






Benefit versus cost trade-offs of masting across seed-to-seedling transition for a dominant subtropical forest species

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Abstract

1. Masting is a common reproductive strategy regulating seedling regeneration in many perennial plant species. The evolutionary origins and functional benefits of masting have been explained by well-supported hypotheses relating to economies of scale of seed production. Nevertheless, our understanding of the potential costs of masting for the plant seed-to-seedling transitions remains limited.
2. We tracked the seed fate and documented changes in the seed spatial distribution patterns during the seed-to-seedling transition process of *Castanopsis fargesii*, a dominant species of subtropical evergreen broad-leaved forests in China under natural conditions for more than 6 years.
3. Masting resulted in a high proportion of seeds escaping predation by vertebrates and rodents, supporting the predator satiation hypothesis. However, it increased the pre-dispersal seed predation by insects, and decreased the seed germination rate due to a negative effect on seed mass. This resulted in seed-to-seedling transition rates during mast years to be roughly half as much as during non-mast years. In addition, masting negatively affected the spatial rearrangement of seeds, resulting in a spatial aggregative distribution pattern of newly germinated seedlings. The combined negative effects of smaller seeds and spatially aggregated seedlings reduced the survival rate of newly germinated seedlings at seedling establishment stage.
4. *Synthesis.* Considering the whole seed-to-established seedling transition process, the benefits of masting on seedling recruitment due to the effective seed predator situation by vertebrates and rodents were decreased by the additional costs on seed mass, seed germination, seed spatial arrangement and seedling establishment. Our results highlight the importance of considering both the positive and negative effects of masting at each stage of the seed-to-seedling transition. Inferences based on seed predation and recruitment of newly germinated seedlings alone would lead to an overly optimistic conclusion about the benefits of masting.

KEYWORDS

benefits, *Castanopsis fargesii*, costs, evergreen broad-leaved forest, masting, seed-to-seedling transition

1 | INTRODUCTION

The seed-to-seedling transition is one of the most critical phases in the life cycle of plants (Muscarella et al., 2013; Wang & Smith, 2002) and a major bottleneck in plant demography, thereby influencing population dynamics and species coexistence (Poorter, 2007). Importantly, the seed-to-seedling transition is a unique mobile stage in the life cycle of flowering plants for determining their spatial distribution (Swamy et al., 2011). Elucidating the ecological mechanisms that regulate the seed-to-seedling transition is important for gaining a better understanding of both plant regeneration dynamics and the origin of spatial distribution patterns of adult trees (Fricke et al., 2014; Muscarella et al., 2013; Piironen et al., 2017). Nonetheless, our understanding of the factors that influence the seed-to-seedling transition of plants, such as the effect of masting, is still limited.

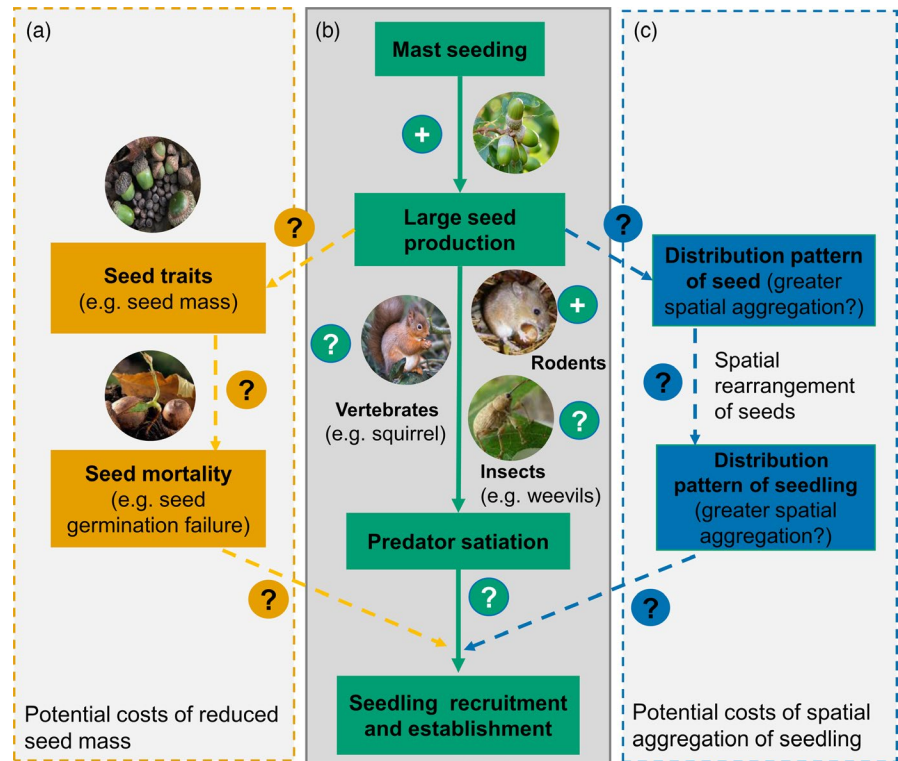
Characterized by the intermittent production of seeds, masting is a common reproductive strategy influencing the seed-to-seedling transition of many perennial plant species (Bogdziewicz, Ascoli, et al., 2020; Bogdziewicz, Szymkowiak, et al., 2020; Kelly & Sork, 2002; Minor & Kobe, 2017; Pearse et al., 2016; Pesendorfer et al., 2016; Zhang et al., 2020). Hypotheses that attempt to explain the selective advantages and evolutionary origins of masting are mainly related to the economies of scale, such as enhanced pollination efficiency and satiation of seed predators during mast years (Kelly et al., 2001; Kelly & Sork, 2002; Pearse et al., 2020; Rapp et al., 2013). Indeed, as a functional benefit of masting, the predator satiation hypothesis (PSH) has been extensively supported (Bogdziewicz, Espelta, et al., 2018; Linhart et al., 2014; Pearse et al., 2020; Wang et al., 2017; Xiao et al., 2013; Zwolak, Bogdziewicz, & Rychlik, 2016; Zwolak, Bogdziewicz, Wróbel et al., 2016). However, these empirical studies have evaluated the benefits of masting at either pre-dispersal or post-dispersal stages, with few considerations of the potential costs of masting (Bogdziewicz, Espelta, et al., 2018; Xiao et al., 2013; Zwolak, Bogdziewicz, Wróbel et al., 2016). To date, we still lack clarity about the potential benefits and costs of masting for all phases of the seed-to-seedling transition of forest keystone species (Pearse et al., 2020; Zwolak et al., 2020).

