

Seed–predator satiation and Janzen–Connell effects vary with spatial scales for seed-feeding insects

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Received: 29 June 2016 Returned for revision: 22 August 2016 Editorial Decision: 14 September 2016

- **Background and Aims** The Janzen–Connell model predicts that common species suffer high seed predation from specialized natural enemies as a function of distance from parent trees, and consequently as a function of conspecific density, whereas the predator satiation hypothesis predicts that seed attack is reduced due to predator satiation at high seed densities. Pre-dispersal predation by insects was studied while seeds are still on parent trees, which represents a frequently overlooked stage in which seed predation occurs.
- **Methods** Reproductive tree density and seed production were investigated from ten *Quercus serrata* populations located in south-west China, quantifying density-dependent pre-dispersal seed predation over two years by three insect groups.
- **Key Results** Acorn infestation was nearly twice as high in the low-seed year as that in the high-seed year, with considerable spatio-temporal variation in the direction and magnitude of density-dependent pre-dispersal seed predation evident. Across whole populations of trees, a high density of reproductive trees caused predator satiation and reduced insect attack in the high-seed year. Within individual trees, and consistent with the Janzen–Connell model, overall insect seed predation was positively correlated with seed production in the low-seed year. In addition, there was variation among insect taxa, with positive density-dependent seed predation by *Curculio* weevils in the high-seed year and moths in the low-seed year, but apparent density independence by *Cyllorhynchites* weevils in both years.
- **Conclusions** The overall trend of negative density-dependent, pre-dispersal seed predation suggests that predator satiation limited the occurrence of Janzen–Connell effects across *Q. serrata* populations. Such effects may have large impacts on plant population dynamics and tree diversity, depending on the extent to which they are reduced by counteracting positive density-dependent predation for seeds on individual trees and other factors affecting successful recruitment.

Key words: Conspecific density, density dependence, predator satiation, pre-dispersal seed predators, *Quercus*, seed survival, spatio-temporal variability.

INTRODUCTION

Seed predators are important in the life-history of many tree species, and can kill up to 70–100 % of seed crops, creating direct effects on seedling establishment for a wide range of tree species (Janzen, 1971; Crawley, 1992; Hulme and Benkman, 2002; Fenner and Thompson, 2005). Discussions about the effects of seed production and seed density on seed and seedling recruitment focus on two main hypotheses. The Janzen–Connell model is a well-known explanation for high plant diversity, whereby conspecific negative density-dependence affects survival, growth and recruitment of seeds and seedlings under the parent tree (Janzen, 1970; Connell, 1971; Fig. 1A). The Janzen–Connell model hypothesizes that seeds and seedlings of common species suffer high mortality by host-specific natural enemies close to parent trees. It provides a mechanism for the recruitment of rare species, and has been interpreted more

generally as an effect of conspecific density, not just distance from parent trees (Hammond and Brown, 1998; Wright, 2002; Terborgh, 2012). Evidence indicates that such negative density-dependent recruitment is widespread during the seed-to-seedling transition stage (Blundell and Peart, 2004; Wright *et al.*, 2005; Kobe and Vriesendorp, 2011). In contrast to the Janzen–Connell model, the predator satiation hypothesis predicts that seed attack is reduced in high-seed years or in areas with high seed densities, leading to positive density-dependent recruitment of common species (Fig. 1B) (Silvertown, 1980; Kelly, 1994; Hammond and Brown, 1998). Additionally, density-independent recruitment patterns have been described for different species or geographical areas (Hammond and Brown, 1998; Wright, 2002; Comita *et al.*, 2014). Therefore, we argue that density dependence may be relevant to population and metapopulation persistence of single species at different space and time scales (e.g. Nicholson, 1958; Hanski *et al.*, 1996).

