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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Seed trait-mediated selection by rodents affects mutualistic interactions and seedling recruitment of co-occurring tree species

Hongmao Zhang[1,2] · Chuan Yan[2] · Gang Chang[3] · Zhibin Zhang[2]

Abstract As mutualists, seed dispersers may significantly affect mutualistic interactions and seedling recruitment of sympatric plants that share similar seed dispersers, but studies are rare. Here, we compared seed dispersal fitness in two co-occurring plant species (*Armeniaca sibirica* and *Amygdalus davidiana*) that inhabit warm temperate deciduous forest in northern China. We tested the hypothesis that seed trait-mediated selection by rodents may influence mutualistic interactions with rodents and then seedling establishment of co-occurring plant species. *A. davidiana* seeds are larger and harder (thick endocarps) than *A. sibirica* seeds, but they have similar levels of nutrients (crude fat, crude protein), caloric value and tannin.

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✉ Hongmao Zhang
zhanghm@mail.ccnu.edu.cn

✉ Zhibin Zhang
zhangzb@ioz.ac.cn

Chuan Yan
yanc@ioz.ac.cn

Gang Chang
snow1178@snnu.edu.cn

[1] Animal Behaviour Research Group, School of Life Sciences, Central China Normal University, Wuhan 430079, Hubei, China

[2] State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

[3] Shaanxi Institute of Zoology, Xi'an 710032, Shaanxi, China

More *A. sibirica* seedlings are found in the field. Semi-natural enclosure tests indicated that the two seed species were both harvested by the same six rodent species, but that *A. sibirica* had mutualistic interactions (scatter hoarding) with four rodent species (*Apodemus peninsulae*, *A. agrarius*, *Sciurotamias davidianus*, *Tamias sibiricus*), and *A. davidiana* with only one (*S. davidianus*). Tagged seed dispersal experiments in the field indicated that more *A. sibirica* seeds were scatter-hoarded by rodents, and more *A. sibirica* seeds survived to the next spring and became seedlings. *A. sibirica* seeds derive more benefit from seed dispersal by rodents than *A. davidiana* seeds, particularly in years with limited seed dispersers, which well explained the higher seedling recruitment of *A. sibirica* compared with that of *A. davidiana* under natural conditions. Our results suggest that seed dispersers may play a significant role in seedling recruitment and indirect competition between co-occurring plant species.

Keywords Plant–animal mutualism · Plant regeneration · Seed dispersal · Seed trait · Small rodents

Introduction

Seed dispersal, the movement of seeds away from parent trees, plays a significant role in determining the structure and dynamics of plant populations and communities (Nathan and Muller-Landau 2000). Rodents are prominent seed dispersers of plants because they move seeds from mother trees, partially deposit these seeds into safe sites, and fail to retrieve a portion of them (Jansen and Forget 2001; Zhang et al. 2005). Rodents may generate different seed dispersal patterns among tree species with different seed traits, leading to different plant regeneration and

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community structures (Hollander and Vander Wall 2004; Zhang et al. 2005). Previous studies have indicated that scatter-hoarding rodents are essential in affecting seed fates and seed dispersal patterns of plant species (e.g., Jansen and Forget 2001; Zhang et al. 2005; Beck and Vander Wall 2010; Vander Wall 2010).

Seed trait-mediated selection by animals has been extensively investigated (reviewed by Zhang et al. 2005; Vander Wall 2010; Vander Wall and Beck 2012). Both seed and animal traits affect seed fate of plants, and finally affect the dispersal fitness of plants (Jansen and Forget 2001). In general, seeds with a large size, hard coat, high nutritional content, dormancy and high tannin are more often dispersed by animals, whereas seeds with small size, soft coat, low nutritional content, nondormancy, low tannin, or insect infestations are often consumed immediately by animals (reviewed by Vander Wall 2010; Vander Wall and Beck 2012; Chang and Zhang 2014; Wang et al. 2014; Zhang et al. 2015). But how seed trait-mediated selection by rodents affects on plant–animal mutualism and seedling establishment has rarely been investigated among co-occurring plant species.

Co-fruiting and animal-dispersed plants with different seed traits will have different mutualistic interaction with animals and thus have different dispersal fitness and seedling recruitment. We hypothesized that seed traits may mediate mutualistic interaction between seeds and rodents and then affect seedling recruitment of co-occurring plant species. Because only scatter-hoarded seeds benefit seedling recruitment of plants, the mutualistic interaction of a plant species with animals is measured by the number of animal species which scatter-hoard seeds and the scatter-hoarding intensity of each species.

Wild apricot (*Armeniaca sibirica*) and wild peach (*Amygdalus davidiana*) (Rosaceae) are both found in warm temperate forests in northern China. They have similar habitat requirements and phenological characters, and thus often co-occur in open and sunny habitats after deforestation (Zhang and Zhang 2008). They have similar seed production patterns, seed germination and seedling establishment; but *A. sibirica* trees and seedlings predominate over *A. davidiana* in the field. These species heavily depend upon small rodents to disperse their seeds (Zhang and Zhang 2008). Seeds of the two plants are similar in nutrients, tannin and caloric value, but seeds of *A. davidiana* are larger, heavier and harder (thick endocarps) than those of *A. sibirica* (Table S1). Preliminary observations suggest that *A. sibirica* seeds are more likely to be harvested and scatter-hoarded by rodents than those of *A. davidiana* because of differences in seed coat thickness (Zhang and Zhang 2008). Here, we tracked rodent-mediated seed dispersal processes and seedling establishment across these tree species under enclosure and field conditions. We

sought to test the hypothesis that seed trait-mediated selection by rodents affects mutualistic interaction and seedling recruitment of co-occurring plant species. We predicted that *A. sibirica* (with a higher seedling recruitment under natural conditions) should have more mutualistic interactions with rodents than *A. davidiana* (lower seedling recruitment).