The seed-to-seedling transition is a multiphase process that involves the stages of pre-dispersal, post-dispersal, soil seed bank, seed germination and seedling establishment (Wang & Smith, 2002). Multiple negative density- and distance-dependent effects (e.g. from vertebrates, insects, rodents and fungal pathogens) are the primary agents influencing seed fate and seedling mortality during the full seed-to-seedling transition (Fricke et al., 2014; Lichti et al., 2014, 2017; Tomita et al., 2002; Wang & Smith, 2002; Yang et al., 2015). Given the diversity of predators, masting can shape

different patterns of seed fate such as mortality along the seed-to-seedling transition, due to the balancing of benefits and costs (Figure 1). Generally, at the pre-dispersal stage, insects (e.g. weevils) and vertebrates (e.g. squirrels) are the main seed predators (Linhart et al., 2014; Soler et al., 2017; Tomita et al., 2002; Yang et al., 2015). Some previous studies found that masting reduces seed predation by insects (Linhart et al., 2014; Soler et al., 2017); however, Bogdziewicz, Espelta, et al. (2018) recently showed that the effectiveness of predator satiation for insects on seed mortality can be low. In addition, our knowledge on the effectiveness of predator satiation for vertebrates at pre-dispersal stage in mast years is by far limited. Therefore, the effectiveness of pre-dispersal predator satiation for insects and vertebrates during mast years remains unclear. At the post-dispersal stage, rodents are the main seed predators, consuming an extremely high proportion of the total seed production (Xiao et al., 2013; Yang et al., 2015). Some evidence suggests that masting benefits seeds in escaping from rodent predation (Bogdziewicz, Espelta, et al., 2018; Linhart et al., 2014; Wang et al., 2017; Xiao et al., 2013; Zwolak, Bogdziewicz, Wróbel et al., 2016). This stage is considered to be the main stage when masting brings benefits to seedling recruitment through economies of scale. At the soil seed bank stage, specific fungi can cause seeds to lose vitality (Gallery et al., 2007, 2010; Leishman, Masters, et al., 2000; Tomita et al., 2002). Masting may cause a higher density-dependent seed mortality by fungi due to highly aggregative seeds in the soil seed bank. At the seed germination stage, seed mass largely determines the success of seed germination and seedling emergence (Lebrija-Trejos et al., 2016; Leishman, Wright, et al., 2000). Seed mass is also an important trait that influences seedling establishment (Baraloto et al., 2005; Krishnan et al., 2019; Lebrija-Trejos et al., 2016; Moles & Westoby, 2004). Currently, however, no consensus exists on whether or not trade-offs exist between seed mass and seed production in masting plants (Bonal et al., 2007; Koenig et al., 2009; Wang & Ives, 2017). If, indeed, masting has a negative impact on seed mass, it could counteract the fitness benefits of masting by negatively influencing seed germination or seedling establishment (Figure 1a). The above studies suggest that masting may have costs at the pre-dispersal stage, soil seed bank stage and seed germination stage.

In addition, the spatial distribution of seedlings is important to their survival and growth, thus having a profound consequence on the regeneration and colonization of plant populations (Fricke et al., 2014; Yang et al., 2015). Previous studies have demonstrated that masting events are dominated by some super-producers that are responsible for a disproportionately large total seed production (Bogdziewicz, Szymkowiak, et al., 2020; Minor & Kobe, 2017). As such, the masting of super-producers has the potential to cause a

FIGURE 1 Schematic diagram of the potential benefits and costs of masting on the seed-to-seedling transition of *Castanopsis fargesii*. Panel (a) shows the potential costs of masting on seedling recruitment by reducing seed mass. Panel (b) shows the potential benefits or costs of masting on seedling recruitment by satiation of seed predators; Panel (c) shows the potential costs of masting on seedling recruitment by changing the spatial aggregative distribution pattern of newly germinated seedlings



greater spatial aggregation of seeds. Likewise, masting can directly affect the behaviour of rodents towards seed predation and seed dispersal, thereby reducing the seed dispersal efficiency (Fletcher et al., 2010; Li & Zhang, 2007; Xiao & Huang, 2020). Consequently, masting can potentially result in a greater spatial aggregation of newly germinated seedlings around adults, and at the seedling establishment stage, masting may reduce seedling survival due to the combined negative effects of reduced seed mass on seedling nutrient accumulation and the negative density- or distance-dependent mortality (Connell, 1971; Fricke et al., 2014; Janzen, 1970; Seiwa et al., 2019; Swamy et al., 2011). In this sense, the negative effect of masting on the spatial rearrangement of seeds can also reduce the benefits of masting (Figure 1c).

While masting can create benefits in seeds escaping from predation at the post-dispersal stage, it can also create costs at other stages in the seed-to-seedling transition. Therefore, we hypothesize that the additional costs caused by masting at the pre-dispersal stage, seed germination stage and seedling establishment stage largely counteract the benefits of predator satiation at the pre-dispersal and post-dispersal stages. Specifically, we predict that (a) masting creates a cost at the pre-dispersal stage by insects due to high-intensity predation; (b) masting benefits to seeds escaping predation at both the pre-dispersal stage and dispersal stage are due to vertebrates and rodents achieving predator satiation; (c) masting creates a cost at the seed germination stage due to the negative effects of decreased seed mass on seed germination and (d) masting creates a cost at the seedling establishment stage due to the negative effects of greater spatial aggregation of newly germinated seedlings on seedling mortality. In this study, we tested the above overarching hypotheses by tracing the seed fate and changes in seed

spatial distribution patterns of *Castanopsis fargesii*, a dominant species that is widely distributed in subtropical evergreen broad-leaved forests in China. We studied this species under natural conditions over a 6-year period to understand the potential effects of masting on seed-to-seedling transitions.

2 | MATERIALS AND METHODS

2.1 | Study site and species

The study was conducted in the Jinyunshan National Nature Reserve (GNNR; 29°8'18"–29°17'29"N, 118°2'14"–118°11'12"E; 8,107 ha in area), in Chongqing, China. The region has a subtropical monsoon climate, and the annual mean temperature is 13.6°C. Mean temperatures in January are around 3.1°C, and the mean August temperature is 24.3°C. Mean annual precipitation and relative humidity are 1611.8 mm and 87%, respectively. Vegetation on Jinyun Mountain is comprised of typical subtropical evergreen forest, dominated by *Castanopsis fargesii*, *Machilus nanmu*, *Polyspora speciose* and *Castanopsis carlesii* var. *spinulosa*.

Castanopsis fargesii is one of the dominant species in the subtropical evergreen broad-leaved forests along the Yangtze River in China. Adult *C. fargesii* trees can attain heights of 30 m. The mean seed mass of *C. fargesii* is about 0.5 g, ranging from 0.1 to 1.8 g (Figure S1c). Seeds are predominantly gravity-dispersed, but they are also dispersed to a lesser degree by squirrels and mice. *C. fargesii* has been recognized as a masting species (Xiao et al., 2005). The fruits ripen from October to November, and the peak of the seed rain also occurs between October and November (Yang et al., 2015).

