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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Advantages of masting in European beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis

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Abstract The predator satiation and predator dispersal hypotheses provide alternative explanations for masting. Both assume satiation of seed-eating vertebrates. They differ in whether satiation occurs before or after seed removal and caching by granivores (predator satiation and predator dispersal, respectively). This difference is largely unrecognized, but it is demographically important because cached seeds are dispersed and often have a microsite advantage over nondispersed seeds. We conducted rodent exclosure experiments in two mast and two nonmast years to test predictions of the predator dispersal hypothesis in our study system of yellow-necked mice (*Apodemus flavicollis*) and European beech (*Fagus sylvatica*). Specifically, we tested whether the fraction of seeds removed from the forest floor is similar during mast and nonmast years (i.e., lack of satiation before seed caching), whether masting decreases the removal of cached seeds (i.e., satiation after seed storage), and whether seed caching increases the probability of seedling emergence. We found that masting did not result in satiation at the seed removal stage. However, masting decreased the removal of cached seeds, and seed caching dramatically increased the probability of seedling emergence relative to noncached seeds. European beech thus benefits from masting through the satiation of scatterhoarders that occurs only after seeds are removed and cached. Although these findings do not exclude other evolutionary advantages of beech masting, they indicate that fitness benefits of masting extend beyond the most commonly considered advantages of predator satiation and increased pollination efficiency.

Keywords *Fagus sylvatica* · *Apodemus flavicollis* · Granivory · Scatterhoarding · Seed dispersal

Introduction

Masting, the synchronous and intermittent production of seed by a population, is geographically and phylogenetically widespread among perennial plants (Crone et al. 2011; Allen et al. 2012; Turnbull et al. 2012; Koenig and Knops 2013). This reproductive strategy is intriguing because it entails tradeoffs between current and future reproduction (Pearse et al. 2014; Moreira et al. 2015). Although benefits of masting must outweigh the costs of missed chances to reproduce, the exact nature of those benefits (e.g., increased seed production, survival, or a higher chance of seed-to-seedling transition) remains unresolved (Kelly and Sork 2002; Tachiki and Iwasa 2010; Rapp et al. 2013).

Three hypotheses based on economies of scale have been proposed to explain the evolutionary advantages of masting. The pollination efficiency hypothesis states that occasional high reproductive efforts increase pollination success in wind-pollinated plants (Nilsson and Wästljung 1987; Herrera et al. 1998; Kelly et al. 2001; Moreira et al. 2014). The predator satiation hypothesis posits that seed production during mast events exceeds the consumption

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capacity of local granivore communities, which results in a lower percentage of seeds consumed than in nonmast years. In addition, small seed crops in nonmast years reduce granivore populations to low levels that cannot increase rapidly in response to the next mast event (Kelly 1994; Kelly and Sork 2002). The predator satiation hypothesis is the oldest and the most established evolutionary explanation of masting (Janzen 1971; Silvertown 1980). It has been frequently tested and is generally well supported (e.g., Crawley and Long 1995; Curran and Leighton 2000; Fletcher et al. 2010; Visser et al. 2011; Xiao et al. 2013; Żywiec et al. 2013; Linhart et al. 2014). Alternatively, the predator dispersal hypothesis (Vander Wall and Balda 1977; Ligon 1978) has received much less attention (e.g., Vander Wall 2002; Xiao et al. 2013). It posits that because seeds are too numerous in mast years to be consumed immediately by seed-eating vertebrates, a relatively large proportion are cached and unrecovered in sites favorable for germination and growth.

The predator dispersal hypothesis resembles the predator satiation hypothesis in that both focus on the satiation of granivores in mast years (Kelly and Sork 2002). The crucial distinction between them is the stage at which satiation occurs: before (predator satiation) or after (predator dispersal) removal and caching by seed-eating vertebrates. Even though this distinction is often overlooked, it does have significant consequences because seeds gain benefits associated with dispersal and burial only when satiation occurs after caching (Jansen and Forget 2001; Briggs et al. 2009; Zwolak and Crone 2012).