Materials and methods

Study site

We conducted experiments at the Liyuanling Field Station in Mount Donglingshan (40°00′N, 115°30′E; 800–1400 m a.s.l; 120 km northwest of Beijing city). This mountainous area has a temperate continental monsoon climate and an average annual temperature of 6.5 °C and annual precipitation of 600 mm. Dominant landcover in the study area comprises shrublands, secondary forests and abandoned farmlands. Common plant covers are trees and shrubs such as *Quercus wutaishanica*, *A. sibirica*, *Juglans mandshurica*, *Ulmus laciniata*, *Larix principis-rupprechtii*, *A. davidiana*, annual herbs and sparsely planted trees (e.g., *J. regia*) (Zhang and Zhang 2008). *Niviventer confucianus*, *Apodemus peninsulae*, *A. agrarius*, *Sciurotamias davidianus*, *Tscheskia triton* and *Tamias sibiricus* are common seed-eating and/or -hoarding rodents in the area (Zhang and Zhang 2008).

Enclosure experiments

We conducted enclosure experiments from July to September in 2005 and 2006 using *S. davidianus* (8♂/8♀, 204.9 ± 49.3 g body mass, mean ± SD), *T. triton* (5♂/3♀, 130.2 ± 4.4 g), *T. sibiricus* (10♂/2♀, 69.2 ± 7.0 g), *N. confucianus* (9♂/7♀, 68.3 ± 8.9 g), *A. agrarius* (3♂/5♀, 26.3 ± 2.3 g), and *A. peninsulae* (8♂/8♀, 21.6 ± 2.3 g). We wanted to investigate whethter *A. sibirica* has more seed dispersers (mutualists) than *A. davidiana*.

Four enclosures (10 m × 10 m) were constructed in open areas at the Liyuanling Field Station (see Lu and Zhang 2008). Brick walls of the enclosures (0.3 m thickness) were 1.0 m above ground and 0.3 m below the ground surface. Within enclosures, a layer of sandy soil (5–10 cm) was spread on the ground surface as hoarding substrates for animals. In order to keep animals from entering or leaving, each enclosure was covered with wire mesh (1.2 cm × 1.2 cm grid, supported by a framework of steel tube). Grass was scattered on the mesh to simulate canopy cover in the field (~50 %), and grass, branches, rocks and bricks were dispersed on the ground surface within enclosures to simulate ground cover in the field (~30 %). One

wooden nest box (40 cm × 20 cm × 20 cm, simulating burrow conditions) and a water plate were placed in one corner, and tin-tagged seeds (20 *A. sibirica* and 20 *A. davidiana*) were placed in the center of the enclosures as seed stations for hoarding.

Experimental seeds were collected randomly from 50 *A. sibirica* and *A. davidiana* away from the field experimental plots (plot distance >500 m) during seedfall in experimental years. All seeds of a species collected from different trees were mixed together to create a single sample and spread out on absorbent paper in a dry, well-ventilated room to prevent mildew and fungal damage. Experimental seeds were tagged following the tin-tag method: a unique coded tin-tag (3.0 × 1.0 cm, 0.1 g) was tied to a seed using a 3-cm piece of fine steel wire to facilitate relocation of dispersed seeds (Zhang and Wang 2001). This method is effective at tracking rodent-dispersed seeds under enclosure and wild conditions (Xiao et al. 2006).

We used live-traps (12 cm × 12 cm × 25 cm steel cages) to capture experimental animals near the field station (>500 m from field experiment plots) during July–September in 2005 and 2006. Traps (20–30) were placed along 4–5 transects (150 m long, >50 m apart) at 5-m intervals and covered with a board to protect animals from rain and direct sunlight. Fresh peanuts as bait, small pieces of cucumber as water supply and local dry leaves as nest material were included in each trap. We set traps between 1630 and 1830 hours and checked them for the following 3–5 days at 0600–0730, 1130–1300, and 1730–1830 hours each day. Captured animals were covered and carefully transferred to the laboratory using a nylon bag. Each individual was sexed, weighed, labeled and 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 D/L). Water and nest materials (wood chips or cotton) were provided ad libitum. Commercial mouse chow (Keao Feed, Beijing, China) were provided ad libitum. Seeds and nuts from local plants (*Q. wutaishanica*, *A. sibirica*, *J. mandshurica*, *J. regia* and *A. davidiana*) were provided to ensure a natural diet; 5–10 g of peanuts per animal was provided every 1–2 days as a nutritional supplement. Animals were acclimatized to laboratory conditions at least a full week prior to testing. All animals maintained their health and weight during the period of housing and testing. After experiments, animals were released to the trapping site or kept in the laboratory for other experiments. No pregnant or lactating animals were captured during the trapping season. Animal trapping and usage were approved by the local government, and under a permit provided by our institutes.

Each animal was kept in an enclosure for 2 days during each observation. Subjects were introduced into the enclosure at 1200 hours for habituation on day 1, and removed at the end of day 2 when testing was complete. Tagged seeds were placed in the enclosure at the beginning of day 2, and checked after 24 h (1200–1400 hours). The enclosures were cleared by removing all seeds and their fragments, scarifying the soil and replacing nests and water plates; a break of 1 day was allowed to limit possible interactions between observations.

Seed fates within the enclosure were recorded as intact in situ (IIS) when seeds were intact at the original station; eaten (E) when seeds were eaten in and out of the nest box; scatter-hoarded (SH) when seeds were intact and buried in litter or soil; or larder-hoarded (LH) when seeds were intact in the nest box, similar to the seeds stored in burrow of a rodent in the field. IIS reflects total harvest, SH represents mutualism, and E + LH (defined as PRE) represents a predation relationship between rodent and plant (see also Wang et al. 2014; Zhang et al. 2015). The proportion of each seed fate (IIS, E, SH, LH and PRE) relative to the total number of released seeds was calculated for statistical analysis.