The germination of seeds generally begins in the following April and May. The emergence of seedlings usually starts in July and August and ends in late-October (Figure S1d).

2.2 | Survey of masting pattern and seed-to-seedling transition

In September 2013, we established a 50 m × 100 m permanent monitoring plot that was divided into 50 subplots (10 m × 10 m). We established 86 seed traps within the study plot to sample masting patterns and seed fate in late-September 2013 (Yang et al., 2015). In all, 50 seed traps were installed in the centre of each 10 m × 10 m subplot, and the remaining 36 were placed at the grid intersections (Figure S1a). The closest distance between two seed traps was 7.1 m, which was approximately equal to the average diameter of the crown of *C. fargesii* adult trees. Next, we established soil seed bank quadrats (1 m × 0.5 m) and seedling quadrats (1 m × 0.5 m) along the surface of the left and right sides of each seed trap, respectively (Figure S1b). The boundaries of the soil seed bank quadrats and the seedling quadrats were marked using four pvc tubes (20 cm in height) and nylon threads. We assumed that the seed rain in the soil seed bank quadrats and seedling quadrats were similar to what was actually recorded in the seed traps.

We measured the seed rain from October to December annually from 2013 to 2018. All materials from the seed traps were collected once per week during this period. Seeds collected from the seed traps were defined as mature seeds and categorized into three groups based on careful examination of each seed: (a) intact seeds (seeds intact, without any injury); (b) vertebrate-attacked seeds (eaten by vertebrates (mostly by *Callosciurus erythraeus*) before seeds had fallen) and (c) insect-attacked seeds (suffered from predation by invertebrate such as *Curculio* sp., with obvious holes on the seed surface). We measured the seed mass of all intact seeds using a precision electronic balance.

We measured the soil seed bank in April (in the year following the seed rain) of each year from 2014 to 2019. We defined seeds from the soil seed bank quadrats as surviving seeds, which were categorized into four groups based on a careful examination of each seed: (a) viable seeds (already had an elongated radicle or healthy embryo and cotyledon); (b) fungi-infected seeds (killed by fungal infection, where the embryo and/or cotyledons were covered with hyphae and had decayed); (c) desiccated seeds (killed by desiccation, where the roots and/or cotyledons were withered and brown) and (d) rodent-attacked seed (predation by rodents; mostly by *Rattus flavipectus* and *Rattus norvegicus*).

We sampled newly germinated seedlings every 2 weeks from May to September each year from 2014 to 2019. Newly germinated seedlings were defined as seedlings that had grown at least one true leaf. Seedlings sampled within each seedling quadrat were censused and marked with a numbered label. In late-December of the following year (2015–2020), two growing seasons after seedling emergence, we censused the labelled seedlings that were still alive. We

referred to these individuals as established seedlings (Figure S1e). Based on this information, we established the seed fate pathway in the seed-to-seedling transition (Figure S2).

2.3 | Survey of microhabitat variables

We selected seven microhabitat variables that were expected to affect seed fate, including canopy openness, shrub coverage, herb coverage, litter thickness, light intensity, soil moisture and soil temperature. We investigated microhabitat variables within the soil seed bank quadrats at the same time as we investigated the seeds in the soil seed bank each year. Shrub coverage and herb coverage were estimated as the percentage of shrubs and herbs covering the plot. Canopy openness was defined as the fraction of open sky in a hemisphere that was visible from a point beneath the canopy. Litter thickness was the average thickness of the litter in the quadrats, measured directly using a ruler. Light intensity was measured at 1.3 m above the forest floor using a Light Scout 6 sensor quantum bar (LightScout; Spectrum Technologies, Inc., USA). Soil temperature and moisture were measured using an HH2 moisture meter (Delta-T Devices) at the surface soil layer (0–11 cm depth).

2.4 | Statistical analysis

We defined a mast year as occurring when the mean seed density exceeded the standard deviation over the 6-year period (LaMontagne & Boutin, 2009). We calculated the proportion of seeds killed according to the categories described above (i.e. vertebrate-attacked seed, insect-attacked seed and rodent-attack seed) to estimate the intensity of each seed-killing agent. We defined the seed-to-seedling transition rate as the percentage of seedlings (either newly germinated seedlings or established seedlings) of mature seeds. We calculated the intensity of each type of seed-killing agent, and the seed-to-seedling transition rate for each seed trap in each year. In addition, we defined super seed traps and super seedling quadrats as the top 10 seed traps for seed production and the top 10 seedling quadrats for newly germinated seedling abundance, respectively.

Using generalized linear mixed models (GLMMs), we tested whether or not annual seed production had a negative effect on seed mass with a Gaussian family, identity linked model. Seed trap-level mean seed mass was included as the response variable, log-transformed annual seed production was treated as fixed effect, and the year and trap ID were included as random effects. We tested whether or not annual seed production had a significant effect on the proportion of each type of killed seed using a binomial family, log-linked model. Seed trap-level seed-killing agent intensity was treated as the response variable, log-transformed annual seed production was treated as a fixed effect, and year and trap ID were treated as random effects. We tested whether or not annual seed

production had a significant effect the establishment probability of the newly germinated seedlings using a binomial family, logit-linked model. Seedling establishment (0/1) was included as the response variable, log-transformed annual seed production was included as a fixed effect and trap ID was included as a random effect.

We evaluated the effects of seedling aggregation, seed mass and microhabitat on seedling establishment using a binomial family, logit-linked model. Seedling establishment (0/1) was the response variable, and seed trap-level mean seed mass, seedling quadrats-level seedling density, and microhabitat variables were fixed effects, and year and trap ID were random effects. To measure the partial effect of each variable on the odds of seedling survival, we calculated the odds ratios for each coefficient (exponential of the estimate of each coefficient). An odds ratio >1 indicated positive effects on survival, whereas ratio <1 indicated negative effects.

We estimated the spatial distribution patterns of the cumulative seeds or seedlings imputed in the two mast and four non-mast years using ArcGIS 10.2 (Esri, 2010). We used a simple inverse distance weighting interpolation algorithm to estimate the seed or seedling density across the entire grid surface based on actual numbers of seeds or seedlings collected from the traps or quadrats (Swamy et al., 2011). The search radius for the interpolation was restricted to the two or four nearest seed traps (7.1 m) and the influence of surrounding seed traps on the interpolated value of seed density at any point within the grid was controlled using a power value of 2 as the exponent of distance. This more strongly weights the nearest neighbour seed trap over the linear interpolation (Swamy et al., 2011). We then used Moran's *I* coefficient to evaluate the spatial aggregation of seeds and seedlings at each stage of the seed-to-seedling transition (Legendre & Fortin, 1989). The significance level for Moran's *I* coefficient was corrected after multiple tests (Holm, 1979).

