ORIGINAL ARTICLE

Effects of masting on seedling establishment of a rodent-dispersed tree species in a warm-temperate region, northern China

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Abstract

Masting is an evolutionary strategy used by plants to promote seed survival and/or seed dispersal under animal predation, but its effects on seedling establishment in field condition are rarely tested by long-term experiments incorporating combined effects of seed and animal abundance. Here, we tracked seed production, rodent-mediated seed dispersal, and seedling establishment in *Armeniaca sibirica* from 2005 to 2014 in a warm-temperate forest in northern China, and examined the effects of seed abundance and per capita seed availability on seed fate and seedling recruitment rate. Our results showed that seed abundance or per capita seed availability generally benefited the seedling recruitment of *A. sibirica* through increasing dispersal intensity, supporting predator dispersal hypothesis. However, seedling recruitment showed satiated or even dome-shaped association with per capita seed availability, suggesting the benefit to trees would be decreased when seed abundance were too high as compared to rodent abundance (a satiated effect). Our results suggest that the predator dispersal and satiation effects of masting on seedling recruitment can operate together in one system and conditionally change with seed and animal abundance.

Key words: per capita seed availability, predator dispersal hypothesis, predator satiation hypothesis, rodents, seed dispersal

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INTRODUCTION

Masting, the synchronous and intermittent production of seeds by a population in many perennial plants, is thought to be an important strategy for plants to improve fitness (Kelly 1994; Vander Wall 2010). Several hypotheses (e.g. wind pollination, predator satiation, resource matching, animal pollination/dispersal, hormonal regulation, etc.) have been developed to explain masting in different plant species, with varying levels of

experimental support (reviewed in Kelly & Sork 2002; Bogdziewicz *et al*. 2020). Two of them, the Predator Satiation Hypothesis and the Predator Dispersal Hypothesis, are the most widely studied for explaining the masting in animal-dispersed plants, especially in those dispersed by scatter hoarding animals. The Predator Satiation Hypothesis suggests that masting increases pre-dispersal seed survival by satiating seed predators (e.g. insects, granivorous rodents), consequently, more seeds are likely to survive and germinate following a mast year than in the intervening non-mast years (Sork 1993; Kelly 1994; Koenig & Knops 2000; Kelly & Sork 2002). The Predator Satiation Hypothesis is the most established evolutionary explanation of masting in many plant species (e.g. animal-dispersed plants) and is well supported (Crawly & Long 1995; Curran & Leighton 2000; Vander Wall 2010; Xiao *et al*. 2013; Linhart *et al*. 2014; Wang *et al*. 2017). The Predator Dispersal Hypothesis suggests that for plants that are dispersed by scatter-hoarding animals, masting may improve dispersal fitness by increasing the scatter-hoarding intensity of animals, reducing cache recovery after hoarding, and enhancing dispersal distances (Vander Wall & Balda 1977; Vander Wall 2002). Therefore, more seeds are likely to be dispersed and survive to the period of germination in a mast year than in the non-mast years (Vander Wall 2010). The Predator Dispersal Hypothesis is also supported by a number of studies in different species (Vander Wall 2002, 2008; Jansen *et al*. 2004; Moore *et al*. 2007; Li & Zhang 2007; Zwolak *et al*. 2016; Pesendorfer *et al*. 2016; Pesendorfer & Koenig 2016).

In animal-dispersed plants, seed survival and seedling recruitment depend on the abundances of both seeds and animals (Theimer 2001, 2005). Seed and animal abundance vary greatly from year to year under natural conditions (Xiao *et al*. 2013). Plants therefore experience a trade-off between satiating and attracting seed predators (Crone *et al*. 2011). However, the effects of masting are rarely tested using long-term data by considering the effects of both seed and animal abundance on seed dispersal and final establishment rate (but see Xiao *et al*. 2013).

In this study, we examined the effects of seed abundance and seed availability using a 10-year dataset of seed dispersal of wild apricot (*Armeniaca sibirica*) under rodent predation in a warm deciduous forest in northern China, aiming to identifying the roles of both seed dispersal and satiation effect on seedling recruitment rate of the tree species. Wild apricot is a widely distributed deciduous tree or shrub that inhabits secondary forests and shrub lands across northern China (Lu & Zhang 2004). Following seedfall, its seeds (dispersal units, each comprising a single seed enclosed in a hard endocarp,

hereafter the seeds) undergo secondary dispersal exclusively by rodents due to the hard woody endocarp that prevents other animals (e.g. birds, insects) from consuming the seeds (Lu & Zhang 2004). We tracked annual seed production, animal abundance, and seed fates of *A. sibirica* seeds from seed to seedlings from 2005–2014, and quantified seed removal, scatter-hoarding, survival, and seedling emergence each year. Because *A. sibirica* seeds strictly dispersed by scatter-hoarding rodents (Lu & Zhang 2004; Li & Zhang 2007) rarely germinate on the ground surface due to drought (Zhang & Wang 2001; Guo *et al*. 2010), and seedlings hardly survive below parent trees due to competition and the lack of sunlight (Zhang *et al*. 2013). We predicted that masting may enhance seed survival and seedling recruitment by increasing dispersal intensity (the Predator Dispersal Hypothesis).