Vander Wall (2010) provided several predictions of the predator dispersal hypothesis that distinguish it from the predator satiation hypothesis, although the hypotheses are not mutually exclusive. According to the predator dispersal hypothesis, seed removal behavior is not satiated by masting events. Satiation does occur, however, after seeds are cached, so many cached seeds escape consumption. Also, seed caching increases the probability of seedling emergence because it provides favorable abiotic conditions for seeds and generally protects them from consumption by other individuals of the caching species and by other granivorous species. Finally, the predator dispersal hypothesis predicts a higher fraction of harvested seed crop and longer seed dispersal distances in mast years (Kelly 1994; Vander Wall 2002, see Table 1 for a summary). Masting would increase seed dispersal distances if scatterhoarders maintained an optimal density of caches, perhaps determined by a tradeoff between density-dependent losses due to pilferage and travel costs (Stapanian and Smith 1978).

We examined whether the defining features of the predator dispersal hypothesis occur in our study system: yellow-necked mice (*Apodemus flavicollis*) interacting with the European beech (*Fagus sylvatica*). Our study lasted 4 years and included two mast and two nonmast years. We evaluated seed and seed-predator abundance, quantified seed removal, and measured seedling emergence. We tested the following predictions: (1) mast and nonmast years do not differ in the proportion of seeds removed from the forest floor (i.e., lack of satiation before seed caching); (2) masting reduces the fraction of cached seeds removed (i.e., satiation after caching); and (3) cached seeds have a higher probability of seedling emergence than noncached seeds (Table 1). We also tested predictions on how masting impacts the proportion of seeds harvested, the distance of seed dispersal, and rodent population size (Table 1). These impacts are considered important aspects of the predator dispersal and the predator satiation hypotheses (Kelly 1994; Kelly and Sork 2002; Vander Wall 2002), even though they cannot be used to distinguish them.

Table 1 Predictions of the predator satiation and the predator dispersal hypotheses

Predicted masting effect	Response variable	Predator satiation	Predator dispersal	Our results
1. Granivore satiation before caching	Proportion of seeds removed from the forest floor	Yes	No[a]	No
2. Granivore satiation after caching	Proportion of seeds removed from caches	Yes	Yes[a]	Yes
3. Caching improves seedling emergence[a]	Seedling emergence from buried seeds vs. seeds left on the forest floor	Not applicable	Yes[b]	Yes
4. Masting increases the fraction of seeds harvested by granivores	Proportion of seeds removed from the forest floor	Not applicable	Yes[c]	No
5. Masting increases seed dispersal distance	Distance of seed dispersal	Not applicable	Yes[b]	No
6. Granivore populations decline between mast events	Abundance of granivorous rodents	Yes	Not applicable	Yes

[a] The effect of caching on seedling emergence is not masting dependent. However, it is a necessary condition of the predator dispersal hypothesis: if seed caching does not increase seedling recruitment, then the stage of satiation (before or after caching: predictions 1 and 2) is irrelevant

[b] After Vander Wall (2010)

[c] After Vander Wall (2002)

Materials and methods

Natural history

European beech (*Fagus sylvatica*) is a large broad-leaved tree (usually 30–40 m tall) that is widespread in temperate Europe and often dominates forests (Standovár and Kenderes 2003). It is monoecious, wind-pollinated, and generally self-incompatible (Packham et al. 2012). *F. sylvatica* is characterized by a pronounced masting pattern, with an average intermast interval of 4–8 years in mainland Europe (Pidek et al. 2010). However, intervals between mast years can be as short as 2 years or as long as 15 years (reviewed by Packham et al. 2012). Beech nuts are relatively large (a single seed usually weighs 0.2–0.3 g), nutritious (5.7 kJ per seed), and readily eaten by small mammals, most notably yellow-necked mice (Grodziński and Sawicka-Kapusta 1970). In a study conducted in a beech forest, seeds comprised 74 % of stomach volume in yellow-necked mice (averages from one mast and one nonmast year: Dróżdż 1966). This rodent species also larderhoards and scatterhoards seeds (Jensen 1985; Wróbel and Zwolak 2013). Beech masting causes strong fluctuations in populations of granivorous rodents, with peaks (1 year after masting) followed by crashes (2 years after masting: Jensen 1982). Other animals that eat and disperse beech seeds include Eurasian jay *Garrulus glandarius*, nuthatch *Sitta europaea*, and marsh tit *Parus palustris* (Nilsson 1985).