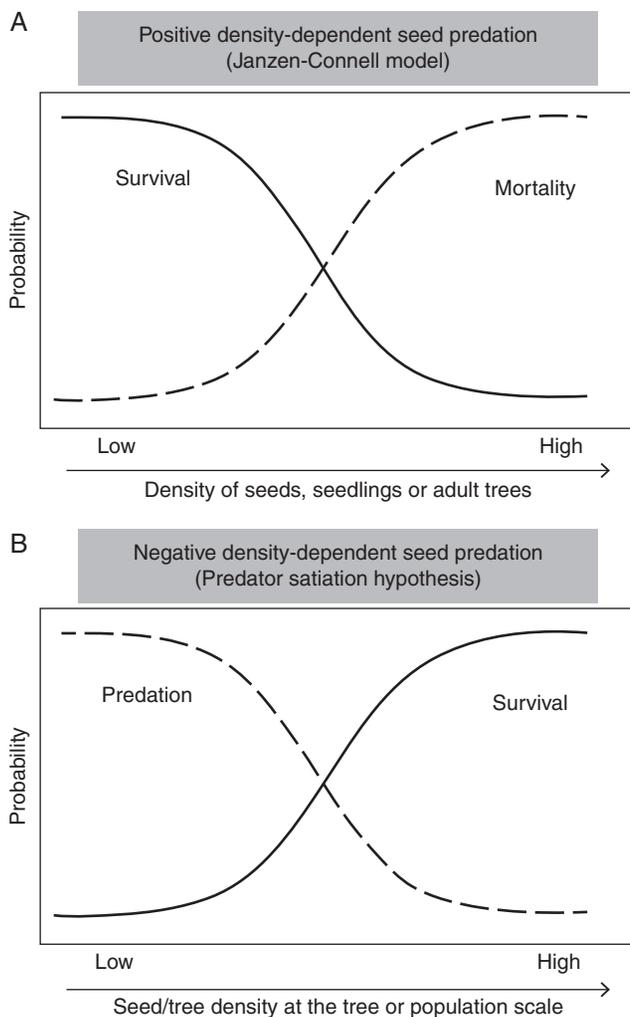


FIG. 1. Hypotheses and predictions about the probability of seed survival or predation as a function of the density of seeds, seedlings or adult trees. (A) Positive density-dependent mortality (modified, the Janzen–Connell model), which predicts that individual plant performance (e.g. survival, growth and recruitment) decreased with increasing conspecific density (Wright, 2002). (B) Negative density-dependent seed predation (the predator satiation hypothesis), which predicts reduced seed predation but increased seed survival when seed density is high enough to satiate seed predators at the tree or population scale (Silvertown, 1980; Kelly, 1994).

Seed predators such as weevils, wasps and moths are responsible for heavy or even complete reproductive failure (Yu *et al.*, 2003; Espelta *et al.*, 2009; Bell and Clark, 2016). While most vertebrate seed predators (e.g. rodents) are generalists operating during or after seed dispersal, many insect seed predators are pre-dispersal specialists (Sallabanks and Courtney, 1992; Hulme and Benkman, 2002). Indeed, a key difference between pre- and post-dispersal seed predators is that the former attack seeds while they are still developing on the tree and their ecological effect is not always readily apparent. Consequently, and as Comita *et al.* (2014) pointed out, studies considering only post-dispersal seed predation can underestimate density-dependent seed mortality. By considering immobile seeds we can, however, simplify thinking about density effects and the Janzen–Connell predictions because it avoids the complication