MATERIALS AND METHODS

Study site

Experiments were conducted at the Liyuanling field station, Donglingshan Mountains, northwest of Beijing city (40°00′N, 115°30′E; 800–1800 m above sea level) (see Zhang *et al*. 2013). The area has a temperate continental monsoon climate. Annual precipitation is 600 mm and average annual temperature is 6.5 °C. Principle land cover (i.e. shrublands, secondary forests, and abandoned farmlands) are undergoing gradual natural secondary succession after over cultivation and grazing. Dominant plants include Liaodong oak (*Quercus wutaishanica*), *A. sibirica*, wild walnut (*Juglans mandshurica*), elm (*Ulmus laciniata*), larch (*Larix principis-rupprechtii*), and wild peach (*Amygdalus davidiana*) in the secondary forests. Primary plant species in the shrublands are young *Q.wutaishanica*, *A. sibirica*, *U. laciniata*, and chaste tree (*Vitex negundo*). In the abandoned farmlands, dominant plants are annual herbs, younger stems of *A. sibirica* and *V. negundo*, and some sparsely distributed cultivated trees (e.g. *J. regia*) (see Zhang *et al*. 2017). The dominant trees mast synchronously every 3–5 years but their interactions are uncertain (unpublished data). Common rodent species are Chinese white-bellied rats (*Niviventer confucianus*), Korean field mice (*Apodemus peninsulae*), and Père David's rock squirrels (*Sciurotamias davidianus*) across the main landcover; striped field mice (*A. agrarius*), greater long-tailed hamsters (*Tscherskia triton*), and Siberian chipmunks (*Tamias sibiricus*) are found in the study area (Zhang & Zhang 2008). All of these rodents affect seed regeneration and plant community structure because they engage in eating and scatter- and/or
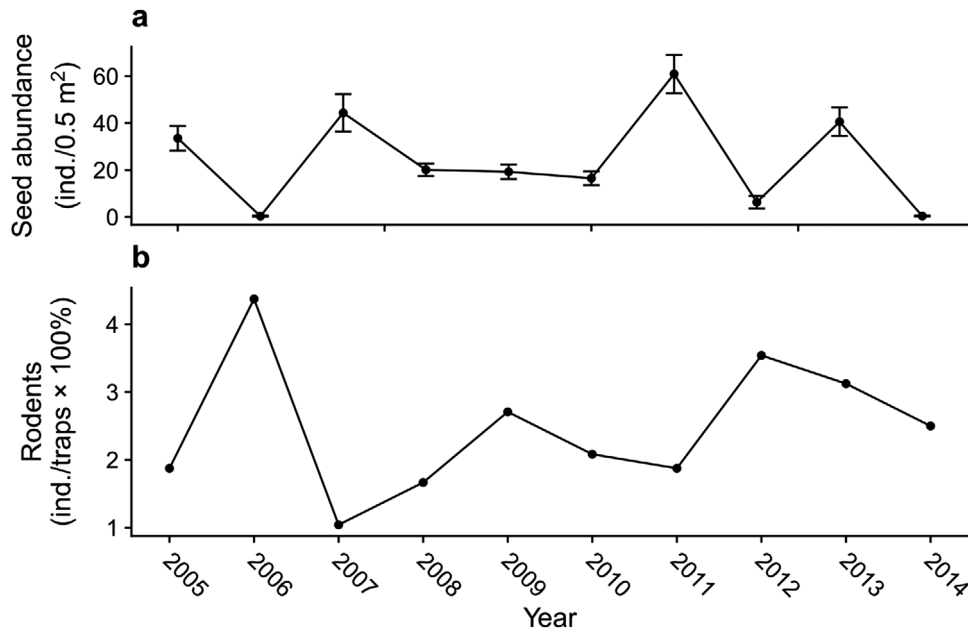
FIGURE 1 The change of annual abundance of *Armeniaca sibirica* seeds (a, mean ± SE) and rodents (b) along years.

larder-hoarding seeds (Zhang & Zhang 2008; Zhang *et al*. 2015). No large ungulates (e.g. deer, boar) or carnivores (e.g. bear, badger) eat *A. sibirica* fruit in the study area (Lu & Zhang 2004; Zhang & Zhang 2008).

Focal plant

In the study area, *A. sibirica* is a dominant plant species scattered across secondary forests, shrublands, and abandoned farmlands, where it also forms patches (Zhang *et al*. 2013). Fruits of *A. sibirica* mature and begin falling in early July, lasting around 30 days. The seed crop of *A. sibirica* varies considerably among years, and seed production is synchronous at population-level in masting years (Fig. 1a) (Li & Zhang 2007). *A. sibirica* seeds have a high crude fat content (53.1%) and high caloric value (25.5 kJ·g^{-1}), are of medium size (1.2 ± 0.2 g mass; 22.1 ± 1.6 mm long, 9.8 ± 0.8 mm wide, including endocarp, mean ± SD, $N = 50$), and have a hard woody endocarp (1.1 ± 0.2 mm thickness) (Zhang & Zhang 2008). *A. sibirica* seeds are dispersed strictly by rodent species in forests due to the hard endocarp preventing access by other animals (e.g. jays) (Lu & Zhang 2004; Zhang *et al*. 2013). Many seeds are deposited at safe sites with 1 to 3 seeds per cache by small rodents during seedfall, and seedlings often emerge the following spring (April to May) (Zhang *et al*. 2013). In the study area, *A. sibirica* is an ideal model for studying mutualistic

dispersal mediated by rodents because its seeds are strictly dispersed by small rodents, and are the main food supply of rodents from July to August (Zhang *et al*. 2013).

