

Contributions of economies of scale in pollination efficiency and predispersal predation to seed viability effects of masting

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Abstract

Economies of scale (EoS), reduced individual costs when plant populations produce large numbers of seeds, are considered a central adaptive benefit of masting, the spatial synchronization of interannual variation in seed production. Throughout the development of seeds in wind-pollinated trees, multiple EoS mechanisms such as increased pollination efficiency and reduced predation rates have been identified. It is unclear, however, whether the same EoS mechanisms apply to co-occurring species and how sequential mechanisms interact to determine seed fate. Here, we use a long-term data set of seed production of beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), and silver fir (*Abies alba*) in a primeval montane forest to investigate the relationship between seed production, pollination efficiency, and predispersal predation by insects. Our results show that the three species differed in presence and extent of EoS mechanisms. In silver fir, only pollination efficiency increased exponentially with seed density, while in Norway spruce only the rate of insect predation decreased with crop size. In beech, both EoS mechanisms had dramatic effects on seed quality and, importantly, our results suggest that pollination efficiency mediated the extent of predispersal predation. Furthermore, we found that both pollination and predation rates only increase strongly in the lower range of seed production, and that predation rates also depend on the extent of seed production the previous year. These findings illustrate that economy-of-scale effects are not universal and that multiple mechanisms in sequence can interact to shape seed fate.

Introduction

In temperate Europe, forest-forming tree species present considerable variation in interannual fruiting (Fernández-Martínez et al. 2017, Pesendorfer et al. 2020). Such temporally variable and spatially synchronized seed production in plant populations, called masting, is thought to provide individuals fitness benefits associated with economies of scale (hereafter “EoS”) which decrease the cost of reproduction per surviving offspring with increasing extent of seed production (Norton and Kelly 1988, Pearse et al. 2016). Two main mechanisms of such EoS in masting are reduced pollen limitation in years of extensive flowering and satiation of seed predators in years of bumper crops (Kelly and Sork 2002). In species in which these mechanisms operate, recruitment peaks after mast years when seed predators are satiated and higher pollination efficiency during mass flowering increases relative seed viability (Crawley and Long 1995, Clark et al. 1998, Zwolak et al. 2016). However, patterns of seed production are changing worldwide in response to climate change (Pearse et al. 2017, Shibata et al. 2020, Clark et al. 2021). For the many species that regenerate through masting, such changes include altered synchrony and interannual variation in seed production, which can all affect reproduction success if economies of scale determine plant regeneration, population dynamics, and community structure (Pearse et al. 2017, Shibata et al. 2020, Bogdziewicz et al. 2020b). We thus need to understand whether economies of scale operate across plant species to understand how changes in reproductive patterns affect plant fitness and regeneration. Despite rising interest in mast-seeding and its underlying mechanisms (Koenig et al. 2021; Pesendorfer et al. 2021), there are few examples of economies of scale (Nilsson and Wastljung 1987; Norton & Kelly 1988), and the interactions of underlying mechanisms are poorly understood. Here, we use a long-term

data set of high spatial resolution to investigate how pollen limitation and predispersal predation vary with annual seed production in Central Europe's few remaining old-growth montane forests.

The pollination efficiency hypothesis suggests that increased pollination success in high flowering years selects for mast-seeding (Kelly et al. 2001), providing the highest fitness to temporally variable and spatially synchronous trees (Bogdziewicz et al. 2020b). Generally, the role of pollen limitation in driving reproduction of wind-pollinated plants was long underestimated (Koenig & Ashley 2003). A series of recent studies, mostly based in North America and New Zealand, found that pollination efficiency correlated positively with flowering density, thus supporting the hypothesis (Houle 1999, Kelly et al. 2001, Rapp et al. 2013, Moreira et al. 2014, Bogdziewicz et al. 2020b). In beech (*Fagus sylvatica* L.), density-dependent pollen limitation was found when correlating the proportion of hollow, unpollinated seeds with stand size across a Swedish landscape, so that trees in larger stands had a higher proportion of viable seeds (Nilsson and Wastljung 1987). Similarly, across England, beech trees that are more responsive to temperature variation and thus more synchronous with their respective populations have lower proportions of unpollinated seeds (Bogdziewicz et al. 2020b). However, it is unclear to what extent the pollination-efficiency EoS occurs across European forest trees and whether it interacts with other EoS mechanisms such as predator satiation. While pollination dynamics are an important driver of fruiting dynamics in oaks (Koenig et al. 2012; 2015; Bogdziewicz et al. 2017, Schermer et al. 2019), pollination efficiency is not always improved by masting. For example, pollen limitation was not relieved by masting in *Sorbus aucuparia* L. or in *Aciphylla squarrosa* J.R. Forst. & G. Forst, two insect-pollinated species (Pías and Guitián 2006, Brookes and Jesson 2007). Furthermore, intraspecific variation in masting behavior and its underlying mechanisms has been observed in several species (Nussbaumer et al. 2018) and is therefore unclear whether pollination EoS apply universally across species ranges.

The predator satiation hypothesis proposes that seed predators are satiated by bumper crops ("mast years") so that a larger proportion of seeds survives than in years of lower reproduction (Kelly and Sork 2002, Zwolak et al. 2022). