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ORIGINAL ARTICLE

Seed density affects post-dispersal seed predation: evidence from a seed removal experiment of 62 species

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Abstract

Post-dispersal seed predation plays an important role in plant demography and biodiversity maintenance. However, the effects of seed density on seed predation from previous studies have been inconsistent. We dissected the effects of density on the 2-step processes of seed predation using 101 520 seeds from 62 plant species in an alpine pine forest for 3 consecutive years. In this study we explained the current controversy surrounding the effects of density on seed predation. Seed encounter frequency (at least 1 seed being predated from an experiment depot) showed positive density dependence, while seed exploitation (the proportion of seeds being predated of the encountered depots) showed negative density dependence. Both density effects showed a consistent trend but with different magnitudes of effect across years. Final seed predation is the combination of seed encounter and seed exploitation. Final seed predation could be either positively or negatively density-dependent and was contingent on the magnitude of the difference between positive density-dependent seed encounter and negative density-dependent seed exploitation. Our results also indicated that studies including only a few species would produce biased results, because the density effect on seed predation differed greatly among plant species. Future studies should include a large number of plant species that possess a wide range of diverse seed traits to avoid potential bias and produce more comprehensive and accurate results.

Key words: density, rodent, seed encounter, seed predation, seed removal

INTRODUCTION

Post-dispersal seed predation is one of the most important determining factors for plant demography, biodiversity maintenance and evolutionary processes (Janzen 1971; Hulme 1998; Larios *et al.* 2017; Hegstad & Maron 2019). During the fruiting season, dispersed seeds often form different spatial patterns that depend on their dispersal syndromes, which leads to a large spatial variation in seed density that may influence the intensity of post-dispersal seed predation and has attracted a lot of attention in recent decades (Stapanian & Smith 1984; Lott *et al.* 1995; Hulme & Hunt 1999; Romo *et al.* 2004; Jansen *et al.* 2014; Cornils *et al.* 2017). The response of seed predators to changes in seed densi-

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ty is a crucial component of many ecological processes, including soil seed bank dynamics, seedling regeneration and species coexistence (Hulme 1998; Jansen *et al.* 2014; Garzon-Lopez *et al.* 2015). Currently, research on the effects of seed density on post-dispersal seed predation are mainly focused on 2 competing hypotheses: positive density dependence predation, known as the Janzen-Connell hypothesis (Janzen 1970; Connell 1971) and negative density dependence, known as the predator satiation hypothesis (Silvertown 1980; Kelly 1994).

Granivorous rodents are important seed predators and are ubiquitous in almost every ecosystem (Moles *et al.* 2003; Zhang *et al.* 2017; Dittel & Vander Wall 2018). Many studies have examined density-dependent effects on post-dispersal seed predation by rodents, but the results of these studies remain controversial, as studies have shown positive (Baraibar *et al.* 2012; Pardini *et al.* 2017) and negative density-dependent patterns (Romo *et al.* 2004; Daedlow *et al.* 2014) and density-independent results (Lott *et al.* 1995; von Allmen *et al.* 2004; Haught & Myster 2008; Rosin & Poulsen 2018). Several scenarios have been proposed to explain these inconsistent results. First, changes in local food abundance and/or rodent population dynamics may mediate density-dependent effects; this scenario is primarily used to explain the inconsistent density effects among habitats, seasons or years (Willson & Whelan 1990; Hulme 1994, 1998; Pannwitt *et al.* 2017). Second, seed burial can also change density-dependent effects by disproportionally decreasing seed predation between low and high seed densities (Hulme 1998; Hulme & Borelli 1999). Third, density-dependent seed predation also differs among plant species (Hulme & Borelli 1999; Myster 2003) and seed size is believed to be a critical factor that mediates the intensity of density-dependent effects (Hulme & Borelli 1999; Perez-Ramos *et al.* 2017). Furthermore, other seed traits, such as nutrient content and physical and chemical defenses, may also influence density-dependent seed predation and require further study.