Study site

Research was conducted in Gorzowska Forest (western Poland, 52.77°N, 15.07°E, elevation 60–80 m), a temperate forest with an average annual precipitation of 523 mm and mean monthly temperatures ranging from −4 °C in January to 23 °C in July. Four experimental sites (80 × 80 m) were established in mature (>80 years old) beech stands located within continuous managed forest. Within each site, we established a grid of reference points with numbered wooden stakes. Grid points were spaced 10 m apart in an 8 × 8 square. Distances between adjacent sites averaged 1.0 km (SD = 0.5 km), and in all cases were sufficiently large to prevent substantial exchange of yellow-necked mice between sites: only 0.06 % of individuals were recaptured between sites (12 out of 1928 marked individuals over 4 years; Zwolak, unpubl. data). Because the selected beech stands contained only single trees of other species, i.e., Scots pine (*Pinus sylvestris*), pedunculate oak (*Quercus robur*), European larch (*Larix decidua*), and black alder (*Alnus glutinosa*), seed production by beech largely determined the total availability of tree seeds in each stand.

Index of beech seed availability

Seed availability was estimated by counting beech seeds on the ground in October (Hilton and Packham 1997). Sampling was conducted in a stratified random manner: each site was divided into four subplots, with six (2009) or three (2010–2012) random reference markers per subplot used as sampling points. At each sampling point, we collected and counted all seeds within 0.5 × 0.5 m quadrats. We chose this method because frequent disturbance by humans prevented the use of seed traps. While counting seeds on the ground might underestimate seedfall because some seeds are immediately removed by animals, it reliably distinguished mast from nonmast years (see "Results").

Abundance of small mammals

At each site, we set up a live-trapping grid, with one wooden live trap ("dziekanówka" type, widely used in Poland, size 21 × 8 × 9.5 cm) placed at each reference point (64 traps per site except in 2009, when we used smaller, 8 × 6, trapping grids). We used rolled oats or a mixture of rolled oats and sunflower seeds as bait.

Sites were trapped in September 2009 and in monthly sessions from June to September 2010–2013. Each session consisted of five consecutive days of trapping. Traps were checked in the morning (08:00–12:00) and in the evening (18:00–20:00). We identified captured rodents to species and marked them with uniquely numbered ear-tags. We used the number of different individuals captured per trapping session, averaged over months and sites, as an index of small mammal abundance in a given year. (The number of individuals trapped was highly correlated with capture–recapture estimates of population size, Pearson's $r = 0.99$: Zwolak et al. 2016).

Rodent exclusion trials

At each study site, we placed 20 rodent exclusion cages, arranged in five sets of four cages. The wire cages (18 × 18 × 18 cm, mesh size 13 mm) were buried 5 cm into the ground. Sets were located along three sides of the square-shaped sites, with one set at each midpoint of three adjacent sides of the site and the remaining sets at the two corners formed by those sides (i.e., a U-shape). We employed a 2 × 2 factorial design such that each set contained (1) a rodent access cage (with 40 × 65 mm openings cut in each side) with beech seeds placed on the leaf litter, (2) a rodent exclusion cage (without openings) with seeds placed on the leaf litter, (3) a rodent access cage with seeds buried 1 cm into topsoil, and (4) a rodent exclusion cage with seeds buried in the same manner. Seeds placed on the

leaf litter simulated seeds that fell from trees, and seeds buried in topsoil simulated caching by yellow-necked mice (R. Zwolak, pers. obs.). Cages within each set were positioned ~2 m from each other in a square pattern. Five beech seeds were added to all cages in October 2009–2012. When possible (mast years in 2009 and 2011), seeds were collected locally. In 2010 and 2012, we used seeds collected from a wider area in Poland by personnel at the Gryfino Forestry Office. Soil in cages was covered with leaf litter to the same depth adjacent to the cages.

The proportion of seeds removed was inferred from seedling emergence in access vs. exclusion cages, as described in "Data analysis" (note that seed removal is not equivalent to seed predation because some of the removed seeds could be cached elsewhere). Seedlings were counted the following May or June, when emergence was complete (i.e., no new seedlings were subsequently found). Some cages ($\bar{x} = 19$ %, SD = 15 %) were destroyed by large animals before we could quantify emergence. The proportion of cages destroyed varied from 9 % (7 out of 80 cages) in 2013 to 41 % (33 out of 80 cages) in 2011. This annual variation in trap damage does not confound the interpretation of the results because it was not associated with the number of seeds naturally available (i.e., frequency of cage damage was not reduced in mast years).