Seed crop size, rodent abundance, and seed availability

Seed crop measurements were conducted in a typical forest of *A. sibirica* during seedfall in July from 2005 to 2014. A 3-ha secondary forest was selected for seed crop measurement. This plot was located on a northeast-facing slope of 30–45° and adjacent to shrublands and abandoned farmland at the foot of the slope. Dominant trees and shrubs in the plot were *A. sibirica*, but *Q. wutaishanica* and *L. principis-rupprechtii* were also common. Annual herbs, young trees, shrubs, and litter were common under the canopy cover. The total canopy cover was more than 60%. A total of 20 *A. sibirica* trees (3.7 ± 8.9 m high, 9.9 ± 5.4 cm diameter at breast height, mean ± SD, >10 m interval) were selected for seed crop measurement. A 0.5-m^2 circular seed trap was set up under each focal tree to collect seeds. The funnel-form seed traps were made of steel wire (5.0 mm diameter) and nylon mesh (2.0 × 2.0 mm grid). The nylon mesh was tied to the steel wire ring using a small steel wire (0.5 mm diameter). Each trap was 1.0 m high from the ground, strutted by three bamboo stems, and covered by a steel

wire mesh (2.5 × 2.5 cm grid) to prevent rodents, especially squirrels and chipmunks, from accessing seeds in the traps (see Xiao *et al.* 2013). Seed traps were set up at the end of June and taken back after seedfall in early August. Seed traps were checked every 2 days, and the amount of seeds in each trap was recorded. Seed density of a given tree was reflected by the total seeds collected by the trap under the tree (also see Wang *et al.* 2017). Average seed density (average seed number per trap per 0.5 m^2) was used to measure seed abundance (crop size) each year (Fig. 1a). Following Koenig *et al.* (2003), we calculated several classic seed masting metrics: At the population level, coefficient of variation (CV_p) = 0.83, 1-year lagged autocorrelation ($ACF1_p$) = −0.63, synchrony index (r_p, mean correlation of 20 traps) = 0.5; at the individual trap level, mean CV_i = 1.16, mean $ACF1_i$ = −0.37. These metrics suggested the focal species was masting (Koenig *et al.* 2003).

In order to estimate rodent abundance during seed dispersal, 3 consecutive days of animal-trapping were conducted within the seedfall experimental plot at the end of the seedfall (at the end of July), and within the plots of seed dispersal experiments (see below) at the end of seed dispersal (see Zhang *et al.* 2013, 2016). Forty live-traps (12 cm × 12 cm × 25 cm steel cages) were set up in each plot along a 4 × 10 trapping grid, 7 m apart. Each trap was covered with a board to protect animals from rain and direct sunlight. Fresh peanuts were used as bait; small pieces of cucumber as water supply and local dry leaves as nest material were included in each trap. Traps were set up between 1630 and 1830 hours and checked for the following 3 days at 0600–0730 hours and 1730–1830 hours each day. A total of 360 trap-days were conducted in each experimental season. Captured animals were released immediately at trapping sites after species identification, weighing, and marking with black ink to avoid duplicate recording. Animal-trapping was approved by the local government, and under a permit provided by our institutes. Trapping success (number of captured individuals/total trap-days × 100%) was used as index of abundance (Fig. 1b).

Following Xiao *et al.* (2013), per capita seed availability (PCSA) was calculated by seed production (average crop size per tree, ACS) and metabolic rodent abundance (the sum of metabolic-scaling body mass from each rodent species each year, AMRA), representing the seed availability for metabolic needs of rodents. Per capita seed availability is a function of ACS and AMRA as follows (Xiao *et al.* 2013; Wang *et al.* 2017):

$$PCSA = ACS/AMRA$$

where,

$$AMRA = \sum_{i=1}^{k} N_i BM_i^{0.75}$$

where, k = the number of rodent species, N_i = the population size of a given rodent species in a given year i, and $BM_i^{0.75}$ = the average metabolic-scaling body mass of rodent species i.

Seed dispersal

Seed dispersal experiments were carried out during the seed dispersal period of *A. sibirica* (July–August from 2005 to 2014). Two 3-ha experimental plots (300 m apart) were selected for seed dispersal experiments in shrubland and secondary forest (see Zhang *et al.* 2013, 2016). The shrubland plot was located on a southeast-facing slope of 20–40° and dominated by *U. laciniata*, *A. sibirica*, and *Q. wutaishanica* shrubs with an average height of 2.1 ± 1.6 m (mean ± SD, n = 100) and >60 % shrub cover. Grasses, young shrubs, and leaf litter were common below the shrub canopy. The secondary forest plot was located on a northeast-facing slope of 30–45° and dominated by the trees *Q. wutaishanica*, *A. sibirica*, and *L. principis-rupprechtii* with an average height of 7.8 ± 3.6 m (n = 100) and >75 % canopy cover. Herbaceous and surface layers below the forest canopy were occupied by annual herbs, young trees, shrubs, leaf litter, and bare ground. Common rodents in the two plots were *A. peninsulae*, *N. confucianus*, and *S. davidianus* (Zhang *et al.* 2013, 2016).