Most studies evaluate density-dependent effects by directly comparing final seed predation or removal among different seed densities (Lott *et al.* 1995; Myster 2003; von Allmen *et al.* 2004; Pannwitt *et al.* 2017; Perez-Ramos *et al.* 2017). Logically, the final seed predation pattern is determined by 2 successive processes (Fig. 1), the encounter of a seed patch and the subsequent exploitation of the seeds after the initial encounter, and seed density may influence these 2 processes in a variety of ways (Willson & Whelan 1990; Hulme 1994; Hulme & Hunt 1999). For example, high seed density may increase the probability of seed encounter by increasing the apparency of seeds, while high density may decrease the proportion of seed exploitation after being encountered based on the predator satiation hypothesis (Feeny 1976; Silvertown 1980; Kelly 1994). Therefore, for a specific range of seed densities, final seed predation may show either negative or positive density dependence as it is the result of 2 linked processes.

In this study, we dissected the effect of density on the 2-step processes of seed predation by monitoring 62 plant species in an alpine pine forest for 3 consecutive years. We predicted that: (i) high density would increase the frequency of seeds being encountered because it would be more apparent and easier to be detected; (ii) once encountered, high density would decrease the proportion of seeds being exploited (the predator satiation hypothesis; Silvertown 1980; Kelly 1994); and (iii) the final proportion of seed predation would either be density-independent, positively density-dependent or negatively density-dependent, and would be contingent on the difference in the magnitude of effect of density on seed encounter and seed exploitation (Fig. 1).

MATERIALS AND METHODS

Study site

This study was carried out in an alpine pine forest in the Shangri-La Alpine Botanical Garden (27°54′N, 99°38′E, altitude 3456 m) of the Yunnan Province in south-western China. The study forest in the garden is not isolated from the natural forest that covers several hundreds of square kilometers. *Pinus densata* is the dominant tree species in this site and it coexists with several *Quercus* and *Rhododendron* species. The ground flora is poorly developed and holds a few herbs and mosses (Wang & Chen 2009; Gong *et al.* 2015). The experiments were conducted from September to November over 3 consecutive years (2004–2006). No apparent annual differences in seed production (e.g. mast seeding phenomenon) were observed during the 3 years (based on personal field observation of *P. densata* and some other common species). In the study forest, 2 nocturnal rodent species, *Apodemus latronum* (Thomas, 1911) and *Apodemus chevrieri* (Milne-Edwards 1868), are the dominant seed predators and dispersers and present similar body sizes and foraging behaviors (Wang & Chen 2009, 2011). Based on our live-trap survey (300 trap-nights each year; i.e. 50 traps × 6 nights), more rodent individuals were captured in 2006 ($n = 16$) than in either 2004 or 2005 (9 and 8 individuals, respectively).

Study species

In total, 62 seed species were used in our experiments: 18 species in 2004, 41 species in 2005 and 35 species in 2006; and 9 species were used in all 3 years (Suppl. Table S1–S3). All the seeds came from 2 sources and were either collected directly from the forest (*n* = 26) or bought from the Seed and Seedling Company of Yunnan (*n* = 36) to enlarge the sample size of seed species. No apparent differences in seed predation by rodents were detected between local and alien plant species in our study forest (Gong *et al.* 2015). Furthermore, some of the data analyzed here was reported in 2 previous papers, both of which covered topics different from those discussed in the current study. Gong *et al.* (2015) tested the relations between seed traits and seed predation of 30 species without any discussion about density effects, while Wang and Yang (2007) mainly discussed the difference in seed predation among the 18 species in 2004; they also reported the density effect on the final seed predation but without disentangling the predation process into seed encounter and seed exploitation. Therefore, to enlarge the sample size (i.e. totally 3 consecutive years and 62 species), we included the reported data in this study.