Field experiments

We conducted field experiments in two stands (3.0 ha each, >500 m apart to ensure independence) in a shrubland and a secondary forest near the field station. We conducted experiments during the period of seedfall of *A. sibirica* and *A. davidiana*, and when the caching activities of small rodents are high (July–September in 2005, 2006 and 2007). The shrubland has a 20°–30° southeastern-facing slope dominated by young *Q. wutaishanica*, *U. laciniata* of 2.4 ± 1.9 m (mean ± SD, *n* = 100) height and 70 % total cover, and covered by annual herbs, dwarf shrubs and litter under shrub cover. The secondary forest is located on a northeastern-facing slope of 30°–40°, dominated by *Q. wutaishanica*, *U. laciniata*, *A. sibirica*, *L. principis-rupprechtii* and *J. mandshurica* with 8.5 ± 3.4-m-tall (*n* = 100) and nearly 100 % canopy cover, with litter, bare ground, annual herbs and some dwarf shrubs beneath the canopy. We located 20 seed stations in 2005, and 15 seed stations in 2006 and 2007 (1.0 m × 1.0 m, >30 m apart) along three parallel transects (150 m long, >30 m apart) within each experimental stand for seed placement. The intervals between stations (>30 m) basically ensured independence because more than 95 % of primary caches of seeds hoarded by small rodents in shrubland and forests were less than 30 m from the seed stations in the study area (*Q. wutaishanica*, Zhang et al. 2008; *A. sibirica*, Zhang et al. 2013; *J. mandshurica*, Zhang et al. 2014).

Experimental seeds were collected during seedfall in experimental years and marked using the tin-tag method above. During the dispersal period of *A. sibirica* and

A. davidiana seeds (July–August) in the field, tagged seeds (20 *A. sibirica* and 20 *A. davidiana* seeds in 2005; 30 *A. sibirica* and 30 *A. davidiana* seeds in 2006 and 2007) were placed at each seed station as food sources for small rodents for eating and hoarding. A total of 1,300 seeds of each species were released over the 3 years. Daily checking (between 1030 and 1500 hours) began after seed placement and stopped when few seeds remained at the seed station and few primary caches remained at their original sites (23 days in 2005, 20 days in 2006 and 23 days in 2007 in total). On each day, the seeds remaining at each seed station were recorded and dispersed seeds were relocated within the plot and nearby area (~50 m around each plot). Seed harvest rate was defined as the proportion of remaining seeds relative to the total number of released seeds at each seed station. For each relocated cache, seed fate, dispersal distance (distance between cache site and seed source), cache density (nearest distance between neighbors), cache site characteristic (vegetation type, substrate, and canopy cover), and cache survival time (time of a cache remained at the original site) were recorded (see Zhang et al. 2013). Cache sites were mapped and marked for later checking. Surviving seeds and seedlings established from rodent-made caches were recorded the following spring (April–May). Proportions of seed survival at different stages and seedling establishment the following spring were defined as seed or seedling numbers relative to the total number of cached seeds.

Following our previous studies (e.g., Zhang et al. 2008, 2013), seed fates at seed stations were defined as: (1) intact in situ (IIS); (2) eaten in situ (EIS) when eaten at the seed stations; seed fates after removal were defined as: (3) scatter-hoarded (SH); (4) intact after removal (IAR) when intact and left on the ground surface after removal (probably due to disturbances by predators and competitors); (5) eaten after removal (EAR) when eaten out of the seed stations; and (6) missing (M) when not relocated and their fate not confirmed. SH represents the benefits of plants from seed dispersers because only SH seeds likely become seedlings. The proportion of each seed fate relative to total released seeds was calculated for statistical analysis.

Vegetation type at cache site were classified as: (1) under shrub (US) when seeds were buried under dense shrub cover; (2) shrub edge (ES) when caches were located at the edge of shrub cover (±0.5 m), near open areas where light penetrated the forest floor; (3) bare ground (BG) when caches were in open ground outside any cover; and (4) open grassland (OG) when caches were buried in open grassland without shrub cover. Cache substrate, the materials directly covering seeds, were classified as: (1) soil (S) when caches were covered soil only; (2) litter (L) when caches were covered with leaves and/or twigs; and (3) grass (G) when caches were covered by grass only. Canopy cover

by trees or high shrubs (≥1.5 m) over a cache site was measured using a spherical densitometer. The proportion of each category relative to total cached seeds was calculated for statistical analysis.

Three consecutive days of animal trapping was conducted as above in each plot at the end of the experiments to estimate rodent abundance during the experimental years. Forty live-traps were set up in each plot along a 4×10 array, about 7 m apart. A total of 480 trap-days were conducted in each year. Captured animals were marked with black ink and released immediately after species identification. Trapping success (number of captured individuals/total trap-days $\times$ 100 %) denoted rodent abundance.

Mature trees of ten 100 m $\times$ 3 m transects (>50 m apart) near the field station were recorded to estimate tree abundance in the study area, and 20 of each species were randomly selected to assess seed abundance per tree each year. Seed abundance in the study area was measured by seed abundance per tree $\times$ tree abundance. New seedlings in these transects were recorded in the following spring (May) to estimate natural seedling recruitment of the two tree species.

Relationships among seed abundance, seed dispersal, seedling establishment and rodent abundance of the two species were analyzed.

Kernel-eating test

To investigate the effects of seed coat on the seed preferences of rodent species, we used seed kernels from the two tree species to feed common rodent species (*S. davidianus*: 4♀/4♂, 270.7 ± 20.2 g body mass; *A. peninsulae*: 4♀/4♂, 22.8 ± 2.3 g body mass; and *N. confucianus*: 4♀/6♂, 62.2 ± 8.5 g body mass; mean ± SD) under captive conditions in September 2006. The animals used in this experiment were captured around the field station and maintained in the laboratory following methods described above. A total of 30 g *A. sibirica* and 30 g *A. davidiana* kernels for *S. davidianus*, and 10 g *A. sibirica* and 10 g *A. davidiana* kernels for *A. peninsulae* and *N. confucianus* were provided to each animal within 24 h. All kernels were mixed together in a plate (5.0 cm diameter). Subjects were food-deprived at least 6 h before tests by removing all food items in cages. Kernels were provided at 1200 hours and remains were collected and weighed separately after 24 h. The mass eaten was defined as the mass of the remains subtracted from the total mass provided to an animal.