We constructed a piecewise structural equation modelling (piecewise SEM) approach to investigate the hypothesized causal relationships among seed-to-seedling transition rates, with the two most important seed-killing agents (predation and seed germination failure), seed density and measured microhabitat variables at the seed trap scale. Piecewise SEM incorporates several linear or nonlinear models into a single analysis pathway using directional separation (d-separation) tests to statistically identify causal relationships and missing links (i.e. pathways) in a directed acyclic graph. An initial path model was built based on our conceptual path diagram (Figure S3). We used linear mixed models to connect the variables, with year and trap ID being included as random effects. We refined the original model by dropping non-significant links, starting with the least significant link, and continuing stepwise until changes in the AICc were <2.

All statistical analyses were performed in R version 4.0.3 (R Development Core Team, 2020). Generalized linear mixed models used the lme4 package (Bates et al., 2014). The calculation of Moran's *I* coefficient was implemented with package 'VEGAN' (Oksanen et al., 2013). Structural equation modelling and model testing were conducted using the 'PIECEWISE SEM' package (Lefcheck, 2016).

3 | RESULTS

3.1 | Masting pattern

A total of 30,466 mature seeds were collected from 86 seed traps from 2013 to 2018. Annually, seed densities ranged from 25.8 to 315.3 seeds/m² across the 6 years, and masting occurred during 2014 and 2018 (Figure 2a). Annual mean seed mass ranged from 0.43 to 0.65 g (Figure S4) and decreased with annual seed production ($\chi^2 = 23.63$, $p < 0.001$; Figure 2b; Table S1).

3.2 | Seed fate in the seed-to-seedling transition

At the pre-dispersal stage, the probability of seed attacked by insect increased with annual seed production ($\chi^2 = 6.31$, $p = 0.012$; Figure 3a; Table S1). Insect attack caused a removal of 16.33% of the mature seeds in the highest production year, which was 1.92 times higher than that in lowest seed production year (Figure 4g). The probability of seed attacked by vertebrates decreased with annual seed production ($\chi^2 = 4.32$, $p = 0.037$; Figure 3b; Table S1). Vertebrate attack caused a loss of 8.04% and 13.88% of mature seeds in the highest and lowest seed production year, respectively (Figure 4f). At the post-dispersal stage, the probability of seed attacked by rodents decreased with annual seed production ($\chi^2 = 9.25$, $p = 0.0023$; Figure 3c; Table S1). Rodent attack caused a loss of 46.15% and 61.12% of mature seeds in the highest and lowest seed production year, respectively (Figure 4h). At the soil seed bank stage, the probability of seed killed by fungi and desiccation did not change significantly with annual seed production (Table S1). At the seed germination stage, the probability of seed germinated failure increased with annual seed production ($\chi^2 = 73.87$, $p < 0.001$; Figure 3d; Table S1). Germination failure caused a 21.75% loss of mature seeds in the highest seed production year, which was 7.4 times higher than that in lowest seed production year (Figure 4k). Annual abundance of newly germinated seedling ranged from 102 seedlings to 513 seedlings, seed-to-seedling transition rates ranged from 3.83% to 8.79% (Figure 4e).

3.3 | Spatial distribution patterns of seeds

The spatial variation of accumulated mature seeds (CV_{trap}) in mast and non-mast years was 1.33 and 1.10, respectively. The super seed traps contributed 42.78% of the total mature seeds in mast years versus 36.95% in non-mast years. The spatial variation ($CV_{\text{seedling quadrat}}$) of accumulated newly germinated seedlings in mast years was higher than in non-mast years (1.11 vs. 0.70). The super seedling quadrats contributed 36.22% and 25.66% of the total newly germinated seedlings in mast and non-mast years, respectively. Correlograms showed a significant positive correlation at the distance class of 7.2 m (minimum distance between two seed traps) for mature seeds, intact seeds, surviving seeds, viable seeds and newly germinated seedlings in mast years, indicating the aggregated

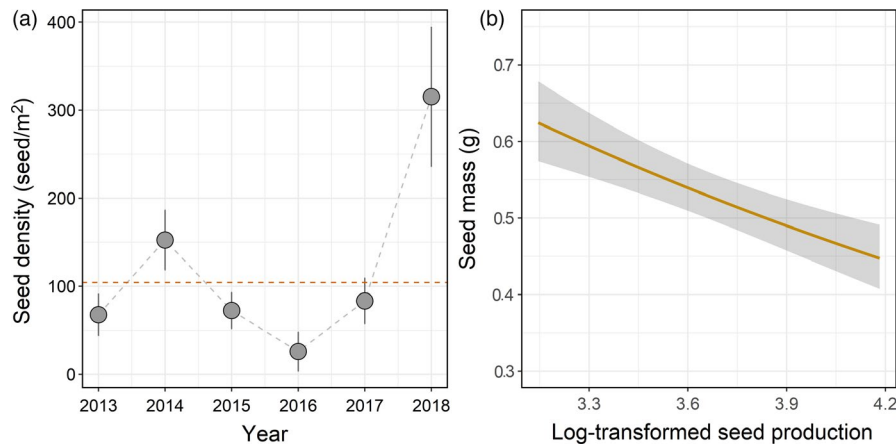


FIGURE 2 Annual changes in *Castanopsis fargesii* seed production (a) and the annual mean seed mass in relation to the annual seed production (log-transformed) (b). In (a), the yellow dotted line represents the standard deviation (SD) of the annual seed density ($SD = 104.3$). Error bars are for SDs of trap-level seed density. In (b), trend line shows statistically significant GLMM model prediction and associated 95% confidence bands (see Section 2 for details)