Seed predation experiment

Five parallel transects were established in the forest at 5-m intervals, and 10 seed-releasing stations were established along each transect at 5-m intervals (Fig. S1). At each station, 2 seed-releasing depots (i.e. plastic plate approximately 12 cm in diameter and 1 cm in height) were set up approximately 1 m apart (Fig. S1). Two seed density levels were selected for all species: either 3 or 15 seeds of the same species. Each species was replicated in 10 randomly selected stations with 5 stations for each density level. For the 2 depots at each station, the same density level of a same species of seeds was used (Fig. S1). At any given time, 3 or 5 species were randomly selected for a 6-day seed predation experiment, depending on the total number species used in that year. For each predation experiment, we placed seeds on the depots at 1900 hours and checked seed fates at 0700 hours the next morning. Seed fate was classified as either seeds ignored (intact seeds remaining at or near the depots) or seeds harvested (including seeds consumed at or near the depots and seeds removed; i.e. absent from the depots). After checking for seed fate, all ignored seeds and residual seed fragments were removed in the morning and new seeds were added in the afternoon. During the 6-day survey, data collection would be suspended if heavy rains or strong winds occurred at night and an additional survey day was added. Finally, 1080 seeds per year were released for each species (high density depots: 15 seeds × 2 depots × 5 stations × 6 days = 900 seeds; low density depots: 180 seeds). In total, 101 520 seeds were used during the 3 years.

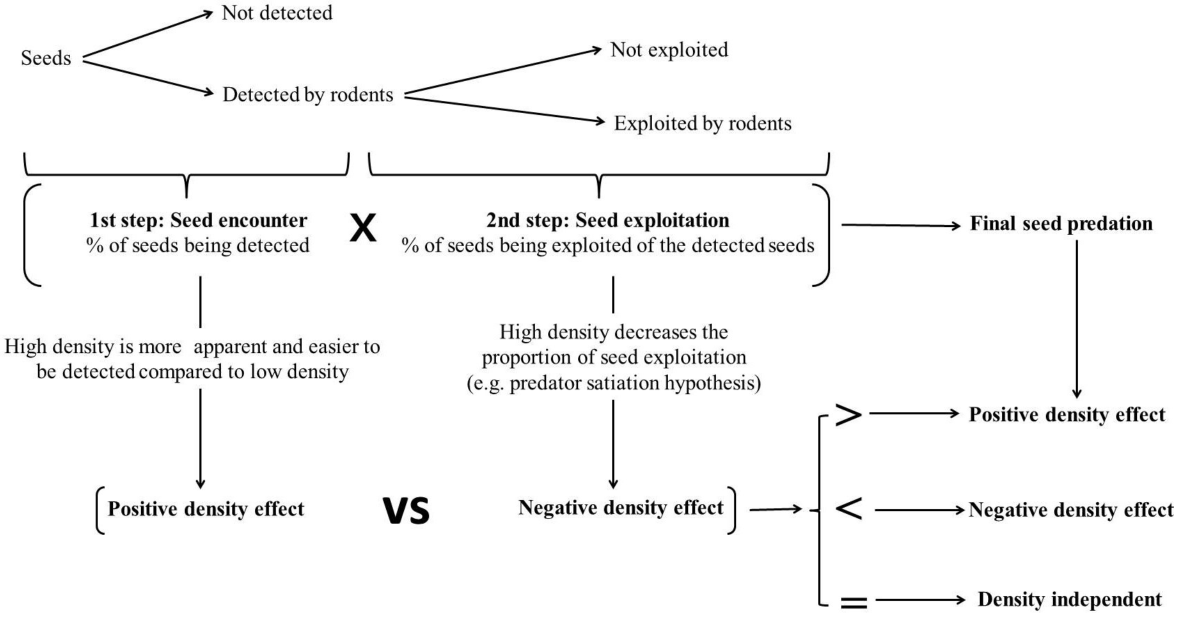

Figure 1 A conceptual diagram of density effects on seed encounter, seed exploitation and final seed predation.

In this study, the proportion of seeds harvested was used to estimate seed predation intensity. It might be a little problematic to assume seed removal as seed predation because removed seeds might have been scatter-hoarded by rodents (Vander Wall *et al.* 2005). However, most of scatter-hoarded seeds in our study area were finally retrieved and consumed by rodents within a few days after being cached (Wang *et al.* 2012; Wang & Yang 2014; Wang & Ives 2017); therefore, we included the removed seeds when estimating seed predation. In this study, seeds were directly released on the plastic plate, and were open to all kinds of seed predators. However, we only considered seed predation by rodents because our previous study indicated that other animals, such as ants or birds, seldom consumed or removed our experimental seeds (Wang & Yang 2007; Wang *et al.* 2012; Gong *et al.* 2015; unpublished camera trap data).