that dispersal changes seed density in space and time. Consequently, insect seed predators attacking immobile (pre-dispersal) seeds are an ideal system in which to explore the roles of density dependence and predator satiation in seed predation. The direction of any density-dependent effects on seed predation, and the spatial and temporal scales at which density dependence operates, may have important consequences for seedling recruitment and ultimately both for population persistence and for the evolution of masting, which is hypothesized to relate to predator satiation (Silvertown, 1980; Kelly, 1994; Curran and Leighton, 2000; Kelly and Sork, 2002). More generally, there may be interplay between spatial and temporal dynamics affecting seed predation. Seed predator populations may build up in areas where conspecific host tree density remains consistently high but persist at lower average abundance in areas where lower conspecific host tree density is reduced or shows greater spatio-temporal variation. Additionally, if seed production is spatiotemporally variable, averaging across space may enable seed predators to deal with temporal variation. Different insect seed predators probably have different abilities to locate seeds and aggregate on them, and may attack fruits or seeds at different developmental stages. Consequently, this kind of niche partitioning could yield important variation in the densities of unattacked seeds available to pre-dispersal seed predators. Pre-dispersal seed predation, like other sources of spatio-temporal variation in plant species recruitment success (see Kelly *et al.*, 2014), may also help to explain how diversity is maintained in diverse forest ecosystems. Consequently, a fuller understanding of this interaction is important from a perspective of ecological theory and application to forest management. To the best of our knowledge, however, no study to date has investigated how different pre-dispersal insect seed predators respond to spatio-temporal variation in seed production.

Consequently, we investigated how variation in population density and associated acorn production of the East Asian oak (*Quercus serrata*) was related to density-dependent pre-dispersal seed predation by three insect groups at different acorn developmental stages over a 2-year period of high and low acorn crops. Specifically we tested the following hypotheses:

1. Insect seed predation is reduced with increased seed production at either individual tree or tree population scales as predicted by the predator satiation hypothesis (Fig. 1B).
2. The proportion of seeds attacked by insects is positively related to seed or tree density at the individual tree or tree population scales (Janzen–Connell model) (Fig. 1A).
3. Seed attack by different insect groups will show similar positive or negative responses to seed or tree densities at both individual tree and tree population scales regardless of these insect groups attacking different acorn developmental stages.

MATERIALS AND METHODS

Study site and study species

Fieldwork was performed in the Banruosi Experimental Forest (altitude 700–1000 m, 31°4'N, 103°43'E) of Dujiangyan City, Sichuan Province, south-west China. The Dujiangyan region is in the northern part of the Hengduan Mountains. Located on the

western border of the Sichuan Basin the area represents an ecotone between two biogeographical regions, the Qinghai–Tibetan Plateau and Chengdu Plain. It lies in the middle subtropical zone, characterized by evergreen broadleaved forests. The weather is often cloudy and foggy, with a mean annual temperature of 15 °C, an annual precipitation of 1200–1800 mm and annual hours of sunlight typically in the range 800–1000.

Quercus serrata is widely distributed in east, south and south-west China (Chun and Huang, 1998) and Japan (Fukumoto and Kajimura, 2001), and is one of the most common tree species in our study area (Xiao et al., 2004a). Its fruit-ripening period occurs from September to December, and acorn size is relatively large (mean 0.97 g; range 0.5–2.1 g). *Quercus serrata* trees [diameter of breast height (dbh) > 0.5 cm] can produce their first acorns 5–8 years after sprouting from a seed or after resprouting (Z. Xiao, pers. observ.). Like many oak species (Koenig and Knops, 2014; Koenig et al., 2015), *Q. serrata* shows considerable spatio-temporal variation (masting) in acorn production [from 2004 we observed regular mast events in 2007, 2008, 2011 and 2013 in a local population (Z. Xiao, unpubl. res.)]. However, it is unclear how density-dependent seed predation influences *Q. serrata* population dynamics in the study region (Xiao et al., 2003, 2004a, 2008; Chang et al., 2009). In the study region, *Q. serrata* acorns are infested by several insect groups, such as *Cyllorhynchites ursulus* (hereafter *Cyllorhynchites* weevils), *Curculio* weevils (e.g. *Curculio haroldi* and several other unidentified species) and moths (e.g., *Cydia* sp., *Archips* sp. and one unidentified gelechiid moth) (Xiao et al., 2004b, 2007; Z. Xiao, unpubl. res.). Based on our observations, *Cyllorhynchites* weevils lay eggs on young acorns and often cut the branch, leaving acorns containing eggs during the early stage of fruit development (from mid-August to late September). *Curculio* weevils infest nearly mature acorns from mid-September to the end of the fruiting season, and moth infestation occurs throughout the fruiting season. We found very few simultaneous infestations: during the 2-year sampling period, only two acorns were simultaneously infested by both *Cyllorhynchites* and *Curculio* weevils, or by both *Cyllorhynchites* weevils and moths.