Fresh and intact seeds used in the experiments were collected from *A. sibirica* forests at least 300 m away from the field experimental plots at the beginning of July (seedfall and natural dispersal period) each year. Seeds were kept in a dry and ventilated room to prevent rotting and mildew growth. Experimental seeds were marked using a tin-tag: a 0.5-mm hole was drilled at the basal part of endocarp of each seed and a unique coded tin-tag (30 × 10 mm, 0.1 g) was tied to each seed with a 3-cm piece of fine steel wire (Zhang & Wang 2001). We drilled the hole very carefully to ensure the kernel was not damaged. We could track the experimental seeds from seed to seedling by searching for the numbered tags (see Zhang *et al.* 2013, 2016). This method is widely used in rodent-mediated seed tracking, although the tags may delay seed removal and be cues for cache retrieval by animals (Xiao *et al.* 2006; Kempter *et al.* 2018).

Five seed stations (0.5 m^2, 30 m apart) were established along each of 3 (2006–2014, n = 15) or 4 (2005, n = 20) parallel transects (150 m long and 30 m apart)

within each experimental plot (see Zhang *et al*. 2013, 2016). Twenty seeds in 2005; 30 seeds in 2006, 2007, and 2009; and 40 seeds in all other years were placed at each seed station in the forest and shrubland plots in July–August. A total of 10,700 tagged seeds were released over 10 years. Each station was checked between 1030–1500 hours every 2–4 days up to a 30-day period. On each visit, seed fates were recorded and dispersed seeds were located within the plot and nearby area (≈50 m around each plot) by visually searching for the tags. Dispersed seeds indicate those seeds were moved away from the seed stations and cached in the soil or litters by small rodents (Zhang *et al*. 2013). For each located seed, seed fate and dispersal distance (distance between cache site and seed station) were recorded, and the cache site was mapped and marked with a branch for revisiting. The branch was about 50 cm away from the cache site and looked natural, but we did not assess its effects on cache recovery. Three consecutive days of animal-trapping was conducted as above in each plot at the end of seed assessment to estimate rodent abundance during experimental seasons. Survived seeds and seedlings established from released seeds (seedling of released seeds, SR) were recorded again in the following spring (April to May) (see Li & Zhang 2007; Zhang *et al*. 2013, 2016).

We set up 5 belt transects (≈200 m long, 10 m wide, 50–100 m apart) to measure the probability of natural seedling establishment from seed banks in secondary forests, shrub land, and abandoned farmlands (15 transects in total) (see Zhang *et al*. 2016). All new seedlings established in spring were recorded each year (seedling from the seed bank, SN).

Considering the whole process from seed release to seedling establishment, we focused on testing effects of seed abundance on the following seed fate variables (with data resolution described): total removal (TR), eaten *in situ* (EIS), intact *in situ* (IIS), eaten after removal (EAR), and scatter hoarded (SH) for each seed station in each plot; seed survival of released seeds (SSR) for each plot; and seedling establishment rate of released seeds (SR) which was summarized from two plots because of low seedling establishment (see definitions in Zhang *et al*. 2013, 2016). Median survival time (MST) of released seeds *in situ*, an index of seed harvest speed by rodents at the seed sources, was calculated for each plot by the Life Table method, implemented in SPSS version 16.0 (see Sun & Zhang 2013). The average dispersal distance (DD) of dispersed seeds was calculated from all the removed seeds for each plot. Seedling rate *in situ* (SIS) was also surveyed, but not a single seed survived and became established at the seed station during the study period.

Data analysis

Structural equation modeling (SEM) is a multivariate statistical modeling technique focusing on estimating multiple and interrelated dependence in a single model framework. Thus, we applied piecewise structural equation models (Lefcheck 2016) to analyze pathway effects (linear) of seed abundance and per capita seed availability on seed-fate variables in this study because of the interdependent pathway process from seed release to seedling establishment among these variables. In order to test the two hypotheses, we divided the dispersal stage into before seed dispersal (at seed stations) and after seed dispersal (seeds removed away from the seed stations by rodents) (for pathway assumption, see Fig. S1, Supporting Information). Based on the seed dispersal processes, we assumed two main pathways: (i) Before seed dispersal: seed abundance or per capita seed availability → intact or eaten *in situ* → seedling rate *in situ* → seedling from the seed bank (because SIS is always zero in our data, we connected IIS with SN in SEM); (ii) after seed dispersal: seed abundance or per capita seed availability → total removal → scatter hoarded or eaten after removal → survival of released seeds → seedling of released seeds → seedling from the seed bank (Fig. S2, Supporting Information). The piecewise SEMs were composed of a series of generalized linear mixed models (GLMM, Table S1, Supporting Information). In order to avoid statistical pseudo-replications (Hurlbert 1984), seed stations nested within plots were incorporated as random factors in the GLMMs for seed fates of total removal, eaten *in situ*, intact *in situ*, eaten after removal, and scatter hoarded after removal, while plots were incorporated as random factors in the GLMMs for survival and seedling of released seeds. Overall fit of piecewise SEM was evaluated using Shipley's test of d-separation, which provides Fisher's C statistic and P value (if $P > 0.05$, the model is an appropriate fit; Lefcheck 2016). Correlated variables that have no direct relationship were incorporated as correlated errors in the SEM. The path coefficients of SEMs are listed in Tables S2 and S3, Supporting Information.