Data analysis

According to Hulme (1994) and Hulme and Hunt (1999), 3 seed predation components were examined: seed encounter (the probability of at least 1 seed being harvested from the depots), seed exploitation (the proportion of seeds being harvested from encountered depots) and final seed predation (the proportion of seeds being harvested from all depots, including both encountered and non-encountered depots).

A generalized linear mixed model (GLMM) was used to analyze the effect of density on seed encounter (encountered *vs* not encountered) with a binomial error distribution and logit link function (function glmer, package "lme4") (Bates *et al*. 2014). A GLMM was also used to analyze the density effect on the proportion of seed exploitation and final seed predation using the cbind function. First, we analyzed all the species together, considering species nested in experimental day as random effects. Second, we ran the same models for each species separately, considering experimental day as the random effect. The overdispersion of the GLMM was tested using overdisp_fun function (Bolker *et al*. 2009). A quasibinomial model was used to correct the standard errors when overdispersion was detected (function glmmPQL, package "MASS") (Ripley *et al*. 2013). All the statistical analyses were performed in R 3.5.2 (R Development Core Team 2016, www.R-project.org).

RESULTS

Seed encounter

In 2004, seeds from high-density depots were encountered 37% more frequently than seeds from low-density depots (66% *vs* 49%; generalized linear mixed model, $Z = -10.02$, $P < 0.001$; Fig. 2a, Table S4). The frequency of seed encounter differed among the 18 species and ranged from 0 to 100% for high-density depots and 0 to 98% for low-density depots (Table S1). Nine species showed similar positive density-dependent seed encounter responses, 3 species showed negative density dependence (with seeds from low density depots being encountered more frequently), while the 6 remaining species showed a density-independent response (Table S1).

Similar patterns were detected in the following years. In 2005, high seed density increased the seed encounter frequency by 32% compared to low seed density (36% *vs* 27%; $Z = -8.18$, $P < 0.001$; Fig. 2d, Table S4). The seed encounter frequency differed among the 41 species and ranged from 3% to 97% and 2% to 82% for high-density and low-density depots, respectively (Table S2). In total, 14, 1 and 26 species showed positive density dependence, negative density dependence and density independence, respectively (Table S2).

In 2006, high seed density slightly increased the seed encounter frequency compared to low seed density (83% *vs* 79%; $Z = -4.48$, $P < 0.001$; Fig. 2g, Table S4). The seed encounter frequency also differed among species and ranged from 7 to 100% and 10 to 100% for high-density and low-density depots, respectively (Table S3). Given that most of depots were encountered in this year, most species showed density independence ($n = 32$), and the remaining 3 species showed similar positive density dependence as the overall pattern (Table S3).

Seed exploitation

Negative density effect was detected in all 3 years. Of the encountered depots in 2004, the proportion of seed exploitation was 15% greater in low-density depots compared to high-density depots (83% *vs* 72%; linear mixed-effects model, $t = 3.29$, $P = 0.001$; Fig. 2b, Table S5). Seed exploitation differed among species and ranged from 40% to 98% for low-density depots and 9% to 100% for high-density depots (Table S1). Five species showed similar negative density-dependent seed exploitation responses overall, while 4 species showed the opposite pattern, and the remaining 9 species showed density-independent seed exploitation (Table S1).

Of the encountered depots in 2005, seed exploitation from low-density depots was 30% greater compared to high-density depots (83% *vs* 64%; $t = 8.84$, $P < 0.001$;

Fig. 2e, Suppl. Table S5). Seed exploitation differed among species and ranged from 33% to 100% and 7% to 99% for low-density and high-density depots, respectively (Table S2). Fourteen species presented the same negative density-dependent pattern overall and 1 species showed the opposite pattern, while the remaining 26 species showed a density-independent pattern (Table S2).

In 2006, low-density density depots increased seed exploitation by 8% compared to high-density depots (95% *vs* 88%; $t = 11.04$, $P < 0.001$; Fig. 2h, Table S5). Seed exploitation differed among species and ranged from 33 to 100% and 7 to 100% for low-density and high-density depots, respectively (Table S3). A total of 12 species presented the same negative density-dependent pattern overall and only 1 species showed positive density dependence, while the remaining species showed density independence (Table S3).