Seed tracking

To determine dispersal distance, seeds were tracked using the technique described in Xiao et al. (2006). A 0.8-mm-diameter hole was drilled through cotyledons and a stainless steel wire (100 mm in length, 0.2 mm in diameter) with a red, uniquely numbered plastic tag (20 × 40 mm) was secured through the hole. The wire and the tag weighed 0.141 ± 0.004 g. Although seed tagging (and most other methods used to mark seeds for subsequent tracking) may influence rodent behavior, our objective was to compare the fates of identically manipulated seeds in mast and nonmast years (Wróbel and Zwolak 2013).

Tagged seeds were placed in Petri dishes (diameter 80 mm; four seeds per dish). In 2009, dishes with seeds (hereafter "seed depots") were arranged in two transects per site, with each transect containing eight seed depots spaced 10 m apart. The two transects were separated by 50 m. All depots were deployed on the same day. Depots were checked the following night and then at 1–14 day intervals for 1.5 months. In subsequent years, depots were placed at random locations in a stratified random manner: each site was divided into four quadrats, and an equal number of seed depots was placed in each quadrat. Depots were deployed three or four times in weekly intervals at a new set of random locations each time. Seeds were tracked after one night. The number of depots per site (and consequently the

number of tagged seeds) varied from 16 (in 2009 and 2010) to 36 (in 2012). In total, we put out 1600 seeds over the course of the study. As with the seedling recruitment cages, seeds were collected locally in 2009 and 2011 and obtained from the Gryfino Forestry Office in 2010 and 2012.

Seeds were placed in depots at dusk (19:00–21:00). The next morning we searched at least 20 m in every direction from the source depot and often further (up to ~40 m) until we had searched ~10 m beyond all discovered seeds. Each search lasted several hours, and each site was searched once per deployment. In total, we found 61 % of the removed seeds. The probability of finding removed seeds did not differ among years ($\chi^2 = 4.59$, $df = 3$, $p = 0.205$). For each seed that was removed and found, we measured the distance from the depot and categorized the fate of the seed as (1) consumed, (2) left on the forest floor, or (3) cached in soil or litter. Dispersed seeds were collected; we did not attempt to record possible secondary dispersal from caches (Vander Wall 1994).

Data analysis

Data were analyzed with generalized linear mixed models in R using the lme4 package (Bates et al. 2013). Beech seed abundance data were analyzed using a generalized linear mixed model with year as a fixed factor and site as a random factor. Small mammal abundance was analyzed using Poisson-family log-link models with year as a fixed effect and month and trapping site as random effects. We used the log-transformed number of traps per trapping grid as an offset to account for smaller grids in 2009. Seedling recruitment was analyzed using a generalized linear mixed model (binomial family and logit-link function). Fixed effects included beech masting (mast vs. nonmast years), rodent access (open vs. closed cages), and seed burial (cages with seeds on the forest floor vs. cages with seeds buried in topsoil). Random effects included year, study site, and block. Our initial model included all two- and three-way interactions among the fixed-effect variables. We arrived at the final model through backward elimination of nonsignificant terms.

We used parameter estimates from the final model to test three predictions of the seed dispersal hypothesis (Table 1). The first prediction—that removal of seeds from the forest floor is similar during mast and nonmast years—was tested by comparing the probability of seedling emergence in open and closed cages with seeds on the forest floor in mast vs. nonmast years. Removal of seeds on the forest floor ($SR_{SURFACE}$) was estimated as

$$SR_{SURFACE} = 1 - SE_{OPEN, SURFACE}/SE_{CLOSED, SURFACE},$$

where $SE_{OPEN, SURFACE}$ is the probability of seedling emergence in open cages where seeds were left on the forest

floor and $SE_{CLOSED, SURFACE}$ is the probability of seedling emergence in closed cages where seeds were on the forest floor.