Measuring tree density at the population scale

The study region is a mosaic of small stands fragmented by agricultural development, highways and villages. We randomly selected ten isolated stands separated by approx. 100–1000 m. In 2013, vegetation survey transects were established to record at least 100 stems of at least 1-cm dbh (1.3 m above ground). This resulted in two, four or eight transects per site, according to the area of each site. One of these transects was 10–15 m from the edge and others were interior within each site. Each transect consisted of 6–11 circular plots (each 5 m in diameter, area 19.6 m²) spaced at 10-m intervals along the transect. Within each circular plot, we tagged, measured the diameter and identified all trees. We used only *Q. serrata* trees of ≥ 4 -cm dbh to estimate reproductive tree density in each site although most trees with dbh of 1–4 cm can also produce acorns.

Acorn production and pre-dispersal seed predation by insects

Seed traps were used to collect fallen acorns from 55 fruiting individuals across whole fruiting seasons in 2013 and 2014. For each of the ten populations, we randomly chose and marked five *Q. serrata* fruiting trees (ten trees in one old-growth site; total $n = 55$ trees) to measure acorn production and insect seed predation in 2013. We measured dbh, tree height and canopy area for each marked tree. We also established one 1-m² seed trap under the canopy of each marked tree at the end of July 2013 and 2014. We collected acorns in the seed traps at 2-week intervals, and all acorns (2013, $n = 2369$; 2014, $n = 1432$) were dissected and categorized as uninfested or infested by three insect groups: *Cyllorhynchites* weevils, *Curculio* weevils and moths. Each insect group attacked acorns on the tree, and was easily identified from larvae or damage signs.

Data analysis

Although the number of available acorns for attack may change through the season due to sequential attack by different insect species, we used the initial acorn numbers from seed traps to determine densities for use in our analyses. This reflects that some simultaneous infestation by different insect species may occur and the amount of overlap in timing was not quantified. The number of seeds per tree was calculated by multiplying total seeds collected in the seed trap by tree canopy area. We used reproductive tree density (reproductive individuals of ≥ 4 -cm dbh per hectare in each site) to measure seed density at the population scale. For each tree, seed infestation was calculated either for all insects or for each insect group, but infestation was not analysed if we were unable to collect at least ten seeds from a given tree. Generalized linear mixed models with a binomial distribution and site as a random factor were used to test the effects of seed density per tree, tree density per site and their interactions on the proportion of seed predation by all insects, and separately for each insect group for each year (Package lme4, Bates et al., 2013; R 3.2.0, R Development Core Team, 2015).

RESULTS

Variation in acorn production and pre-dispersal seed predation by insects

Acorn production varied greatly among the ten populations and between the two years (Appendix 1). The average number of acorns produced per tree was higher in 2013 (1356 ± 273 acorns) than in 2014 (865 ± 181 acorns; paired *t* test for log+1-transformed data, $t = 3.94$, $df = 54$, $P < 0.001$, Appendix 1).

The proportion of acorns attacked by each insect group, in particular *Cyllorhynchites* weevils or moths, was higher in 2014 than in 2013 (Fig. 2). The overall proportion of attacked acorns by insects was nearly twice as high in 2014 ($70.3 \pm 3.8\%$) as that in 2013 ($38.5 \pm 3.4\%$), and also varied greatly among the ten populations (2013, range 23–54%; 2014, range 45–90%).