Data analyses

For enclosure tests, the generalized linear mixed (GLM) multivariate model was used to test the effects of tree species, animal sex (fixed factors) and their interactions on

seed fate (dependent variables) for each rodent species. Paired-sample *t* tests were used to compare differences in seed fate and kernel eating between the two tree species.

For field tests, the Cox regression was used to identify differences in seed survival at seed stations between tree species, stand, year and their interactions. The linear mixed model (LMM) was used to test the main effects of tree species on seed fate, dispersal distance, cache density, cache survival time, and cache site characteristics (canopy cover, vegetation type and substrate) by taking stand and year as random factors first, then to test the interactive effect of tree species with either year or stand by taking stand or year as a random factor. The Wilcoxon test was used for pairwise testing between two tree species with respect to canopy cover, each category of cache substrate and vegetation type, dispersal distance, cache density and cache survival time in different stand in 2006 (data in 2005 and 2007 were not analyzed because of the small sample size of *A. davidiana* seeds). Independent samples *t* tests was used to test differences in seed abundance and seedling abundance between two tree species in each year.

All proportion data (seed fates, vegetation types) were arcsine square root-transformed to achieve normal or approximate normal distributions before analysis. SPSS v.16.0 (SPSS, Chicago, USA) was used for statistical analyses. All statistical tests were two-tailed, and differences were significant when *P* < 0.05.

Results

Enclosure tests

Tree species affected the seed fates of seeds handled by all rodents except *T. triton*. Rodent sex had no effect on seed fates except for *A. peninsulae* where females harvested and hoarded more seeds than males (Fig. 1). No significant interaction between tree species and the sex of rodents was observed. As compared to seeds of *A. davidiana*, *A. sibirica* seeds were harvested more by all rodent species (the proportion of *A. sibirica* vs. *A. davidiana* for *S. davidianus*: 47.5 vs. 11.6 %; for *T. triton*: 95.6 vs. 90 %; for *T. sibiricus*: 16.2 vs. 0.8 %; for *N. confucianus*: 37.5 vs. 3.4 %; for *A. agrarius*: 29.1 vs. 5.0 %; and for *A. peninsulae*: 47.5 vs. 2.2 %); eaten more (for *S. davidianus*: 22.2 vs. 1.6 %; for *T. triton*: 26.9 vs. 11.9 %; for *T. sibiricus*: 4.2 vs. 0 %; for *N. confucianus*: 19.7 vs. 1.9 %; for *A. agrarius*: 5.3 vs. 0 %; and for *A. peninsulae*: 20.9 vs. 0 %); scatter-hoarded more by four rodent species (for *S. davidianus*: 24.4 vs. 7.8 %; for *T. sibiricus*: 6.5 vs. 0.8 %; for *A. agrarius*: 14.4 vs. 2.5 % and for *A. peninsulae*: 10.6 vs. 0.6 %); and larder-hoarded more by three rodent species (for *T. sibiricus*: 9.1 vs. 0 %; for *N. confucianus*: 14.4 vs. 1.6 % and for *A. peninsulae*: 17.8 vs. 0.9 %) (all *P* < 0.05) (Fig. 1). *A. sibirica* showed mutualism (represented by SH) with four rodent species (*S. davidianus*, *T. sibiricus*, *A. agrarius*