The second prediction—that removal of cached seeds is lower during mast than nonmast years—was tested in the same way as the first, but by using cages in which seeds were buried (cached):

$$SR_{CACHED} = 1 - SE_{OPEN, CACHED}/SE_{CLOSED, CACHED}.$$

We estimated 95 % confidence intervals for seed removal (first and second predictions) using parametric bootstrapping. Note that these tests use the difference in seedling emergence between rodent-accessible and -inaccessible seeds as a measure of seed removal. In testing the two predictions, we assume that seed removal by rodents was solely responsible for differences in seedling emergence between open and closed cages within the same seed treatment (i.e., either left on forest floor or buried). We saw no evidence to the contrary (see "Discussion").

The third prediction—that burial improves seedling emergence—was tested by estimating the odds ratio of seedling emergence from buried and unburied seeds in rodent exclusion cages.

Seed tracking data were analyzed with models that contained mast as a fixed factor and year, site, date, and seed depot as random effects. We analyzed whether mast and nonmast years differed with regard to probability of seed removal and dispersal distance of recovered seeds. In the former analysis, we used a binomial error distribution with logit link, and in the latter we used a Gaussian error distribution with dispersal distances log-transformed.

Results

Beech seed abundance

Beech masting occurred in the fall in 2009 (average and SE 345 ± 80 seeds/m^2) and 2011 (382 ± 83 seeds/m^2). In 2010 and 2012, beech did not produce viable seeds at our study site; no seeds were found on the ground or observed on tree branches.

Small mammal abundance

Small mammal abundance was very low in the mast years 2009 ($\bar{x}$ = 9.1 different individuals captured per grid, 95 % CI 7.0–12.0) and 2011 ($\bar{x}$ = 9.7 individuals per grid, 95 % CI 7.9–12.0). In contrast, small mammal abundance was approximately sixfold higher in the nonmast years 2010 ($\bar{x}$ = 55.9 individuals per grid, 95 % CI 45.9–68.1)
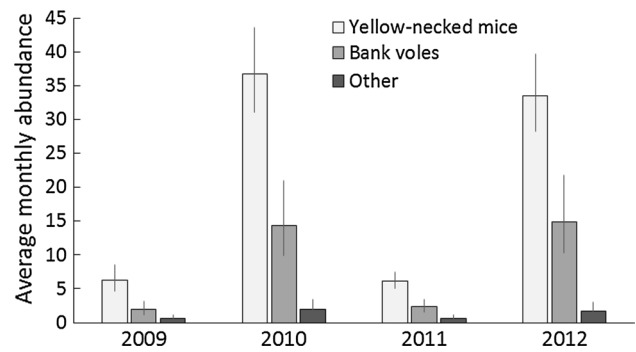
Fig. 1 Monthly abundance (# of captures) of small mammals in beech (*Fagus sylvatica*) stands of Gorzowska Forest, averaged over months and study sites. Recaptured individuals not included. *Whiskers* represent standard errors
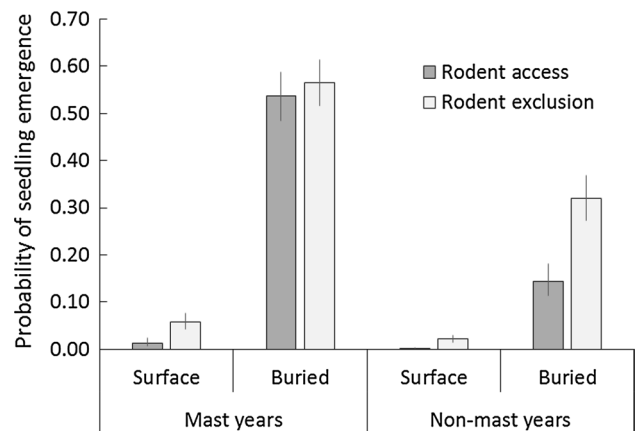
Fig. 2 Estimated probability of beech (*Fagus sylvatica*) seedling emergence in mast and nonmast years. Seeds were buried in topsoil to simulate caching by rodents (*Buried*) or left on leaf litter (*Surface*), simulating seeds that fell from trees. *Rodent access* denotes emergence in open cages, and *rodent exclusion* refers to emergence in closed cages. *Whiskers* represent standard errors

and 2012 ($\bar{x}$ = 53.0 individuals per grid, 95 % CI 43.5–64.5; Fig. 1). These fluctuations in abundance support prediction 6 (declines of granivore populations between mast events).