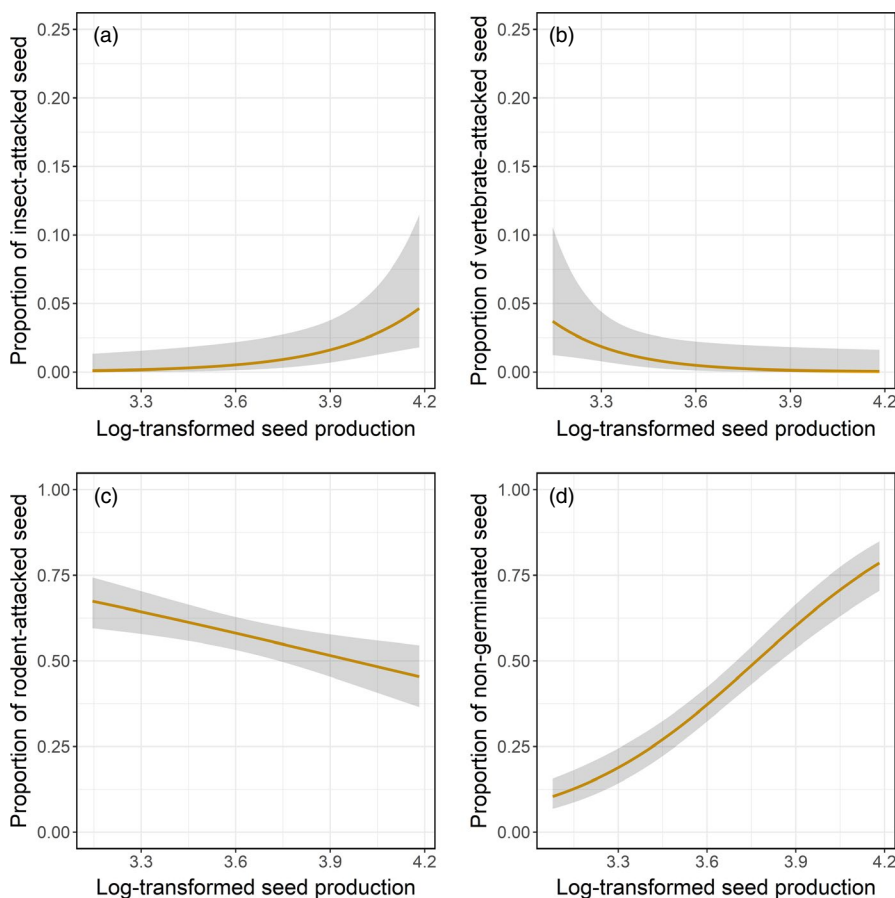


FIGURE 3 The proportion of seed killed by each type of seed mortality factor in relation to the annual seed production (log-transformed). Trend lines show statistically significant GLMM model predictions and associated 95% confidence bands (see Section 2 for details). This figure presents a subset of the seed killing agents in which the relationship was significant

patterns of seeds at this spatial scale. In non-mast years, significant spatial aggregation was only found in mature seeds and intact seeds at the spatial scale of 7.2 m (Figure 5; Figure S5). The spatial distribution of mature seeds and newly germinated seedlings for each year is shown in Figure S6.

The piecewise SEMs explain 69% of the variation of the seed-to-seedling transition rate at the seed trap scale (Figure 6). Seed density had a negative effect on seed-to-seedling transitions, which

was likely due to a positive effect on seed predation by insects and rodent, and a strong indirect negative effect on seed germination by decreasing the seed mass. Litter coverage had a negative effect on seed predation by rodents, and a positive effect on seed germination failure. Canopy openness had a positive effect on the seed-to-seedling transition rate due to a negative effect on seed predation by rodents. Herb coverage had a weak but positive effect on the seed-to-seedling transition (Figure 6).

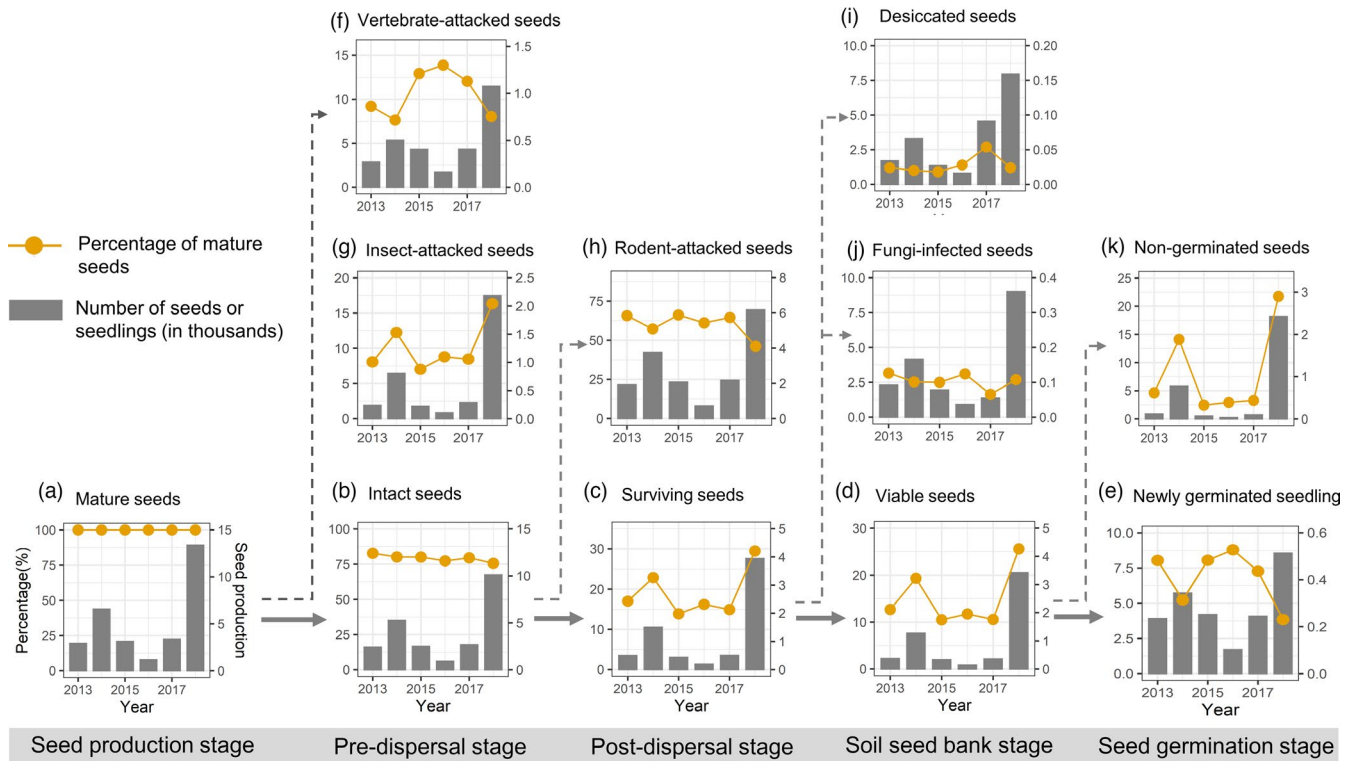


FIGURE 4 Seed fate in the seed-to-seedling transition for seeds produced in each of the 6 years. Solid lines denote survival to the next developmental stage (a–e), and dashed lines denote mortality due to the specified seed mortality agents (f–k), respectively