Fig. 1 Seed fates of *Armeniaca sibirica* and *Amygdalus davidiana* seeds handled by six species of small rodent under semi-natural enclosure conditions. Rodent species are listed in descending order of body weight. Data are proportions of seed number of $\bar{X} \pm$ SE. ****P* < 0.001, ***P* < 0.01 and **P* < 0.05 indicate significant differences in seed number of each seed fate between seeds using paired-sample *t* tests. *IIS* intact in situ, *E* eaten, *SH* scatter-hoarded, *IAR* intact after removal, *LH* larder-hoarded
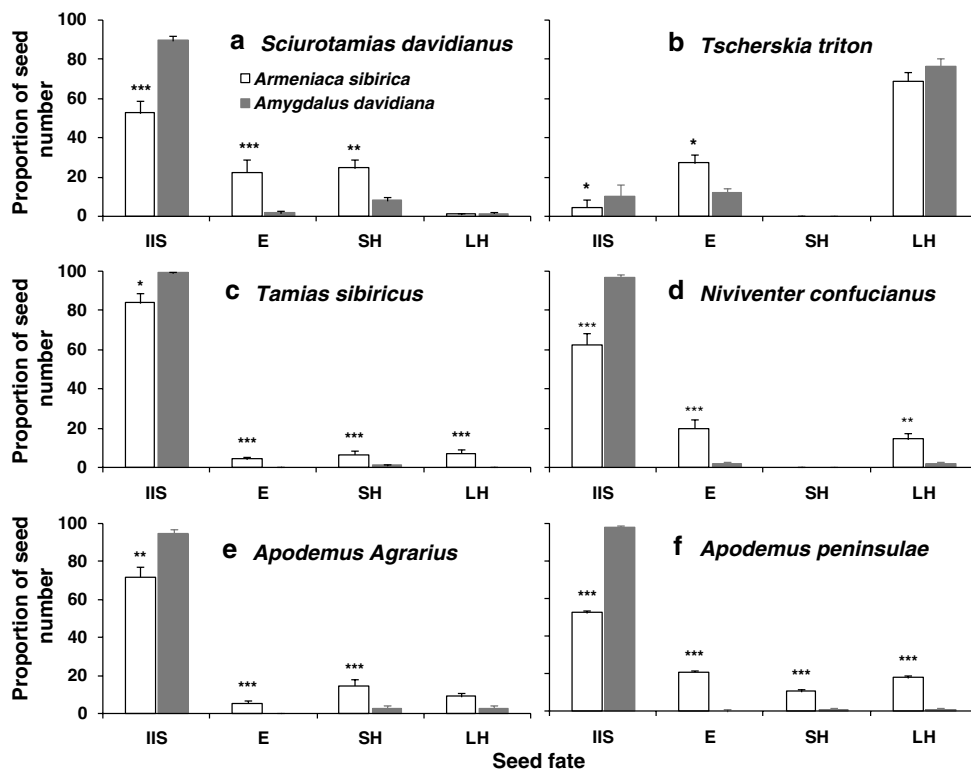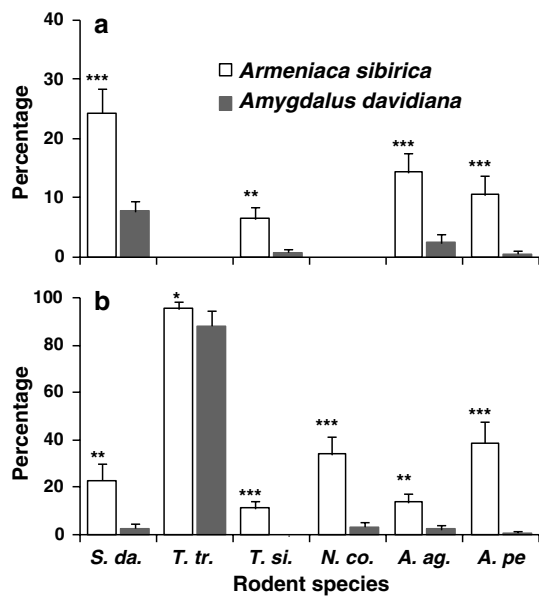
Fig. 2 Interaction strength between six rodent species and two tree species for **a** mutualism (scatter-hoarding) and **b** seed predation (eating and larder hoarding). *S. da. Sciurotamias davidianus*, *T. tr. Tscherskia triton*, *T. si. Tamias sibiricus*, *N. co. Niviventer confucianus*, *A. ag. Apodemus agrarius*, *A. pe. Apodemus peninsulae*. Data are proportions of seeds handled by rodents of $\bar{X} \pm$ SE. ***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$ indicate significant differences in seed number of each seed fate between seeds using paired-sample t tests

and *A. peninsulae*) and predation (represented by LH + E) interactions with all rodent species, while *A. davidiana* showed mutualism with *S. davidianus* and predation interaction with *T. triton* primarily (Fig. 2). These results indicate that *A. sibirica* had greater mutualistic interaction with rodents (as measured by number of seed dispersers and proportion of scatter-hoarded seeds) than *A. davidiana*.

Field test

Seed harvest rates were affected by tree species (Wald $= 142.965$, $df = 1$, $P < 0.001$) and year (Wald $= 76.382$, $df = 2$, $P < 0.001$). Seeds of *A. sibirica* were removed faster than *A. davidiana* seeds in all stands and years (Fig. 3). Using LMM and taking stand and year as random effects, we found a main effect of tree species on IIS (*A. sibirica* < *A. davidiana*, $F_{1,196} = 169.8$, $P < 0.001$), EIS (*A. sibirica* > *A. davidiana*, $F_{1,196} = 17.1$, $P < 0.001$), SH (*A. sibirica* > *A. davidiana*, $F_{1,196} = 71.8$, $P < 0.001$), IAR (*A. sibirica* > *A. davidiana*, $F_{1,196} = 41.5$, $P < 0.001$), and EAR (*A. sibirica* > *A. davidiana*, $F_{1,196} = 57.9$, $P < 0.001$) (Fig. 4a; Table S2). When taking only year as the random effect, we found a main effect of tree species in IIS (*A. sibirica* < *A. davidiana*, $F_{1,196} = 169.8$, $P < 0.001$), EIS (*A. sibirica* > *A. davidiana*, $F_{1,196} = 17.1$, $P < 0.001$), SH

(*A. sibirica* > *A. davidiana*, $F_{1,196} = 69.9$, $P < 0.001$), IAR (*A. sibirica* > *A. davidiana*, $F_{1,196} = 41.5$, $P < 0.001$), and EAR (*A. sibirica* > *A. davidiana*, $F_{1,196} = 57.9$, $P < 0.001$). No significant effect of stand or interaction with tree species was found (Table S2). When taking stand as a random effect, LMM analysis indicated a main effect of tree species on EIS (*A. sibirica* > *A. davidiana*, $F_{1,198} = 17$, $P < 0.001$), IAR (*A. sibirica* > *A. davidiana*, $F_{1,196} = 41.5$, $P < 0.001$) and EAR (*A. sibirica* > *A. davidiana*, $F_{1,196} = 57.9$, $P < 0.001$). *A. sibirica* were more often eaten in situ (EIS) and after removal (EAR) than *A. davidiana*; *A. sibirica* also had more intact seeds after removal (IAR) than *A. davidiana* (Fig. 4b; Table S2). There were significant interactive effects between tree species and year for IIS ($F_{2,194} = 22.1$, $P < 0.001$), SH ($F_{2,193} = 27.6$, $P < 0.001$) and M ($F_{2,194} = 40.7$, $P < 0.001$) (Table S2). Less *A. sibirica* seeds were intact in situ (IIS) than those of *A. davidiana* in all 3 years, and the difference was 2005 > 2007 > 2006 (Table S3). More *A. sibirica* seeds were scatter-harvested (SH) than *A. davidiana* in 2005 and 2007, not in 2006, and the difference was 2005 < 2007 (Table S3). For missing seeds (M), there were differences between *A. sibirica* and *A. davidiana* in 2005 and 2007, but not in 2006 (*A. sibirica* > *A. davidiana* in 2005, *A. sibirica* < *A. davidiana* in 2007; Table S2). These results indicate that *A. sibirica* derives more benefits from seed dispersers as measured by SH (proportion of scatter-hoarded seeds) than *A. davidiana* at the stage of seed caching because rodents preferred to harvest and hoard seeds of *A. sibirica*.