Small mammal communities were dominated by yellow-necked mice *Apodemus flavicollis* (66 % of small mammals captured) and bank voles *Myodes glareolus* (25 %), which consume but do not scatterhoard beech seeds. Other species (striped field mice *Apodemus agrarius*, voles *Microtus* sp., Eurasian harvest mice *Micromys minutus*, Eurasian common shrews *Sorex araneus*, and Eurasian pygmy shrews *S. minutus*) comprised only 5 % of all individuals captured. Overall community composition was similar in mast and nonmast years (Fig. 1).

Table 2 Results of logistic regression for beech (*Fagus sylvatica*) seedling emergence trials

Variable[a]	Regression coefficient ($\pm$SE)	z	P
Intercept	-3.83 ± 0.35	-10.83	<0.001
Masting	1.02 ± 0.27	3.81	<0.001
Rodent access	-2.44 ± 0.73	-3.33	<0.001
Seed burial	3.07 ± 0.31	9.84	<0.001
Masting $\times$ rodent access	-0.90 ± 0.36	2.53	0.011
Rodent access $\times$ seed burial	-1.42 ± 0.70	2.03	0.042

[a] "Masting" denotes seedling emergence in mast relative to nonmast years; "rodent access" denotes seedling emergence in open vs. closed cages; "seed burial" represents seedling emergence from buried seeds vs. seeds on the forest floor. See "Materials and methods" for further explanation

### Seedling emergence and seed removal from experimental cages

The final model of seedling emergence included effects of masting (emergence was higher after mast than non-mast years), burial (more seedlings emerged from buried seeds than from seeds left on the forest floor), rodent access (emergence was lower in open cages than in exclusion cages), an interaction between the effect of rodents and masting (rodent influence was stronger after mast than nonmast years), and an interaction between rodents and burial (the negative effect of rodents on seedling emergence was weaker when seeds were buried; Table 2; Fig. 2). We used parameter estimates from the model to calculate seed removal from experimental cages. In contrast to predictions 1 (satiation before seed caching) and 4 (masting increases seed harvest rates), the estimated removal probability for seeds on the forest floor was similar in nonmast (0.91; 95 % CI 0.63–0.98) and mast (0.78; 95 % CI 0.16–0.94) years. However, prediction 2 (satiation after caching: Table 1) was supported: the removal probability of cached seeds was 0.54 (95 % CI 0.21–0.75) in nonmast years but only 0.05 (95 % CI −0.15 to 0.22) in mast years.

Effects of seed burial on seedling emergence

The odds of seedling emergence from buried seeds were 21.5 (95 % CI 11.8–39.9) times the odds of seedling emergence from seeds left on the forest floor. This result supports prediction 3 (caching improves seedling emergence).

Harvest and dispersal of tagged seeds

In nonmast years, rodents harvested (consumed on the spot or removed) 74 % of the accessible seeds overnight,
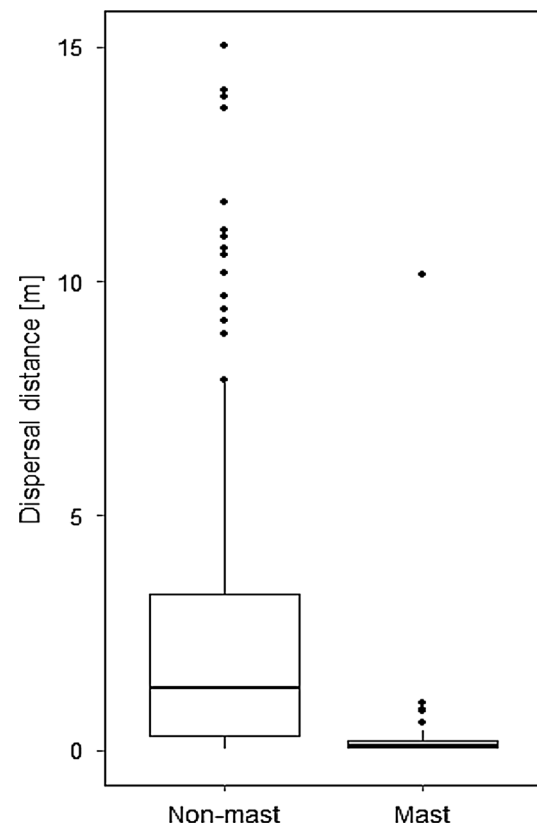
Fig. 3 Dispersal distances of tagged beech (*Fagus sylvatica*) seeds during nonmast and mast years ($N = 334$ and 85 seeds in nonmast and mast years, respectively)