Final seed predation

Unlike the consistent trends observed for seed encounter and exploitation, the effect of density on final seed predation differed across years. In 2004, final seed predation was positively density-dependent and final seed predation was 19% greater at high-density depots compared to low-density depots (48% *vs* 40%; lin-

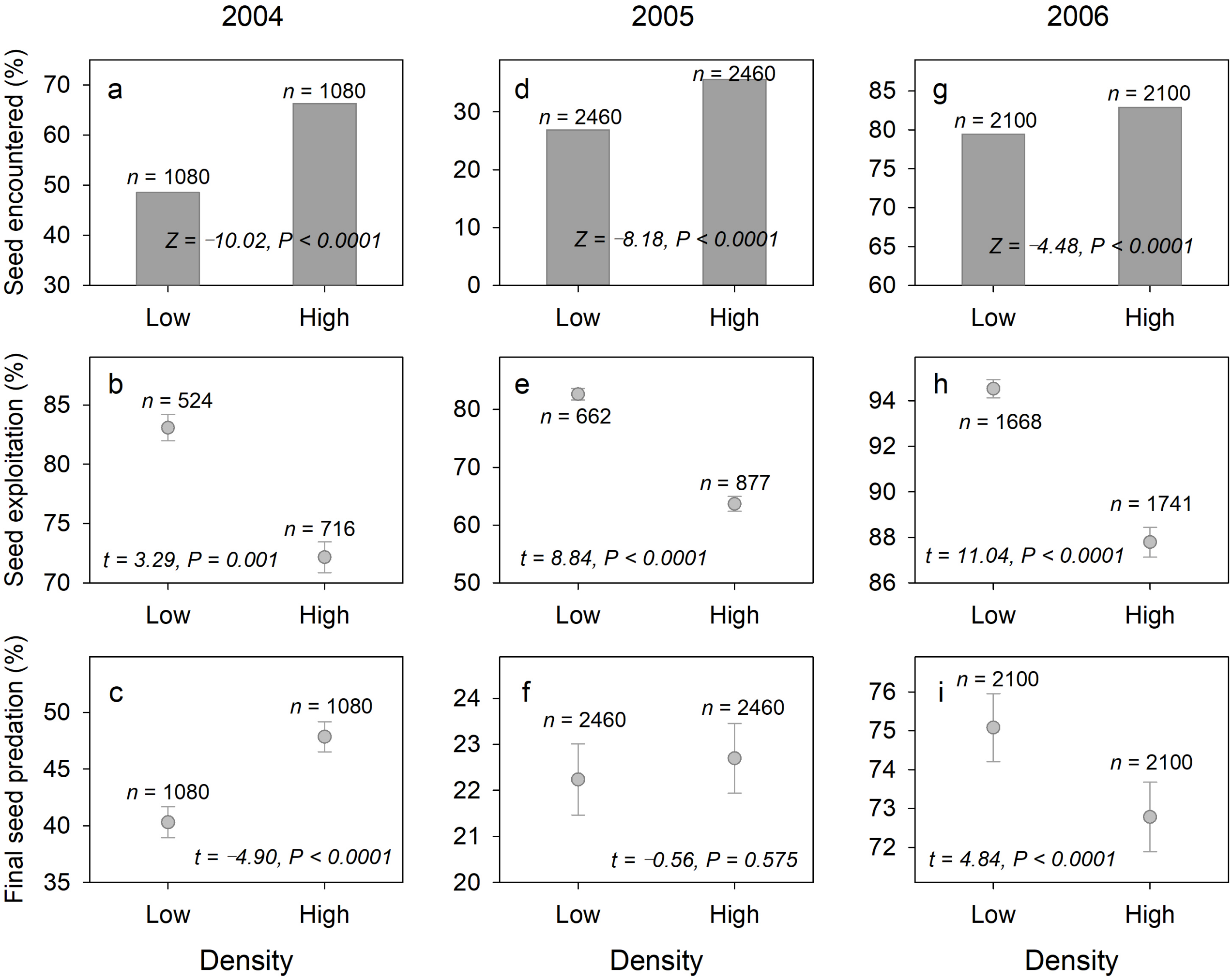

Figure 2 Effects of density on the frequency of seed encounter, seed exploitation after encounter and the final seed predation over 3 years (18 species of seeds were used in 2004, 41 species in 2005 and 35 species in 2006). The numbers in the panels indicate sample sizes (i.e. the number of depots).

