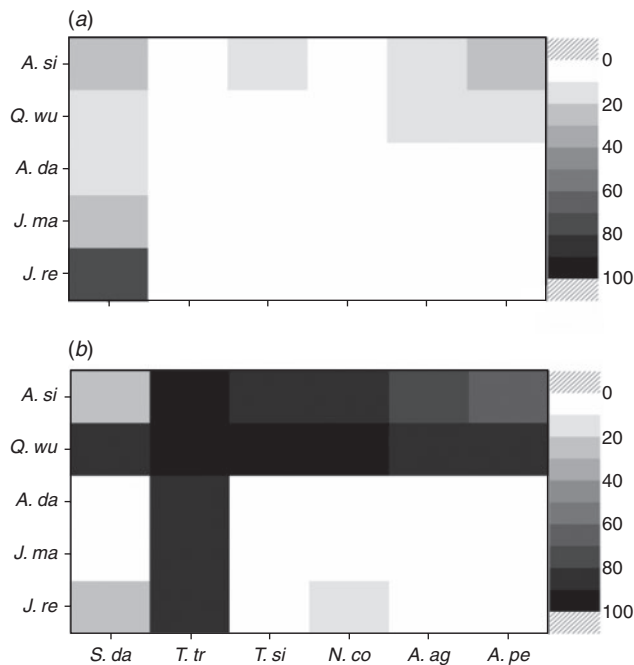


Fig. 3. Interaction strength between six rodent species and five tree species for (a) mutualism (scatter-hoarding) and (b) seed predation. Tree species in a descending order of seed size are as follows: *Juglans regia* (*J. re*), *Juglans mandshurica* (*J. ma*), *Amygdalus davidiana* (*A. da*), *Quercus wutaishanica* (*Q. wu*) and *Armeniaca sibirica* (*A. si*). Rodent species in a descending bodyweight are as follows: *Sciurotamias davidianus* (*S. da*, $n = 15$), *Tscherskia triton* (*T. tr*, $n = 10$), *Tamias sibiricus* (*T. si*, $n = 9$), *Niviventer confucianus* (*N. co*, $n = 16$), *Apodemus agrarius* (*A. ag*, $n = 11$) and *Apodemus peninsulae* (*A. pe*, $n = 16$). Data are proportion of seeds handled by rodents (%), and reflected by the darkness).

et al. 2002) and the body size-structured hypothesis (Ben-Moshe *et al.* 2001; Chang and Zhang 2014; Wang *et al.* 2014). All rodents preferred to eat soft seeds (*Q. wutaishanica*) and hoard hard seeds, supporting the high handling-time hypothesis, whereby an animal would be more likely to cache a seed than to eat it if it takes longer to eat the seed than it does to store (Jacobs 1992; Zhang and Zhang 2008). The high handling-time hypothesis was further supported by the observation that all rodents preferred to eat the nutritional kernels of hard seeds (*J. regia* and *J. mandshurica*) but rejected or hoarded these seeds if the seed coat was intact (Fig. 2, Table 4). However, when rejected seeds were excluded from our analyses, all rodents tended to hoard high-nutrition seeds

(high fat, caloric and a large size) and eat low-nutrition seeds (low caloric, low fat and small size), except *A. agrarius* whose preferences for scatter-hoarding and predation were not correlated with any seed trait (Fig. 2, Table 3). These results support the nutrition hypothesis that high-nutrition seeds are more likely to be hoarded by small rodents (Lewis 1982; Izhaki 2002). Kernel-eating preferences were negatively correlated with crude fibre content and positively correlated with caloric value in all species, further supporting the nutrition hypothesis. We found that high handling-time seeds (large and/or hard seeds) suffered less predation by rodents and enhanced hoarding, suggesting that seed traits (e.g. heavy weight and hard coat) with high handling time may increase rodent mutualism by reducing seed predation (Zhang and Zhang 2008).

Animal behaviour may be altered in enclosures because of spatial limitations, and the absence of competitors or predators. Further, the dispersal and predation of seeds may have been underestimated in our study because seeds do not mature simultaneously in nature and a higher abundance of predators and dispersers may occur during seed fall. Further studies should assess interactions between seeds and rodents under more natural conditions.

In conclusion, we found that different rodent species play different roles in influencing the seed fate of trees. These results have applied implications, namely that so as to foster restoration of degenerated forests, it will be necessary to introduce or protect large-sized seed dispersers (e.g. *S. davidianus*) and reduce the population density of pure seed eaters (e.g. *N. confucianus* and *T. triton*).

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