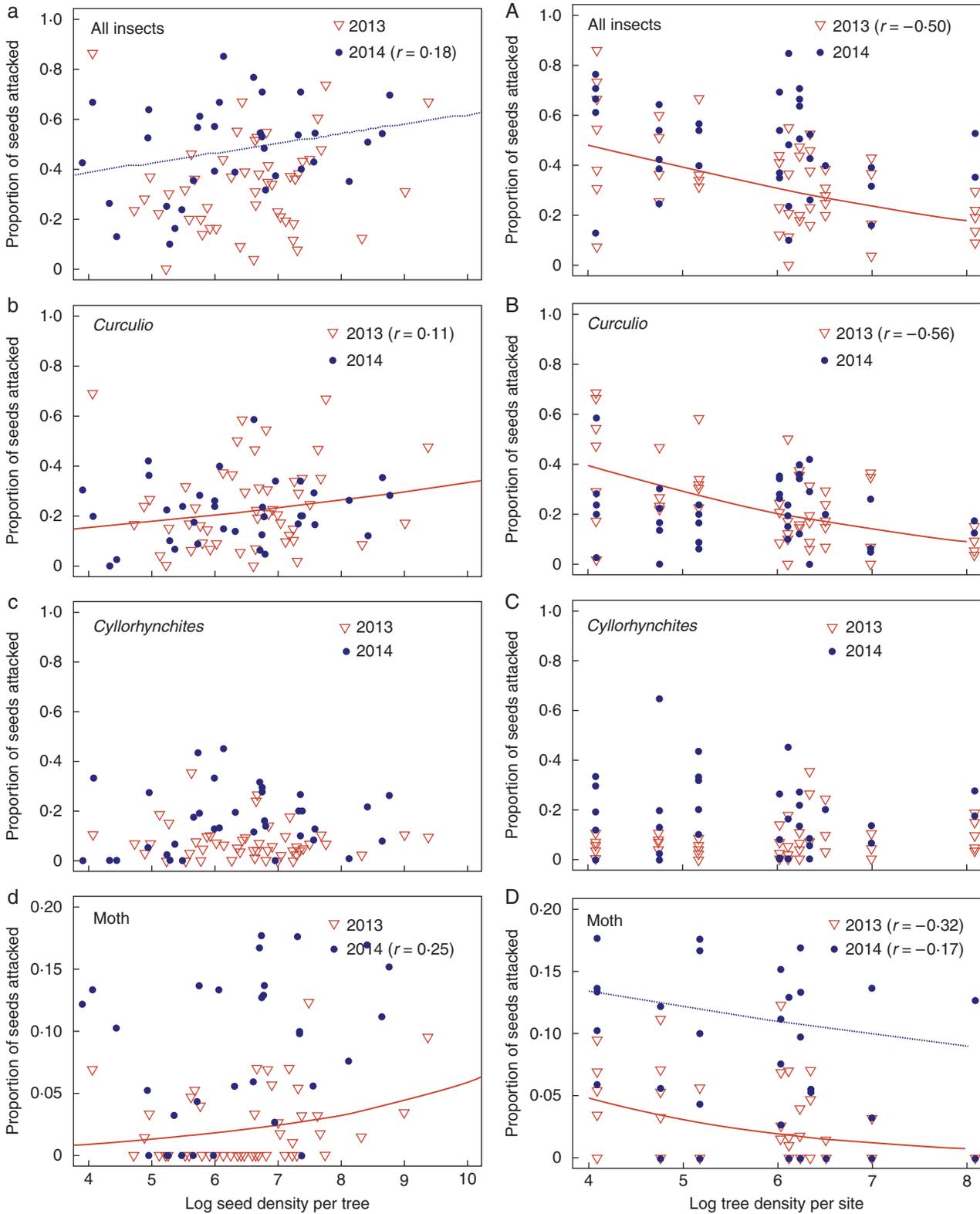


Fig. 2. Pre-dispersal acorn attack of *Quercus serrata* by insects as a function of seed density per tree (a–d) and tree density per hectare in each site (A–D) in each stand in 2013 (the high-seed year; red triangles) and 2014 (the low-seed year; blue dots). Insect seed predators included weevils (*Cyllorhynchites* and *Curculio*) and moths. The trend lines are logistic regression best-fitted estimates, and Pearson's correlation coefficients are shown for the data with $P < 0.05$ (Table 1).