ear mixed-effects model, $t = -4.90$, $P < 0.001$; Fig. 2c, Table S6). Seed predation differed among species and ranged from 0 to 100% for high-density depots and from 0 to 97% for low-density depots (Table S1). Five species showed similar positive density-dependent responses overall, 4 species showed negative density dependence (seeds from low-density depots were subject to stronger predation) and the remaining 9 species showed density-independent responses (Table S1).

In 2005, final seed predation showed a density-independent effect and seeds at both high-density and low-density depots were subject to weak predation (23% *vs* 22%; $t = -0.56$, $P = 0.575$; Fig. 2f, Table S6). Seed predation differed among species for both high-density and low-density depots and ranged from 0.2% to 94% and 0.6% to 77%, respectively (Table S2). Most species showed the same density-independent response overall ($n = 28$) and the remaining species showed positive ($n = 5$) and negative ($n = 8$) density dependence, respectively (Table S2).

In 2006, seed predation was negatively density dependent and final seed predation increased slightly, by 3%, in low-density depots compared to high-density depots (75% *vs* 73%; $t = 4.84$, $P < 0.001$; Fig. 2i, Table S6). Seed predation differed among species and ranged from 3% to 100% for low-density depots and from 0.4% to 100% for high-density depots (Suppl. Table S3). The majority of species ($n = 28$) showed a density-independent response due to the heavy seed predation in this year and the remaining species showed positive ($n = 2$) and negative ($n = 5$) density dependence, respectively (Table S3).

DISCUSSION

The results supported our predictions that seed encounter frequency would show a consistent positive density dependence while seed exploitation would show a consistent negative density-dependent response, although not all species followed the same pattern and some species presented contrasting patterns. However, final seed predation showed inconsistent responses to seed density given the contrasting effects of seed density on seed encounter and seed exploitation and the magnitudes of the effects of density differed greatly across years.

High-seed density increased the probability of seeds being encountered by predators, a result which is similar to that of previous studies (Willson & Whelan 1990; Hulme & Borelli 1999). Generally, a high-density seed patch may be more apparent and easier to detect. Moreover, some seed species contain volatile compounds (Vander Wall 2010; Yi *et al.* 2016) and volatility may increase with increasing seed density, which, in turn, is more attractive to seed predators than low seed density. However, in our study, we were not sure whether the non-encountered depots were not being detected by rodents or if they were ignored after being encountered due to a lack of interest. Nevertheless, seed density showed a positive effect on seed encounter, regardless of whether non-encountered depots were either not detected or detected and then ignored.

With regard to the encountered depots, seed exploitation was negatively related to the density or the absolute number of seeds, which supports the predator satiation hypothesis (Janzen 1971; Silvertown 1980), at least within the seed density range of our study. When rodents handle seeds, regardless of whether the seeds are eaten *in situ* or removed, the handling time may positively relate to the number of seeds handled and longer handling times may increase the risk of the rodent being predated. Therefore, rodents may prefer not to spend much time at the same seed depot. Logically, there should be a limit to the number of seeds that a rodent can handle and remove at any given time. Once a depot was encountered and a specific number of seeds were handled, the proportion of seeds handled was smaller when more seeds were present at the depot (i.e. high seed density). Seed density often varies in both space (e.g. seed production variation among individuals; Wang & Ives 2017) and time (e.g. mast seeding phenomenon; Vander Wall 2010). Our results further indicated that a larger proportion of seeds would escape from rodent predation under trees with larger seed production or in mast seeding years.