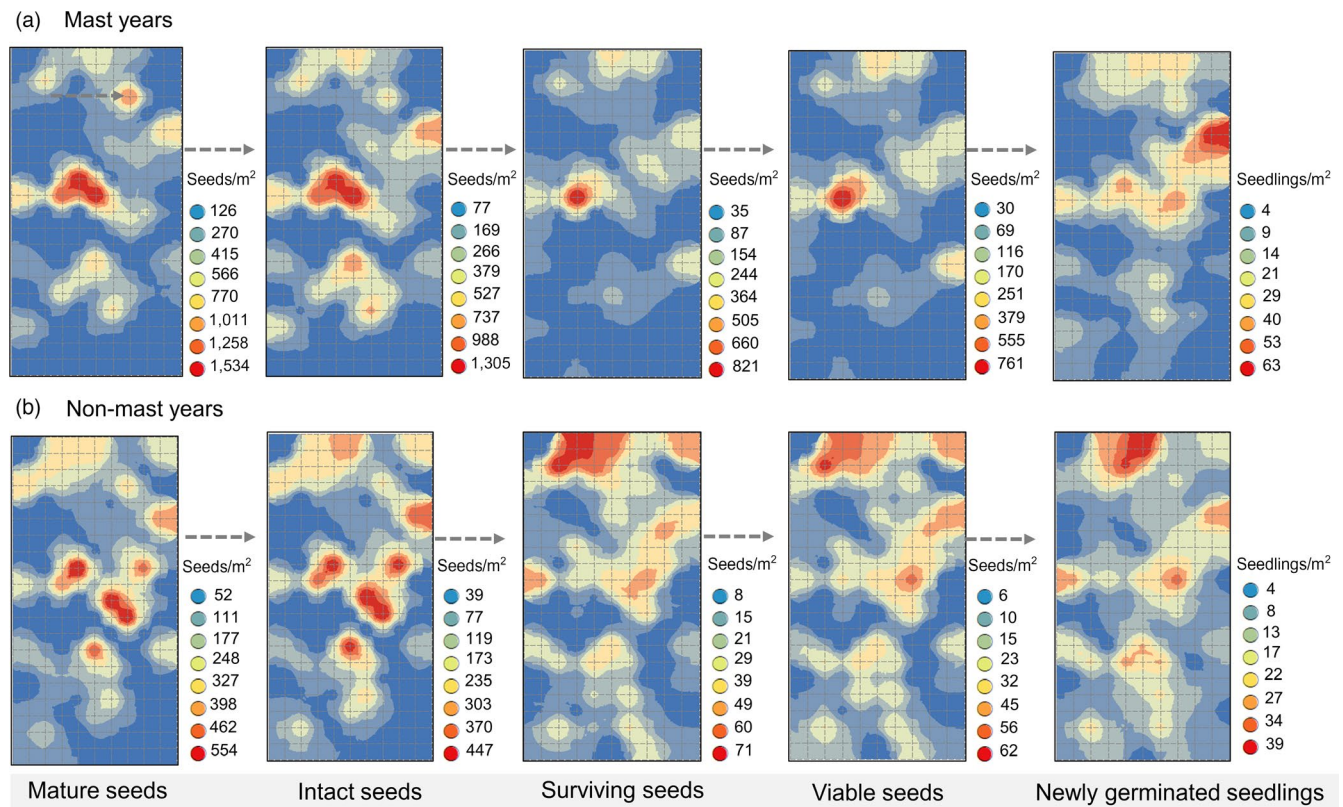


FIGURE 5 Spatial distribution patterns of seeds and newly germinated seedlings at each stage in the two mast years (a) and four non-mast years (b). Maps represent spatial variance and aggregation in the seed and seedling density at each dispersal stage. The seed density across the entire grid surface was estimated using a simple inverse distance weighting interpolation algorithm (see Section 2 for details)

3.4 | Seedling establishment

At the seedling establishment stage, the establishment probability of newly germinated seedlings decreased with annual seed production ($\chi^2 = 13.12$, $p < 0.001$; Figure 7a). Seedling establishment probability was positively affected by seed mass and light intensity, and negatively affected by the seedling density (Figure 7b). Annual abundance of established seedling ranged from 81 seedlings to 212

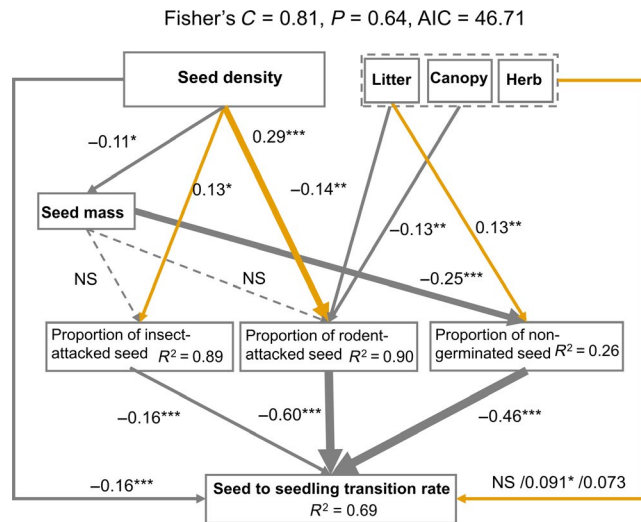


FIGURE 6 Path analysis diagram for seed density, seed mass, microhabitat variables, seed predation, seed germination and seed-to-seedling transition. Arrows represent unidirectional relationships between the variables. Significant effects are depicted at $p < 0.05$ (*), < 0.01 (**), < 0.001 (***), and NS for no significant effect. Arrow size is proportional to the absolute value of the coefficient for each pairwise relationship. Yellow arrows indicate positive effects and grey arrows indicate negative effects. The variance explained (R^2) is shown in the box for each response variable

seedlings, seed-to-established seedling transition rate ranged from 1.59% to 6.98% (Figure 7c).

4 | DISCUSSION

Consistent with our overarching hypothesis, we found strong and multilevel effects of masting on seedling recruitment for *C. fargesii* (Figure 8). Masting resulted in a higher proportion of seeds escaping predation by vertebrates at the pre-dispersal and by rodents at post-dispersal stages and recruitment of more newly germinated seedlings, thus supporting the predator satiation hypothesis. Nevertheless, masting caused higher proportion of seed being predated by insects and dramatically decreased seed germination rates (15.3% in the highest seed production year vs. 75.1% in the lowest year) due to its negative effects on seed mass. This resulted in the seed-to-seedling transition rate in mast years being roughly half of the rate in non-mast years. In addition, masting negatively affected the spatial rearrangement of seeds resulting in a greater spatial aggregative distribution pattern of newly germinated seedlings. More importantly, the combined negative effects of smaller seeds and spatially aggregated seedlings reduced the establishment fitness of the newly germinated seedlings. This resulted in seedlings that were recruited in mast years suffering extremely high mortality (59.9% in the highest seed production year vs. 43.3% in the lowest year) during the seedling establishment stage. Looking at the whole seed-to-established seedling transition process, the benefits of masting were largely outweighed by the additional costs. Our study points to the importance of considering both positive and negative effects of masting across the entire seed-to-seedling transition phase. Inferences based on seed predation and recruitment of new seedlings alone would certainly lead to an overly optimistic conclusion with regard to the benefits of masting.