TABLE 1. The effects of seed density per tree and tree density per site on pre-dispersal seed attack of *Quercus serrata* by weevils (*Curculio* and *Cyllorhynchites*) and moths in 2013 and 2014; fixed factors in bold had significant effects ($P < 0.05$)

Fate and factor	2013			2014		
	Estimate ± s.e.	<i>z</i>	<i>P</i>	Estimate ± s.e.	<i>z</i>	<i>P</i>
Seed predation by all insects						
(Intercept)	0.76 ± 0.63	1.22	0.224	-0.56 ± 0.52	-1.06	0.288
ln(seeds per tree)	0.06 ± 0.05	1.16	0.245	0.21 ± 0.05	4.44	<0.001
ln(trees per site)	-0.33 ± 0.08	-4.39	<0.001	-0.15 ± 0.08	-1.89	0.058
Seed predation by <i>Curculio</i> weevils						
(Intercept)	4.81 ± 1.81	2.66	0.008	-1.44 ± 0.73	-1.98	0.048
ln(seeds per tree)	-0.55 ± 0.26	-2.10	0.036	0.09 ± 0.06	1.50	0.135
ln(trees per site)	-1.23 ± 0.34	-3.57	<0.001	-0.10 ± 0.11	-0.96	0.340
ln(seeds per tree) × ln(trees per site)	0.12 ± 0.05	2.39	0.017	—	—	—
Seed predation by <i>Cyllorhynchites</i> weevils						
(Intercept)	-3.64 ± 1.21	-3.01	0.003	-1.88 ± 0.91	-2.06	0.039
ln(seeds per tree)	0.02 ± 0.09	0.20	0.843	0.07 ± 0.07	0.96	0.336
ln(trees per site)	0.15 ± 0.15	1.01	0.311	-0.03 ± 0.14	-0.21	0.834
Seed predation by moths						
(Intercept)	-0.72 ± 1.89	-0.38	0.702	-2.19 ± 0.51	-4.25	<0.001
ln(seeds per tree)	0.04 ± 0.14	0.28	0.780	0.19 ± 0.06	3.07	0.002
ln(trees per site)	-0.61 ± 0.25	-2.44	0.015	-0.21 ± 0.09	-2.44	0.014

Effects of seed and tree density on seed attack at the tree and population scales

The proportion of acorns attacked by all insects, or separately by *Curculio* weevils or moths, increased with acorn production at the tree scale in each year (Fig. 2; Table 1). In 2013, tree density at each site had strong negative effects on seed attack by all insects, but in 2014, negative effects were apparent only for moth infestation (Fig. 2; Table 1). In addition, the interactions between seed density per tree and reproductive tree density per plot had significant effects on seed attack by *Curculio* weevils in 2013. However, seed or tree density at either tree or population scales had no strong effects on seed attack from predation by *Cyllorhynchites* weevils in either year (Fig. 2; Table 1).

DISCUSSION

The Janzen–Connell model, negative density-dependent seed and/or seedling recruitment as a function of conspecific density or distance to the fruiting plant, is suggested to be a major mechanism for understanding the high diversity of tree species in tropical forests (Janzen, 1970; Connell, 1971). This idea has been supported by a large number of empirical studies working during post-dispersal seed, the seedling and sapling stages. However, there are few studies of such effects while seeds are still on trees (Lewis and Gripenberg, 2008). We demonstrate here that the direction and magnitude of density-dependent seed predation by host-specific insects differed not only between individual tree and tree population scales, but also across different insect groups.