In order to detect the nonlinear effects of seed abundance or per capita seed availability on seed fates of total removal, intact *in situ*, median survival time, survival of released seeds, seedling of released seeds, seedling from the seed bank, and average dispersal distance, we applied GLMM with quadratic terms and the random factors of seed stations nested within plots or only plots. Binomial error terms were used for proportional data of total removal, intact *in situ*, survival of released seeds, seedling of released seeds, while Gaussian error terms for median

FIGURE 2 The pathway linear effects of seed abundance or per capita seed availability of *Armeniaca sibirica* on seedling of seed bank, and seed survival and seedling establishment of released seeds via middle dispersal-fate variables as revealed by using the piecewise structural equation models. The piecewise structural equation modeling suggests that the overall fitted pathway structures are statistically appropriate (for SEM with seed abundance, Fisher's C = 30.42, df = 26, $P = 0.251$; for SEM with per capita seed availability, Fisher's C = 21.89, df = 16, $P = 0.147$). Sold arrows indicate positive effects and dashed arrows indicate negative effects.
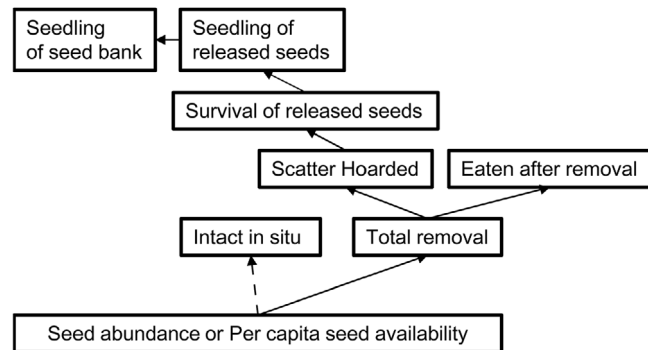
survival time, seedling from the seed bank, and average dispersal distance. The best-fitting models were selected by analysis of deviance (*anova* function in *R* environment) and AICc (small-sample-size corrected Akaike Information Criterion) as shown in Table S4, Supporting Information. The residual temporal autocorrelation of above models were validated by partial autocorrelation function, and no significant autocorrelation was detected (Figs S2 and S3, Supporting Information). The above analyses were applied by using *MuMIn*, *piecewise SEM*, and *lme4* packages in *R* environment.

RESULTS

By using piecewise linear SEM analysis, we found seed abundance and per capita seed availability both showed a positive chain effect from total removal → scatter hoarded → survival of released seeds → seedling of released seeds → seedling of seed bank; a positive chain effect from total removal → eat after seed dispersal; only a negative effect on intact *in situ* before seed dispersal (Fig. 2).

By using GLMMs, we found seed abundance had a U-shaped effect on total removal and a dome-shaped effect on intact *in situ* (Fig. 3a,c). Per capita seed availability showed a nonlinear positive effect on total removal and negative effect on intact *in situ* (Fig. 3b). Seed abundance had a dome-shaped effect on median survival time of released seeds *in situ*, while per capita seed availability had a linear negative effect (Fig. 3d,e). Seed abundance showed a U-shaped effect on dispersal distance (Fig. 3f).

By using GLMMs, we found seed abundance showed a linear or an overall positive effect on seed survival rate of released seeds, seedling rate from released seeds, and seedling from the seed bank, while per capita seed availability showed a satiated or dome-shaped nonlinear positive effect on the survival of released seeds, seedling of released seeds, and seedling of seed bank (Fig. 4).

DISCUSSION

Our SEM results indicated that seedling recruitment rate was generally positively associated with seed abundance or per capita seed availability of *A. sibirica* through scatter-hoarded seeds, suggesting that the Predator Dispersal Hypothesis mostly explained our observations. However, per capita seed availability showed a satiated or even dome-shaped association with the seedling recruitment rate, indicating that the predator satiation effects might occur when seed abundance were too high, as compared to the rodent abundance. Thus, the effects of masting on seedling recruitment rate may be operated by predator satiation and dispersal in our subjects, and conditionally vary with seed and animal abundance.