whereas in mast years, rodents harvested only 3 % of the seeds ($z = -5.12$, $p < 0.001$). In contrast to prediction 5 (masting is associated with increased distance of seed dispersal), the average dispersal distance of removed seeds was almost eight times greater in nonmast than in mast years ($\chi^2 = 11.82$, $df = 1$, $p < 0.001$; Fig. 3).

Discussion

Our results suggest that European beech primarily benefits from masting through consumer satiation after seed caching. This phenomenon is often overlooked because detecting it requires examination of the dispersal and caching processes. Given that seed caching dramatically improved the odds of seedling emergence, we suggest that satiation after caching is likely more beneficial for European beech than satiation before caching. Therefore, whether the satiation takes place before or after satiation is indeed an important influence on plant fitness, as posited by Vander Wall (2010).

Our results more strongly support the predictions of the predator dispersal hypothesis than those of the predator

satiation hypothesis (Table 1). With respect to the first prediction, beech masting did not result in rodent satiation during the seed harvest phase. Evidence for rodent satiation caused by masting comes mainly from short-term seed removal experiments (a higher fraction of seeds removed during nonmast years and a lower fraction removed during mast years, Kelly and Sork 2002) and gross estimates of rodent seed consumption based on rodent abundance and metabolic rates (i.e., too many seeds for rodent populations to consume; Jensen 1982). Results of our seed tracking experiments suggest that seed removal is considerably slower in mast than in nonmast years (see also Crawley and Long 1995; Theimer 2001; Jansen et al. 2004). However, in the long term, rodents may still remove a large proportion of the seeds in mast years: as revealed by our rodent exclusion experiments, when rodents are allowed to forage on seeds throughout fall, winter, and spring, they strongly affect seedling recruitment in both mast and nonmast years (Hulme and Kollmann 2005). Therefore, the most important effect of masting might not be the proportion of seeds harvested but rodent behavior towards cached seeds (Vander Wall 2001; Jansen et al. 2004).

Beech masting satiated rodents during the phase of seed consumption from caches, supporting the second prediction of the seed dispersal hypothesis. This result is consistent with several other studies (Theimer 2001; Vander Wall 2002; Jansen et al. 2004; Yi et al. 2011), but contrasts with Xiao et al. (2013), who rejected the predator dispersal hypothesis largely on the basis of a decline in survival of cached seeds after mast years (see also Hoshizaki et al. 2002). As a caveat, our caching experiments simulated seed pilferage by naive consumers rather than seed retrieval by cache owners. However, both processes are expected to exhibit the same dynamics in response to masting because both are governed mainly by changes in the seed:scatterhoarder ratio (Theimer 2005).

In accordance with the third prediction, seed burial resulted in dramatically improved seedling emergence. In most ecological situations, seeds benefit from caching in topsoil, although the magnitude of this benefit varies (Zwolak and Crone 2012). Cached seeds gain improved radicle penetration of soil and protection from desiccation, frost, UV light, and seed predators that do not cache. Thus, seed burial in topsoil is considered one of the main benefits for plants whose seeds are harvested by scatterhoarders (Briggs et al. 2009; Zwolak and Crone 2012).

Beech masting did not result in a higher proportion of seeds harvested or longer seed dispersal distances compared to nonmast years (Table 1). The notion that masting evolved because abundant seed or fruit crops ensure more frequent visitations by dispersers is generally contested (Koenig et al. 1994; Herrera et al. 1998; Kelly and Sork 2002), although it might operate in North American

nutcracker–whitebark pine and rodent–pine interactions (Vander Wall 2002; McKinney and Tomback 2007; Barringer et al. 2012). In addition, even a lower *proportion* of seeds harvested could mean greatly increased *numbers* of seeds harvested (and presumably cached) during mast than nonmast years (Vander Wall 2010).