Negative density-dependent seed predation due to predator satiation

Our results at the population scale provide strong evidence for the predator satiation hypothesis. The predator satiation hypothesis is widely accepted as an adaptive mechanism for

describing temporal patterns between seed predation by seed-eating animals and annual seed production in many tree species (Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002). We found that pre-dispersal seed predation by insects was nearly double in the low-seed year (70 % in 2014) compared to that in the high-seed year (38 % in 2013), and insect seed predation was negatively related to reproductive tree density at the tree population scale in the high-seed year. In addition, negative density-dependent seed predation by moths was confirmed in the low-seed year, but seed attack by all insect groups, or separately by *Cyllorhynchites* or *Curculio* weevils, was density-independent, resulting from higher seed predation and smaller acorn crops among individual trees in the low-seed year. Most of our results are consistent with the predator satiation hypothesis, and with studies by Jones and Comita (2010), who reported reduced seed attack of *Jacaranda copaia* by wasp seed predators, and Bagchi *et al.* (2011), who showed negative density-dependent post-dispersal seed predation of *Parashorea malaanonan*. It may be common that predator satiation can lead to more tree seeds being available for seed dispersal and late-stage seedling establishment.

It is, however, well known that negative density-dependent recruitment occurs more frequently at the seed-to-seedling transition stage in different plant populations and communities especially in tropical forests (Wright, 2002; Comita *et al.*, 2014). Therefore, it is possible that the positive density-dependent effects of predator satiation in years of high seed predation may be offset later by negative density-dependent recruitment of seedlings, which can cause large impacts on plant population dynamics and tree diversity (Hammond and Brown, 1998; Wright, 2002). As shown by Fedriani *et al.* (2015), such antagonistic density-dependent effects may operate at multiple stages of plant reproduction. They found that fruit initiation was higher for individuals with more neighbours at small distances, but fruit development decreased with an increasing number of nearby neighbours leading to density-independent overall fruit-set. In addition, predator satiation may be a major mechanism for understanding why tree species such as oaks become

dominant in many forests (Hart, 1995), a total contrast to the predictions of the Janzen–Connell model.

*Positive density-dependent seed predation
(Janzen–Connell Model)*

In contrast to strong negative density-dependent seed predation at the population scale, our results supported the Janzen–Connell model at the individual tree scale: overall insect seed predation was positively correlated with seed production in 2014, the low-seed year. Similar results were also seen for *Curculio* weevils in the high-seed year, and for moths in both years. Like our study, Visser *et al.* (2011) also found strong positive density-dependent post-dispersal seed attack of the palm *Attalea butyracea* by specialist bruchid beetles at the population scale. In most conditions, fruits or seeds on individual fruiting trees can represent an abundant and spatially aggregated resource, especially in high-seed years (Crawley, 1992). Insect seed predators may be attracted to these fruiting trees with high seed crops or high-density patches, and thus they are more efficient in locating seeds for feeding and egg-laying. This may be one key reason that higher seed predation can be found in these fruiting trees with high seed crops as shown in this study. However, this positive density-dependent seed predation at the tree scale may be offset by reduced seed predation at the population scale due to predator satiation in high-density populations (patches) or in high-seed years.

Density-independent seed survival from seed predation

We found that negative density-dependent seed predation occurred mostly at the population scale, and positive density-dependent seed predation occurred at the within-tree scale. The direction and magnitude of density-dependent pre-dispersal seed predation, however, were inconsistent between high-seed and low-seed years, and also among three different insect groups attacking different acorn developmental stages. Annual variation in seed production is common in many tree species, but can lead to higher losses to insect predators in lower-seed years (or seed-poor sites), as predicted by the predator satiation hypothesis (Silvertown, 1980; Kelly, 1994). This is probably the reason that density-independent effects were observed in the low-seed year in this study. For *Q. serrata*, *Cyllorhynchites* weevils attacked acorns at earlier developmental stages than *Curculio* weevils or moths, but why did these three insect groups respond differently to seed or tree density? We have two hypotheses: (1) compared to late-infesting insects, early-infesting *Cyllorhynchites* weevils had more seeds available each year even in the low-seed years, and (2) each insect group was highly sensitive to the infestation by other insect groups. The latter hypothesis was supported by the observation that two *Q. serrata* acorns were simultaneously infested by both *Cyllorhynchites* and *Curculio* weevils, or by both *Cyllorhynchites* weevils and moths over the two years.