The Predator Satiation Hypothesis states that massive seed production synchronized over large geographical areas in seed-rich years can satiate most seed predators (Sork 1993; Koenig & Knops 2000). Consequently, more seeds will remain (non-dispersed) at seed sources, survive to the period of germination, and become seedlings in seed-rich years compared to seed-poor years. Several studies of rodent-mediated seed removal have observed that seed removal from the seed source is slower, the proportion of seeds remaining at the seed source is higher during the period of natural dispersal (30–60 days), and that the proportion of seeds surviving to germination (the next spring) is higher in seed-rich years compared to seed-poor years (Crawley & Long 1995; Theimer 2001; Jansen *et al.* 2004; Xiao *et al.* 2005, 2013; but see Vander Wall 2002). Our SEM results indicate that seed abundance or per capita seed availability shows an overall significant negative effect on intact *in situ* (Fig. 2). Besides, we did not find single seedling established from our released seeds. However, GLMM results reveal that when seed abundance is low, seed abundance or per capita seed availability shows a positive effect on intact *in situ* and median survival time (Fig. 3c,d), suggesting the predator
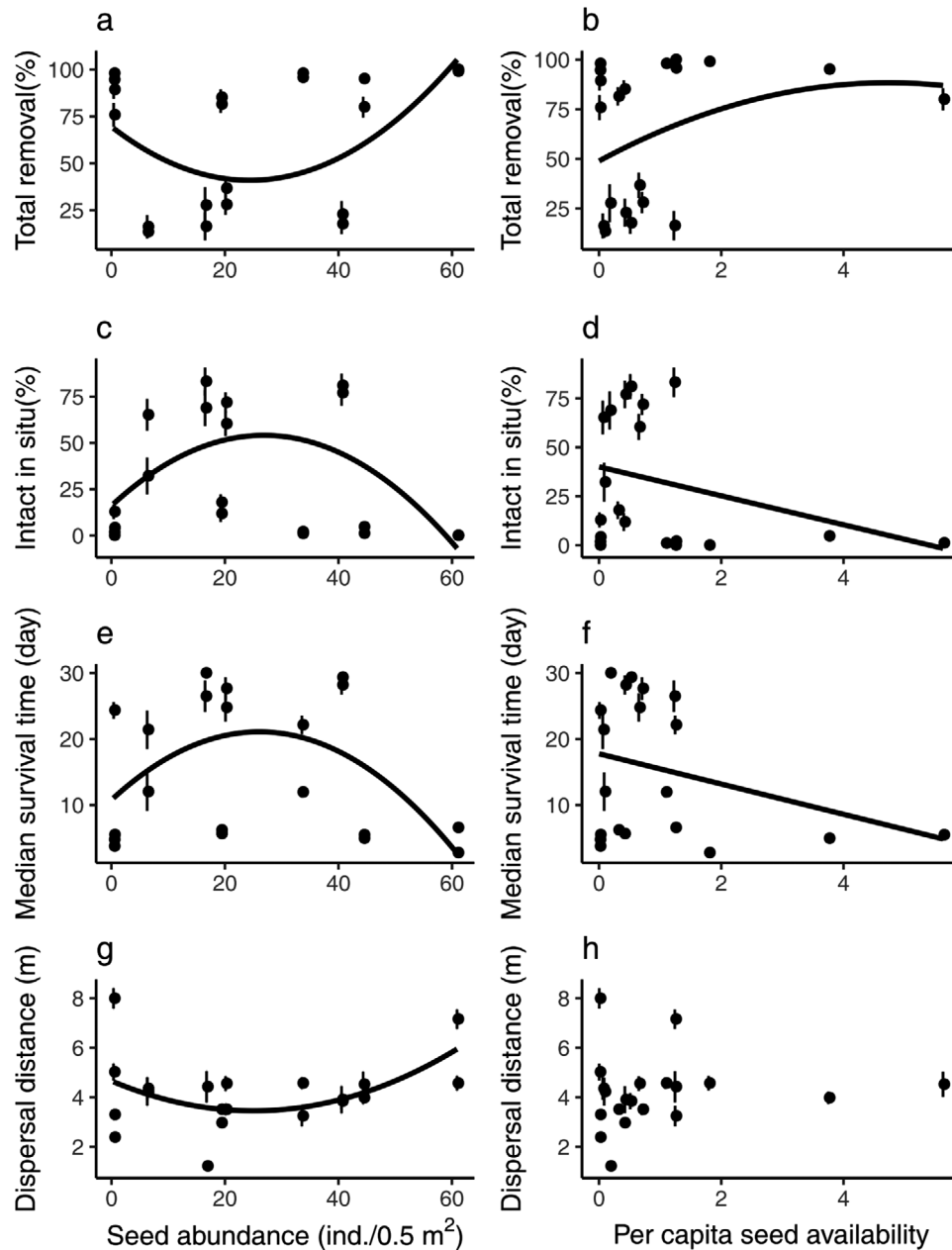
FIGURE 3 The effects of seed abundance and per capita seed availability of *Armeniaca sibirica* on total removal (a,b), intact *in situ* (c,d), median survival time (e,f), and average dispersal distance of removed seeds(g,h). Each data point represents variable in each plot every year (mean ± SE). The regression line was drawn according to generalized linear mixed models as described in the Materials and Methods section.

satiation effects before seed dispersal occurred when seed abundance was lower than a particular threshold. When seed abundance was higher than the threshold, it stimulated the seed dispersal or removal by rodents (Fig. 3a–c).