Using a LMM model with stand and year as random factors, we did not find a main effect of tree species on dispersal distance, cache density, cache survival time and cache site characteristics (canopy cover, vegetation type and substrate) (all $P > 0.05$) (Table S4). Using Wilcoxon tests for pairwise testing in different stands and years, we found that *A. sibirica* seeds were dispersed further than *A. davidiana* seeds in shrubland in 2006 (7.9 ± 5.5 vs. 5.4 ± 4.4 m, mean $\pm$ SD, $Z = -3.768$, $P = 0.036$) (Table S4). These results suggest that the two tree species have similar dispersal fitness when their seeds are cached by small rodents. However, more *A. sibirica* seeds survived until the following spring and became seedlings than *A. davidiana* seeds, implying that *A. sibirica* is more successful in seedling recruitment than *A. davidiana* under rodent predation (Table S4).

There was no significant difference of seed abundance per tree between *A. sibirica* and *A. davidiana*, but *A. sibirica* had significantly higher seed abundance than *A. davidiana* in all years because there are more mature *A. sibirica* trees in the field (Table 1). More *A. sibirica* seedlings were established in the field than *A. davidiana* in all years. Seed abundance was low but rodent abundance was high in 2006, while this was opposite in 2005 and 2007 (Table 1).
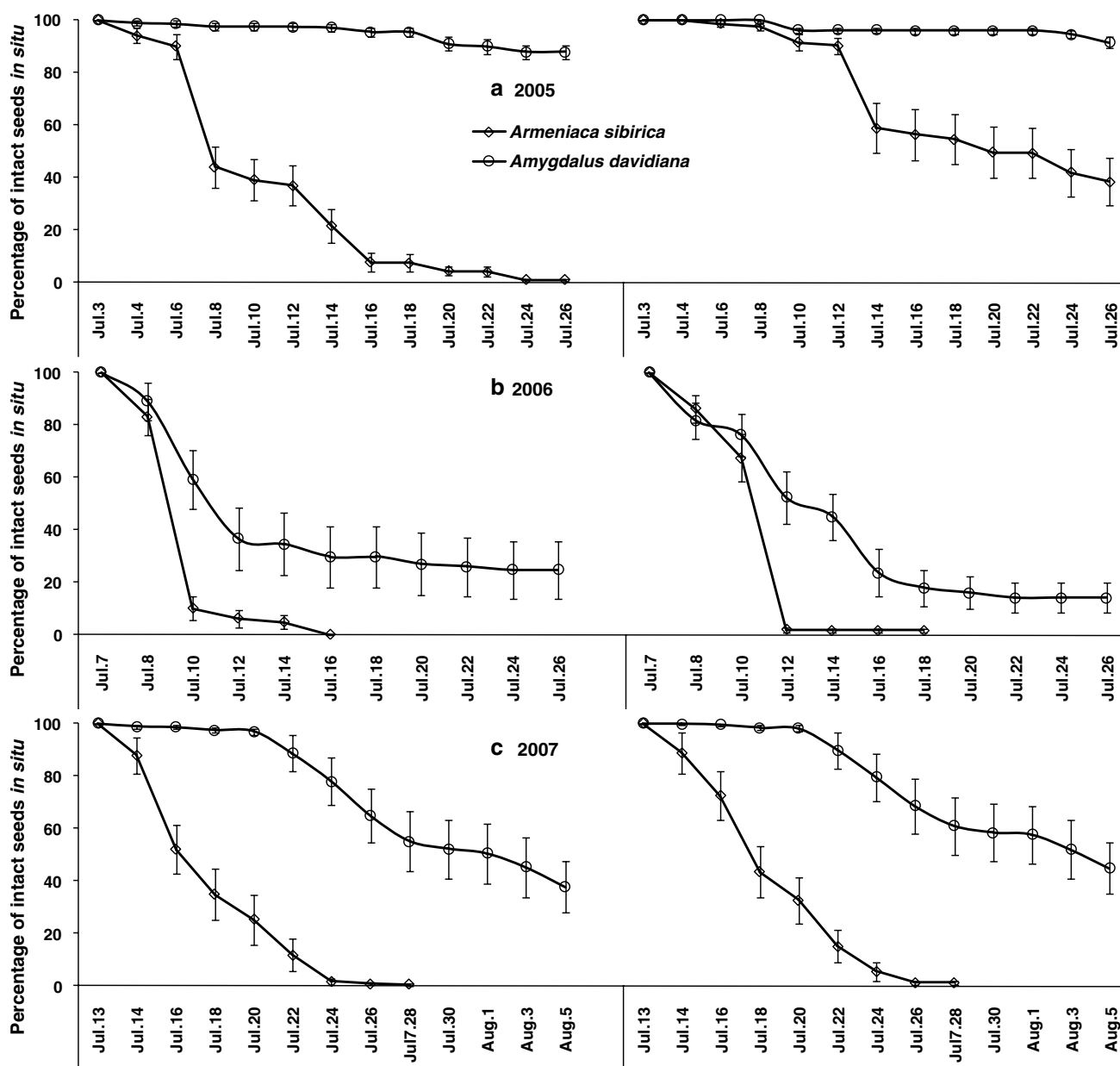
Fig. 3 Dynamics of seeds of *Armeniaca sibirica* and *Amygdalus davidiana* harvested by small rodents within different stands and years in the field. Data are frequencies of $\bar{X} \pm$ SE

Compared to *A. davidiana* seeds, more *A. sibirica* seeds were scatter-hoarded in 2005 and 2007 when seed abundance was high and rodent abundance was low, but the difference was not significant in 2006 when seed abundance was low and rodent abundance was high (Table 1), suggesting that *A. sibirica* seeds had an advantage over *A. davidiana* when competing for seed dispersers when they were limited.