We found considerably longer seed dispersal distances in nonmast than in mast years. Tests of the prediction that masting increases seed dispersal distances (Stapanian and Smith 1978) produced mixed and mostly negative results (increase in seed dispersal distance in Vander Wall 2002; Li and Zhang 2007; Yi et al. 2011; decline in Jansen et al. 2004; Moore et al. 2007; Puerta-Piñero et al. 2010; Xiao et al. 2013; this study). If the distance of seed dispersal decreases rather than increases during masting, then masting entails a trade-off between dispersal distance and seed survival in caches (Jansen et al. 2004; Moore and Swihart 2007). Benefits of increased dispersal distance include escape from the negative influence of parent trees on recruitment (Swamy et al. 2011) and greater scattering of seeds, resulting in lower density-dependent losses (Jansen et al. 2008). However, beech at our study site often forms monospecific stands, which means that escape from density-dependent effects of conspecifics is implausible. Moreover, during mast years, the forest floor is covered with beech seeds; even seeds that were dispersed long distances would be unlikely to avoid density-dependent mortality generated by conspecific seeds and seedlings. Nevertheless, if intraspecific and within-population Janzen–Connell effects occur in beech (Liu et al. 2015), there may be an important threshold associated with escaping mortality close to the maternal plant. In addition, farther dispersal increases the likelihood of colonizing ephemeral habitat patches that are suitable for recruitment, such as treefall gaps.

At our site, the abundance of granivores strongly declined between beech mast events, in accordance with the predator satiation hypothesis (Table 1). It has been argued that if animals act as mutualistic dispersers, population declines between mast events would be disadvantageous for plants (Kelly and Sork 2002). However, a high seed:scatterhoarder ratio (e.g., abundant seeds and rare scatterhoarders) is essential for the survival of cached seeds (Theimer 2005). When seeds are scarce and scatterhoarders numerous, seeds are mostly consumed, and even those that are cached are eventually pilfered and eaten (see "Results"). Therefore, it might be beneficial for plants to keep scatterhoarder populations at relatively low levels.

Limitations of our study include its relatively short time frame (only two mast and two nonmast years) and the use of seeds from two different sources: locally collected seeds during mast years and seeds taken from storage during nonmast years. The use of seeds from two sources was

necessary because beech masting is a large-scale event—during mast years, seeds could only be collected in the field (stored seeds were unavailable, or, at best, stores contained 2-year-old seeds), and naturally occurring seeds were unavailable during nonmast years, requiring us to use seeds collected the previous year. It is conceivable that the fresher seeds used during mast years were more preferred by rodents than the seeds from storage used during non-mast years. However, all results indicated similar or more intense seed removal during nonmast years, suggesting that any preference for fresher seeds was overridden by other factors that change rodent behavior between mast and non-mast years.

Another possible caveat includes potential effects of ambient seed abundance on rodent motivation to engage with the experiments (i.e., remove seeds that were tagged or placed in cages). If rodents avoided experimental seeds in mast years (when food was abundant), but not in nonmast years (when food was scarce), then our experiments would underestimate the magnitude of seed removal in mast years. We note, however, that seed removal is typically unaffected by seed marking (Sork 1984; Li and Zhang 2003; Hirsch et al. 2012; Wróbel and Zwolak 2013), and we left our experimental cages in the field for over 6 months, allowing mice to familiarize themselves with these structures.

In conclusion, our results support the predictions of both the predator satiation and the predator dispersal hypotheses. Importantly, the timing of satiation—after the seeds had been removed and cached—supported the predator dispersal hypothesis. Predictions of these hypotheses are not absolute, however. Not all of the predictions need to hold for the benefits of any to be ecologically or evolutionarily important. Simultaneous consideration of the two hypotheses provides a useful framework as it focuses attention on costs and benefits of masting that apply to interactions with different types of animals. For example, masting may both satiate invertebrate seed predators (Crawley and Long 1995; Maeto and Ozaki 2003; Espelta et al. 2008) and ensure that some seeds are cached and left uneaten by rodents. From this perspective, these two hypotheses do not need to be treated as alternatives. The predator satiation hypothesis applies to seed predation. The predator dispersal hypothesis can be interpreted as a special more-detailed case of the predator satiation hypothesis that applies specifically to scatterhoarders, which can act simultaneously as predators and dispersers.

Compliance with ethical standards

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