The Predator Dispersal Hypothesis is observed in plant-scatter-hoarding animal systems (Vander Wall 2010). It posits that numerous seeds instantly inundate seed-hoarders in seed-rich years and promotes animals to hoard much more seeds than they can consume, and
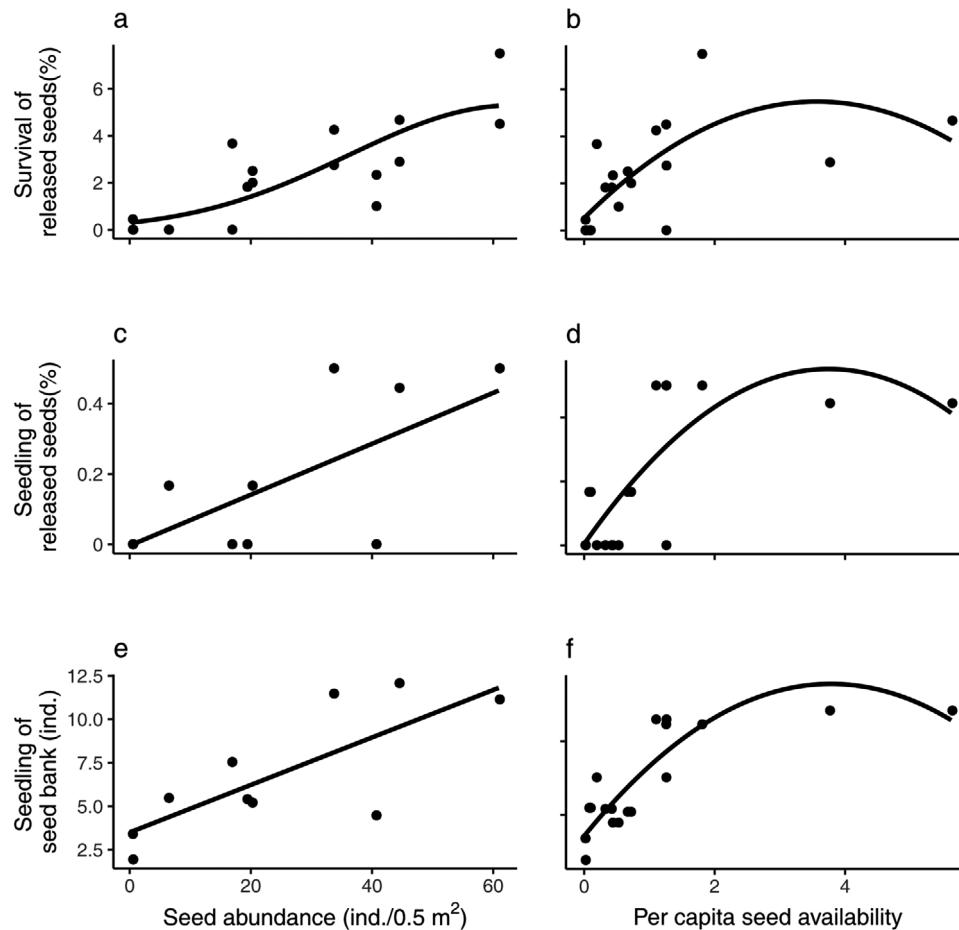
FIGURE 4 Effects of seed abundance and per capita seed availability of *Armeniaca sibirica* on seed survival of released seeds (a,b), seedling of released seeds (c,d), and seedling from the seed bank (e,f). Each data point represents the value in each plot every year for survival of released seeds, and the annual value for seedling of released seeds and seedling of seed bank. The regression line was drawn according to generalized linear mixed models as described in the Materials and Methods section.

hoard seed in further places. This means that a relatively large proportion of seeds is cached and unrecovered in the safe sites, favorable for plant fitness (Vander Wall 2010; Zwolak *et al*. 2016). In contrast with the Predator Satiation Hypothesis which emphasizes high survival before seed dispersal, the Predator Dispersal Hypothesis emphasizes increasing seed dispersal probability and dispersal distance, reduced seed loss after dispersal, and then high dispersal effectiveness and seedling recruitment in seed-rich years (Kelly & Sork 2002; Vander Wall 2010; Zwolak *et al*. 2016). Plants gain benefits from masting only when more seeds are dispersed from parent trees, deposited into places favorable for germination and growth, and then uncovered by animals in seed-rich years (Jansen & Forget 2001; Zwolak & Crone 2012). High seed dispersal occurs in seed-rich years because hoarding behavior of

animals is not easily satiated by masting events, and numerous caches satiate consumption in the later stages of seed dispersal (Zhang *et al*. 2008; Vander Wall 2010). Our SEM results support the Predator Dispersal Hypothesis, and are also consistent with several other studies in animal-dispersed plants (Fig. 2) (Vander Wall & Balda 1977; Li & Zhang 2007; Zwolak *et al*. 2016; Pesendorfer *et al*. 2016). However, GLMM results suggest that per capita seed availability showed satiated or dome-shaped effects on survival of released seeds and seedling of released seeds (Figs 2 and 4b,d), suggesting when per capita seed availability was higher than a particular threshold, seed removal was satiated.

Plants gain advantages from long-distance dispersal because it reduces density-dependent seed loss and seedling competition (Stapanian & Smith 1984; Moore

& Swihart 2007; Swamy *et al.* 2011; Steele *et al.* 2015) and increases likelihood of depositing seeds in safe sites, such as forest gaps, shrub edges, and open places (Li & Zhang 2007; Zhang *et al.* 2013; Zwolak *et al.* 2016). Previous studies have reported that masting increases seed dispersal distance (Stapanian & Smith 1978; Vander Wall 2002; Li & Zhang 2007; Yi *et al.* 2011), but other observations showed conflicting results (Jansen *et al.* 2004; Xiao *et al.* 2013; Zwolak *et al.* 2016; this study). In our study, we found dispersal distance showed U-shaped associations with seed abundance (Fig. 3f). Increase of seed production likely induced shorter dispersal distance under a threshold level of seed production, and then induced longer dispersal distance when seed production is over the threshold. The plasticity of food hoarding strategies of rodents according to food abundance may partially explain the U-shaped change of seed dispersal distance (Niu *et al.* 2020). Rodents appear to move seed further for hoarding to reduce competition and pilferage when seed abundance is relative low, and they tend to rapidly cache seeds around the sources to maximize food harvest when seed production is high and ephemeral (Jenkins & Peters 1992; Galvez *et al.* 2009; Zhang *et al.* 2014).