Kernel-eating test

Under captive conditions, kernels of *A. sibirica* seeds were less eaten by *S. davidianus* as compared to *A. davidiana* (the proportion of *A. sibirica* vs. *A. davidiana*: 14.0 vs. 32.5 %), *N. confucianus* (27.4 vs. 40.1 %) and *A. peninsulae* (20.9 vs. 27.8 %) (all $P < 0.05$). These results indicate that seed coat thickness, instead of kernel value, resulted
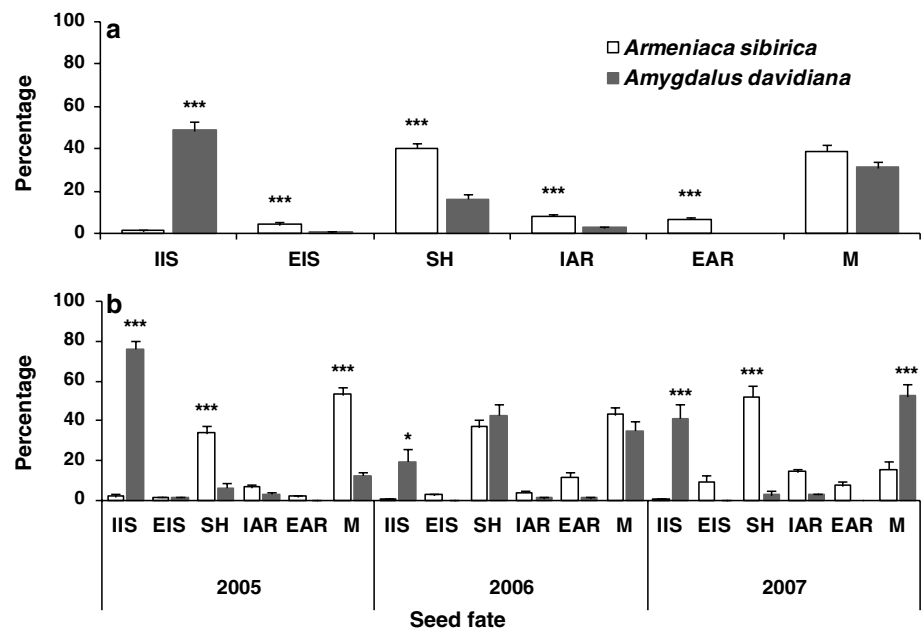
Table 1 Seed abundance per tree, mature tree abundance, seed abundance, seed dispersed by rodents, new seedling abundance of *Armeniaca sibirica* and *Amygdalus davidiana*, and rodent abundance in the three experimental years

Year	Tree species	Seed abundance per tree $\bar{X}$ ($\pm$SD) $n = 20$	Tree abundance $\bar{X}$ ($\pm$SD) $n = 20$	Seed abundance $\bar{X}$ ($\pm$SD) $n = 20$	Seed dispersed n (%)	Seedling abundance $\bar{X}$ ($\pm$SD) $n = 10$[a]	Rodent abundance n (Ts)
2005	*A. sibirica*	251.5 (66.3)	15.6 (12.5)	3923.4 (3154.1)	259 (32.4)	17.2 (16.4)	17 (3.5)
	A. davidiana	229.5 (64.2)	2.7 (3.6)	635.0 (842.0)	52 (6.5)	0.7 (1.2)	
2006	*A. sibirica*	31.0 (12.9)	15.6 (12.5)	483.6 (388.8)	289 (32.1)	2.8 (3.2)	51 (10.6)
	A. davidiana	33.4 (15.6)	2.7 (3.6)	92.4 (122.5)	307 (34.1)	0.5 (1.1)	
2007	*A. sibirica*	140.0 (46.9)	15.6 (12.5)	2184.0 (1755.8)	389 (43.2)	14.8 (17.2)	21 (4.4)
	A. davidiana	127.2 (57.3)	2.7 (3.6)	351.9 (466.6)	19 (2.1)	1.1 (2.1)	

480 traps per year

Ts trapping success

[a] Data of seedlings abundance were investigated by the following spring

in the difference between *A. sibirica* and *A. davidiana* in seed selection and dispersal by rodents under enclosure and natural conditions. Rodents preferred to select and disperse *A. sibirica* seeds with their thinner seed coats over *A. davidiana* seeds with thicker seed coats under natural conditions, although they preferred to eat kernels of *A. davidiana* seeds over those of *A. sibirica* seeds under captive conditions.

Discussion

Although relationships between seed traits and rodent seed dispersal have been well investigated (reviewed by Vander Wall 2010; Vander Wall and Beck 2012), the effects of seed trait-mediated selection by rodents on mutualistic

interaction and seedling establishment of co-occurring plant species are rarely investigated. In this study, we found that *A. sibirica* seeds have higher seedling recruitment under natural conditions and showed a greater array of mutualistic interactions with rodents. The co-occurring species, *A. davidiana*, was found to have lower seedling recruitment and showed fewer mutualistic interactions with rodents, particularly in years with a relatively low rodent density. Seed coat thickness, instead of seed kernel value, contributed to differences in mutualistic interactions between these two plants. Our results suggest that seed trait-mediated selection may affect mutualistic interactions between seeds and rodents and then seedling recruitment, and may cause indirect competition for seed dispersers between co-occurring plant species.