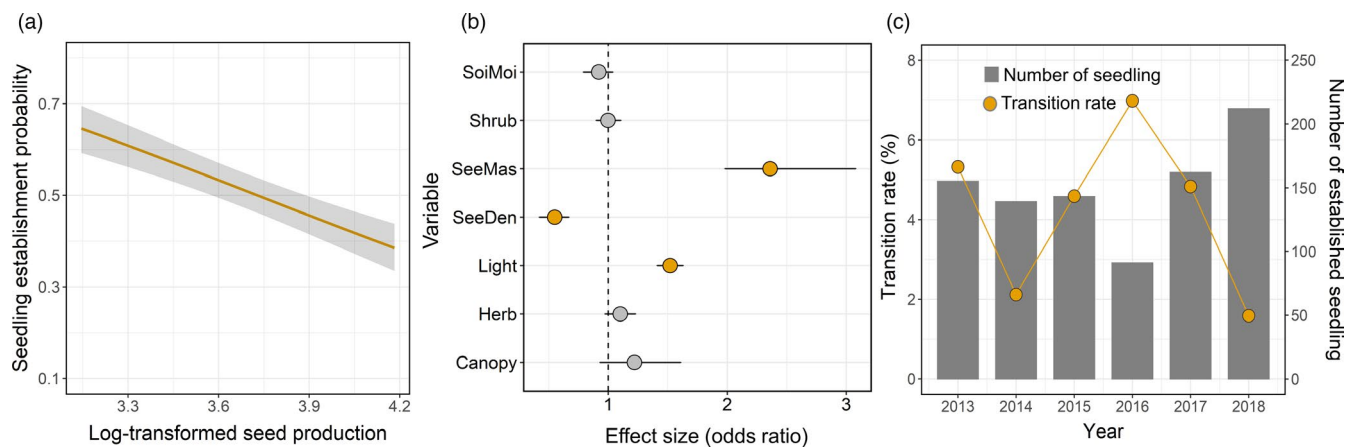


FIGURE 7 Establishment probability of newly germinated seedling in relation to the annual seed production (log-transformed) (a), the contribution of environmental factors to seedling establishment (b) and the number of established seedlings and the seed-to-established seedling transition rate by year (c). Trend line in (a) shows statistically significant GLMM model prediction and associated 95% confidence bands (see Section 2 for details). Codes for environmental factors in (b) are as follows: SoiMoi for soil moisture; Shrub for shrub coverage; SeeMas for mean seed mass of a seed trap; SeeDen for seed density of a seedling quadrat; Light for light intensity; Herb for herb coverage and Canopy for canopy openness

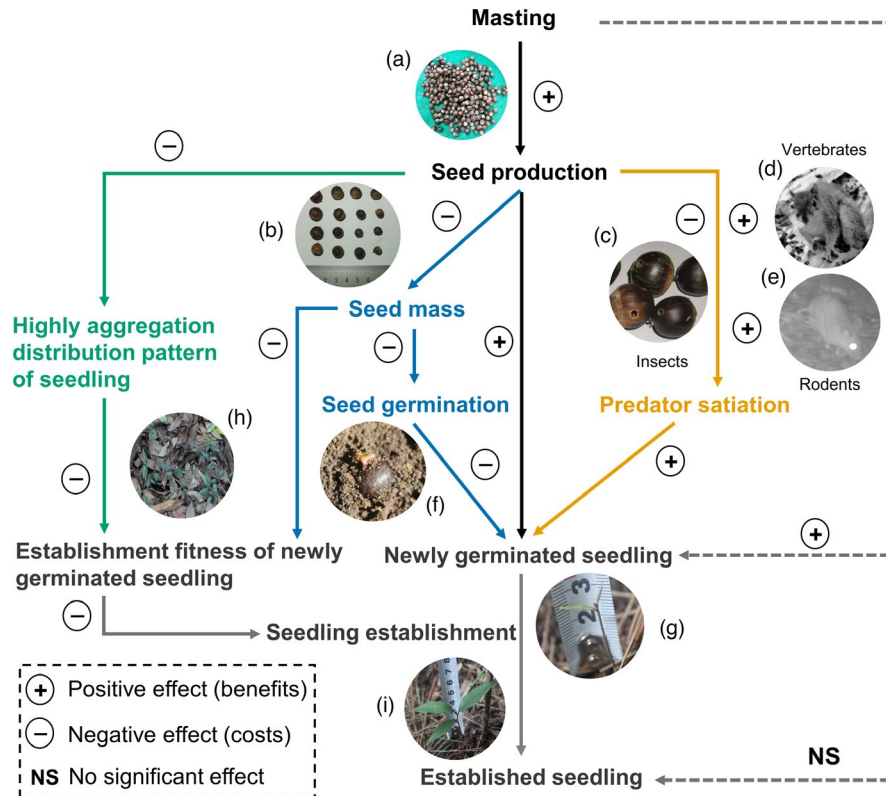


FIGURE 8 Schematic diagram summarizing the benefits and costs of masting on seedling regeneration of *Castanopsis fargesii*. Yellow lines represent the benefits or costs of masting on seed predation. Green lines represent the costs of masting on seedling fitness by influencing the changes in the seed spatial distribution. Blue lines represent the costs of masting on seedling recruitment and seedling fitness by reducing seed mass. Grey dotted lines represent the indirect effects of masting on seedling recruitment. (a) A massive amount of seeds collected in a single seed trap in a mast year; (b) large variation of seed mass; (c) insects as predators of *C. fargesii* seeds; (d) vertebrates as predators of *C. fargesii* seeds; (e) rodents as predators of *C. fargesii* seeds; (f) a germinated viable seed; (g) a newly germinated seedling; (h) a massive amount of newly germinated seedling aggregate distributed around an adult tree in a mast year and (i) an established seedling

The predator satiation hypothesis predicts that plants producing a massive number of seeds during a mast year provide more than enough food for seed predators, which allows higher proportion of seeds to escape predation during the seed dispersal stage (Bogdziewicz, Espelta, et al., 2018; Linhart et al., 2014; Wang et al., 2017; Xiao et al., 2013; Zwolak, Bogdziewicz, Wróbel et al., 2016). In this study, the decrease in seed predation by vertebrates at the pre-dispersal stage and by rodents at the post-dispersal stage, as observed in mast years, was consistent with the past studies (Xiao & Huang, 2020; Xiao et al., 2017). Moreover, the mean newly germinated seedling density recruited during mast years was about twice that recorded during non-mast years, which is similar to observations made in previous studies (Xiao et al., 2013; Zhang et al., 2020). These results suggest that masting of *C. fargesii* benefits seeds escaping predation and seedling recruitment, to some extent, supporting the predator satiation hypothesis in relation to the economies of scale (Xiao et al., 2013; Zwolak, Bogdziewicz, Wróbel et al., 2016).