In conclusion, our study has shown spatio-temporal variation in pre-dispersal seed predation by insects, with the direction and magnitude of density-dependent seed predation changing with spatial scales. Predator satiation limited the occurrence of Janzen–Connell effects across *Q. serrata* populations, and

while the Janzen–Connell model explained seed mortality or recruitment at the local tree scale, the predator satiation hypothesis explained the overall recruitment of seeds at the population level. In tandem, these two processes may potentially help to explain how tree diversity is maintained and also how species abundance patterns change over time and space, although it is apparent that patterns of species diversity and abundance are also contingent on later steps in recruitment from seeds to adult reproductive plants (see Hanley and Sykes, 2009, 2014; Barton and Hanley, 2013). However, in contrast to the density responses of pre-dispersal insect seed predators to seed densities at individual trees or conspecific neighbours, post-dispersal seed predators such as generalist rodents often respond differently to seed density over time and space (Xiao *et al.*, 2013). This occurs because vertebrate seed predators can move long distances and their foraging is not restricted to individual trees (Hammond and Brown, 1998; Hulme and Benkman, 2002). Further studies of the foraging and egg-laying movements of insects need to be made to determine if they are indeed less mobile than vertebrate seed predators. Anthropogenic disturbances such as deforestation, hunting and forest fragmentation have caused population declines and diversity losses affecting both host trees and their seed predators (Bagchi *et al.*, 2011). Understanding the impact of density-dependent seed predation by both pre- and post-dispersal seed predators on forest dynamics in these changing landscapes is essential for future conservation and management of threatened forests.

ACKNOWLEDGEMENTS

We thank Xunlong Wang and Chengqiang Wang for help with fieldwork, the Subalpine Mountain Plant Garden of West-China, CAS and the Forest Bureau of Dujiangyan City of Sichuan Province for field support, and Mick Hanley and two anonymous referees for comments on the manuscript. The experiments comply with the current laws of China. This research was supported by NSF China (31330013, 31270470, 31071929), and CAS Visiting Professorship for Senior International Scientists to Charles Krebs (2010T1S12).

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APPENDIX 1. *Tree density, tree traits and acorn production (mean ± s.d.) of Quercus serrata from ten sites in a Dujiangyan subtropical forest, south-west China, in 2013 and 2014*

Site*	Reproductive tree density per ha. (dbh ≥ 4 cm) [†]	dbh (cm)	Tree height (m)	Canopy area (m ²)	Acorns per tree (2013)	Acorns per tree (2014)
1	59.6	24.04 ± 2.18	16.97 ± 1.06	57.07 ± 10.37	3670 ± 1195	572 ± 165
2	1087.0	6.40 ± 1.01	5.26 ± 0.30	10.44 ± 1.37	1144 ± 391	572 ± 180
3	671.3	14.34 ± 0.95	9.28 ± 0.42	21.71 ± 2.13	306 ± 131	518 ± 284
4	116.0	13.62 ± 1.74	8.54 ± 0.99	17.35 ± 3.43	811 ± 338	557 ± 368
5	3273.8	9.42 ± 1.01	8.38 ± 0.35	10.27 ± 1.88	509 ± 200	254 ± 158
6	572.0	8.08 ± 1.51	7.12 ± 0.50	9.34 ± 2.93	485 ± 141	445 ± 377
7	510.2	21.94 ± 4.10	14.44 ± 1.92	32.06 ± 6.96	906 ± 385	1337 ± 846
8	414.5	21.76 ± 1.27	14.32 ± 0.67	30.44 ± 1.77	1613 ± 701	3402 ± 1233
9	453.5	12.12 ± 2.09	10.42 ± 1.97	18.87 ± 3.50	928 ± 236	360 ± 151
10	177.5	17.46 ± 1.26	14.9 ± 0.40	22.76 ± 7.45	852 ± 197	923 ± 267

**n* = 10 trees for Site 1 or five trees for each other site.

[†]Reproductive individuals with dbh ≥ 4 cm were used in the analysis.