Previous studies suggest that hard seeds and high nutrition seeds have high mutualism with rodents by increasing scatter-hoarding and reducing predation, while soft and/or low nutrition seeds have low mutualism with rodents, but suffer from high predation (Ben-Moshe et al. 2001; Zhang and Zhang 2008; Chang and Zhang 2014; Wang et al. 2014; Zhang et al. 2015). However, very large and hard seeds are rejected by small-sized rodents and very soft seeds often suffer intense predation, in which both circumstances are negative to seed dispersal and regeneration (Xiao et al. 2005; Zhang et al. 2015). In our study, we found a thicker seed coat did not favor mutualistic interaction with rodents, suggesting the response of rodents to seed coat thickness may be non-monotonic. Although the kernels of *A. davidiana* seeds were preferred by rodents, their seeds were only dispersed by *S. davidianus*, probably because their seed coat was too thick for rodents to eat (see also Zhang and Zhang 2008; Zhang et al. 2015). More *A. sibirica* seeds were eaten by small rodents at seed stations and after removal than *A. davidiana* seeds, possibly because their kernels are easily accessible (small size, thin endocarps and flat shape). However, many *A. davidiana* seeds were also dispersed in 2006, suggesting that *A. davidiana* seeds can be well dispersed when rodent populations (especially *S. davidianus*) are high (Fig. 4; Table S4). A high number of *A. davidiana* seeds were not located in the field, perhaps because some were scatter-buried in soil outside the experimental plots by *S. davidianus*, because this squirrel tends to move hard seeds (e.g., *J. mandshurica* and *J. regia*) far from seed sources and scatter-hoard them within the home range (Zhang et al. 2014). Due to extensive human disturbance in this region, the population size of *S. davidianus* is in decline and this may present problems for the seed dispersal of plants that produce large and hard seeds (e.g., *J. mandshurica*, *A. davidiana* and *J. regia*).

We found that *A. sibirica* seeds not only had high mutualistic rates (scatter-hoarding) but also high overall consumption by all species of rodents, possibly due to a relative higher net energy reward (kernel mass/endocarp mass) and easily accessible kernels. *A. davidiana* seeds in contrast were rather infrequently consumed or hoarded by most rodent species; largely because of their large size, hard endocarp and spherical shape, making their kernels harder to access. These results suggest that plants that have more mutualistic interactions with dispersers also suffer higher predation. Therefore, the effects of *A. sibirica* seeds on neighboring *A. davidiana* seeds may be complex. As observed, the presence of *A. sibirica* seeds may reduce dispersal of *A. davidiana* seeds (competitive effects), and at the same time increase survival of *A. davidiana* seeds (facilitative effects). Facilitation between co-fruiting plants sharing similar seed dispersers has been reported in some studies (e.g., Carlo 2005; Saracco et al. 2005). For example, Carlo (2005) found the seed dispersal patterns of *Solanum americanum* by birds were facilitated by the presence of fruiting *Cestrum diurnum* neighbors. The positive and negative effects between co-occurring plants need to be evaluated in detail in future studies.

Rodent-mediated seed dispersal promotion can be detected as a quantitative and/or qualitative increase in a plant's seed dispersal pattern due to the effects of animals (Carlo 2005). Quantitative promotion in seed dispersal can be measured by the net amount of seeds dispersed; qualitative promotion can be measured by the dispersal pattern of individual seeds, such as dispersing further from the seed source, burying at low density, depositing more seeds at safe sites, surviving longer, and establishing more seedlings (Carlo 2005). In this study, more *A. sibirica* seeds were harvested and scatter-hoarded than *A. davidiana*, but there were no differences in cache site characteristics (canopy cover, vegetation type and cache substrate), seed dispersal distance, cache density, and seed survival time between the two plant species. The increasing effects of plant–rodent mutualism on seed dispersal of *A. sibirica* correspond to increased quantitative rather than qualitative components of the dispersal process. High seed predation is a major limitation of regeneration for *A. sibirica* and *A. davidiana* because they mature in summer (July) when seed eaters are at high abundance but co-fruiting species are low (Li and Zhang 2007; Zhang et al. 2015). Our results in the field support this conclusion because very few seeds survived to the next spring and very few seedlings were established from rodent caches (Table S4).

Competition for resources occur between sympatric plants when resources are limiting (McGoey and Stinchcombe 2009; Thorpe et al. 2011). Many factors mediate competitive results between co-occurring plant species and influence the structure, dynamics, and evolution of plant communities (reviewed by Connolly et al. 2001; Bell et al. 2005; Thorpe et al. 2011). Mutualists, such as seed dispersers, are important resources for plants, but their role in mediating plant competition and community structure is poorly understood. A few studies have investigated interspecific competition for seed dispersers and effects of plant–disperser mutualism on plant competition and community structure (Carlo 2005; Saracco et al. 2005; Rejmánek and Klinger 2010). For example, frugivore visitation of *Schefflera morototoni* can be facilitated by certain fruit–plant species but hampered by other species (Saracco et al. 2005). However, seed disperser competition between co-occurring plants in plant–rodent systems is unknown. *A. sibirica* and *A. davidiana* often co-occur in open and sunny forests and shrublands in our study area, have similar habitat requirements and phenological characters, and have similar rodent dispersers (Zhang and Zhang 2008; this study). In fact, we have some evidence of competition

for seed dispersers of rodents between *A. sibirica* and *A. davidiana*. In 2005 and 2007, seed abundance was high but rodent density was low. In 2006, seed rain was low but rodent density was high (Table 1). Thus, seed dispersers were limited in 2005 and 2007, while they were not limited in 2006. When seed dispersers are limited, *A. sibirica* seeds were more scatter-hoarded by rodents in 2005 and 2007 than *A. davidiana* seeds (Fig. 4; Table 1). In 2006, the difference of seed hoarding by rodents on the two species was not obvious (Fig. 4; Table 1). These results suggest that *A. sibirica* seeds had competing advantages for seed dispersers over *A. davidiana* seeds when seed dispersers were limited. Future studies should be directed to test the potential effects of mutualists in regulating indirect competition between *A. sibirica* and *A. davidiana* in the field. Establishment of long-term monitoring plots that exclude seeds or add seeds of the other species are needed in order to measure competition for seed dispersers between these two species.

Author contribution statement Z. Zhang and H. Zhang designed the study; H. Zhang conducted the experiments; and all authors contributed to writing of the manuscript.

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