Despite these findings, the benefits of masting for seeds escaping predation from vertebrates and rodents were reduced by the additional costs at the pre-dispersal and seed germination stages. First, this study found that masting caused a significantly higher proportion

of seeds being attacked by insects at the pre-dispersal stage (Figures 3 and 4), which is similar to the observations of certain oak species (Bogdziewicz, Marino, et al., 2018; Xiao et al., 2017). Second, this study found that the strong trade-off between inter-annual seed production and seed mass resulted in the production of smaller seeds in mast years than in non-mast years (Figure 2b; Figure S4). The overall disadvantage of small seeds on the seed germination rate has been widely discussed in previous studies (reviewed by Leishman, Wright, et al., 2000). The seed germination rate of *C. fargesii* seeds is also positively correlated to seed mass (Gao et al., 2016). In this study, the reduction in seed mass dramatically decreased the seed germination rate during mast years (Figures 3d and 4k). These two costs resulted in the mean seed-to-seedling transition rate during mast years being only half of the rate seen in non-mast years (4.5% vs. 8.9%, Figure 4e). During the entire seed-to-seedling transition, the benefits of masting for seeds escaping predation were largely outweighed by the disadvantages from the reduced seed mass on seed germination.

The spatial distribution patterns of newly germinated seedlings have profound effects on seedling fitness and the demography of plant populations (Nathan & Muller-Landau, 2000; Yang et al., 2015). In this study, a large change in the seed spatial pattern

was observed during the seed-to-seedling transition in non-mast years (Figure 5b). The spatially aggregated distribution of seeds became segregated at the seed dispersal stage, which is similar to a previous study on *Fagus crenata* (Tomita et al., 2002). This change was mainly associated with spatially non-random predation and the effectiveness of seed dispersal. The probability of rodent-attack was mostly density-dependent, which caused the seeds at the microsites with a greater seed density to suffer relatively intensive predation (Figure 6). In addition, an increase in the density of viable seeds was observed in the 14 soil seed bank quadrats where the density of mature seeds was initially low during the non-mast years. This result indicates that some seeds in patches of high seed density had been transported to patches of low seed density, which is similar to other recent studies (Hirsch et al., 2012; Huang et al., 2020; Zhang et al., 2020). In contrast, such changes in the seed spatial distribution pattern were not observed during mast years (Figure 5a). The production of a massive number of seeds and the existence of some super-producers in the mast years led to a highly spatially aggregated seed distribution pattern (Minor & Kobe, 2017). In addition, masting provides abundant food resources for rodents, which negatively affects the rodents' scatter-hoarding behaviour (Wang et al., 2017; Xiao et al., 2005, 2015). As a result, a notably aggregated distribution of seeds and newly germinated seedlings was observed in mast years, despite multiple mortality factors causing a large proportion of lost seeds.

This study demonstrates that the combined negative effects of smaller seeds and the spatial aggregation of seedlings can reduce the fitness of newly germinated seedlings at the seedling establishment stage. First, the reduced seed mass caused by masting negatively affected the survival of newly germinated seedlings. Seed mass is recognized as a key functional trait that affects offspring fitness, with smaller seeds having a distinct disadvantage due to their increased sensitivity to competition, shading, drought and nutrient limitation (Leishman, Wright, et al., 2000; Moles & Westoby, 2004). For *C. fargesii*, its seedling emergence occurs at the end of October, when droughts and cold winter temperatures are only a few weeks away. Moreover, the understorey environmental conditions of the *C. fargesii* forests that we surveyed were characterized by low-light intensity. Seedlings from large seeds can benefit from early survival by maximizing development of deep root systems, and thus are able to defend against the unfavorable environment. Therefore, seed mass of *C. fargesii* largely determines the fitness of seedlings at the establishment stage. This study found that the reduced seed mass had a negative effect on establishing the newly germinated seedlings of *C. fargesii* (Figure 7b), similar to previous studies (Lebrija-Trejos et al., 2016; Seiwa et al., 2019). Second, seedlings recruited during mast years had a notably aggregated spatial distribution surrounding conspecific adult trees, which is similar to the distribution pattern of mature seeds (Figure 5a). Thus, they may suffer from a relatively higher impact from negative density- and distance-dependent mortality agents (Murphy et al., 2017; Seiwa et al., 2019; Terborgh et al., 2014; Yang et al., 2015; Zhu et al., 2015). In fact, this study found that the 2-year survival rate of seedlings decreased

with annual seed production (Figure 7a), and seedling recruited in mast years had higher establishment rate than in non-mast years. Moreover, no significant difference was seen between the abundance of the established seedlings recruited in mast and non-mast years (Figure 7c). This result suggests that the negative effects of masting on early survival of the newly germinated seedlings further outweigh the benefits of masting on seedling recruitment.

In conclusion, considering the whole seed-to-established seedling transition, the benefits of masting on seedling recruitment due to the effective seed predator situation by vertebrates and rodents were decreased by the additional costs on seed mass, seed germination, seed spatial arrangement and seedling establishment. Inferences based on seed predation and recruitment of newly germinated seedlings alone would lead to an overly optimistic conclusion regarding the benefits of masting. For *C. fargesii*, due to the limited resources for reproduction, the strategy of producing large number of smaller seeds in mast years is not as effective as we expected for offspring recruitment. Further observation and targeted studies are warranted to assess how masting indirectly affects the long-term dynamics of seedling recruitment.

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AUTHORS' CONTRIBUTIONS

L.H. wrote the manuscript with input from all authors; Y.Y. and L.H. were involved in planning and supervising the work; C.J., L.Z. and S.Q. performed the field measurements; D.L., L.Z., K.S., B.C., E.Y. and R.M. performed the analyses. All authors discussed the results and contributed to the final manuscript.

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Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4qrfj6q9m> (Huang & Yang, 2021).

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SUPPORTING INFORMATION

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