The Predator Satiation Hypothesis and the Predator Dispersal Hypothesis are not mutually exclusive. Some previous studies support the Predator Satiation Hypothesis, while others support the Predator Dispersal Hypothesis. The difference among these studies may be caused by differences in seed-handling costs (e.g. seed coat hardness). For example, it has been demonstrated that rodents tend to disperse seeds with hard seed coats (not eaten *in situ*.) to avoid high predation risks (Zhang & Zhang 2008; Wang *et al.* 2014; Zhang *et al.* 2015). In studies using plant species that produce seeds with a hard coat (e.g. *Pinus* spp., *Corylus* spp., *Fagus* spp., *Carapa procera*, and *A. sibirica* of this study), the Predator Dispersal Hypothesis was supported (Vander Wall 2002; Jansen *et al.* 2004; Li & Zhang 2007; and this study), while in studies using plant species with a soft seed coat (e.g. *Quercus* spp., *Fagus crenata*, *Camellia oleifera*), the Predator Satiation Hypothesis was supported (Sork 1993; Kelly 1994; Kon *et al.* 2005; Xiao *et al.* 2013). Our study site is located in dry warm-temperate forest, and seeds of *A. sibirica* cannot germinate without seed dispersal and burial away from the parent trees due to their hard seed coat and drought (Fig. S4, Supporting Information; Zhang & Wang 2001; Guo *et al.* 2010). Therefore, it is reasonable that the Predator Dispersal Hypothesis provides a mechanism for masting in *A. sibirica*. Our results suggested that the relative significance of the Predator Satiation Hypothesis and the Predator Dispersal

Hypothesis in explaining masting effects may be largely related to seed traits of the focal plant species and the combined effects of seed and animals abundance.

In our study, we found the effects of per capita seed availability on seed fates and seedling recruitments were satiated or dome-shaped when they reached a certain threshold (Figs 3 and 4). If seed availability is too low, the seedling establishment rate would be low because rodents would consume most of the seeds; if seed availability was too high, there might be more seeds undispersed, and are not able to establish seedlings. Thus, per capita seed availability becomes a conflicting selective pressure on seed dispersal fitness under rodent predation, resulting in the observed nonlinear effects of seed abundance or per capita seed availability on seed fates and seedling recruitment. Recent studies indicate that satiated or dome-shaped interaction between species is a key factor in maintaining biodiversity and stability (Yan & Zhang 2014). Therefore, it is necessary to further investigate the nonlinear effects of seed abundance or per capita seed availability on seed dispersal and seedling establishment by considering the combined effects of both seed abundance and rodent abundances (i.e. per capita seed availability).

In summary, our results suggest that both the Predator Satiation Hypothesis and the Predator Dispersal Hypothesis are important in explaining masting phenomenon in plant–animal dispersal systems, and which is obvious probably depends on abundance of seeds and animals. It is necessary to make more long-term investigations in more broad forest systems (taking into account more plant species) in order to further examine the ultimate causes of masting.

AUTHOR CONTRIBUTIONS

H.Z. and Z.Z. designed the research. H.Z., J.S., and H.L. conducted the field work and collected data. C.Y. and H.Z. performed analyses. H.Z., C.Y., Z.Z., X.Y., and S. W. contributed to the writing and revising.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 The model lists of piecewise structural equation models (SEM) with seed abundance or per capita seed availability (PCSA). The models assumed the pathway effects of seed abundance or PCSA on seed fates. The brackets are random effects in generalized linear mixed models (GLMMs), following lme4 packages in R software. (1|Plot/Station) indicates random effects of stations nested within plots, and (1|Plot) indicates random effects of plots.

Table S2 The path coefficients from the best-fit piecewise SEM models explaining the effects of seed abundance on seed fates.

Table S3 The path coefficients from the best-fit piecewise SEM models explaining the effects of per capita seed availability (PCSA) on seed fates.

Table S4 The models for selecting nonlinear (quadratic terms) effects of various exploratory variables for total removal (TR), intact in stitu. (IIS), seed survival rate (SSR) and seedling rate from released seeds (SR), seedling from the seed bank (SN), Median survival time (MST) and dispersal distance (DD).

Figure S1 Assumptions of pathway effects of seed abundance and PCSA on seed fates by using piecewise structural equation modeling (SEM). IIS, intact in situ; EIS, eaten in situ; IIS, intact in situ; TR, total removal; SH, scatter hoarded; EAR, eaten after removal; SSR, seed survival of released seeds; SIS, seedling establishment rate in situ; SR, seedling establishment rate of released seeds. SN, seedling establishment rate from the seed bank. Because SIS is always zero in our data, we connected IIS with SN during piecewise structural equation modeling.

Figure S2 The residual autocorrelations of different models (response variable ∼ independent variable), arranged as Fig. 2 in main text. No test for "Dispersal distance ∼ per capita seed availability" because the relationship is not significant.

Figure S3 The residual autocorrelations of different models (response variable ∼ independent variable), arranged as Figure 3 in main text.

Figure S4 Difference of germination rate of Armeniaca sibirica between seeds left on the ground surface and buried in the soil. Redrawn by using the data (mean ± SE) from Zhang and Wang (2001).

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