Final seed predation showed distinct density-dependent responses across years; specifically, a positive density dependence was observed in 2004, a negative density dependence was observed in 2006 and a density independence was observed in 2005. Current studies have also found similar inconsistent density effects on seed predation and several possible reasons have been suggested, including rodent population size, food abundance, seed burial and seed traits (Willson & Whelan 1990; Hulme & Borelli 1999; Myster 2003; Vander Wall 2010; Pannwitt *et al.* 2017; Rosin & Poulsen 2018). In our study, food abundance in the forest was similar across years and the experimental seeds were not buried. The rodent abundance and seed species present were different across years, which may have contributed to the different density responses observed. Surprisingly, these factors did not change the effect of density on seed encounter and exploitation.

Although the frequency of seed encounter was positively density dependent in all 3 years, the magnitude of the effect of density differed greatly across years. For example, high-seed density increased the frequency of seed encounter by 37%, 32% and 4% in 2004, 2005 and 2006, respectively. The same pattern was present for seed exploitation; low-seed density increased the proportion of seeds harvested from encountered depots by 15%, 30% and 8% in 2004, 2005 and 2006, respectively. The density response for final seed predation is the combined effect of positive density-dependent seed encounter and negative density-dependent seed exploitation. Therefore, the density response for final seed predation may depend on the difference in magnitude of the effects of seed encounter and seed exploitation. In 2004, the increase in positive density-dependent seed encounter was greater than the increase in negative density-dependent seed exploitation (37% *vs* 15%); therefore, final seed predation showed positive density dependence. A contrasting pattern existed in 2006, and the effect of density on final seed predation showed negative density dependence because the magnitude of negative density-dependent seed exploitation was greater than positive density-dependent seed encounter (8% *vs* 4%). In 2005, the increased frequency of negative density-dependent seed exploitation was similar to the increase in positive density-dependent seed encounter (30% *vs* 32%); thus, final seed predation was density independent.

When analyzing our data for each species, we found that many species followed the same density-dependent patterns as the combined dataset. However, a certain proportion of species did not show a clear density response, and a few species showed contrasting patterns. Similar interactive effects between seed density and plant species on seed predation have been reported in other studies (Willson & Whelan 1990; Hulme & Borelli 1999; Myster 2003; Perez-Ramos *et al.* 2017). Seed traits, such as seed size, are important factors that can influence the foraging behavior of seed predators (Hulme 1994; Perez-Ramos *et al.* 2017; Rosin & Poulsen 2018). In our study, seed size could not completely explain the overall interspecific variation in density-dependent seed predation. Our experimental seeds contained a large range of sizes each year, and seeds with similar seed size often showed inconsistent density responses for seed encounter, seed exploitation and final seed predation (Tables S1–S3). This result further indicates that seed traits other than seed size may also play important roles in density-dependent seed predation.

In conclusion, our results indicated that seed encounter and seed exploitation showed consistent and contrasting responses to seed density; however, the magnitude of both density effects differed across years and possibly depended on rodent population size and overall food abundance, which, in turn, resulted in final seed predation showing a distinct response to seed density. For example, when the food abundance is very low or rodent population is extremely large, rodents may increase their foraging activity and encounter most of the seeds available in the forest; thus, final seed predation may follow the same pattern as seed exploitation and show negative density dependence. However, when total food abundance is high or the rodent population is small, rodents may only encounter a small portion of seeds; thus, final seed predation may follow the same pattern as seed encounter and show positive density dependence. Furthermore, density dependence varied among plant species, which may indicate that studies using only a few seed species may bias density effect results. Therefore, studies that use many plant species and that include a large range of a diverse of seed traits may avoid the aforementioned bias to some extent and reveal more comprehensive results.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found in the online version of this article at the publisher's website.

Table S1 Effects of density on the frequency of seed encounter, seed exploitation after encounter, and the final seed predation in 2004

Table S2 Effects of density on the frequency of seed encounter, seed exploitation after encounter, and the final seed predation in 2005

Table S3 Effects of density on the frequency of seed encounter, seed exploitation after encounter, and the final seed predation in 2006

Table S4 Generalized linear mixed model for the effects of density on the frequency of seed encounter during the 3 years

Table S5 Generalized linear mixed model for the effects of density on the proportion of seed exploitation after encounter during the 3 years

Table S6 Generalized linear mixed model for the effects of density on the proportion of final seed predation during the 3 years

Figure S1 Schematic diagram of seed release in the field.

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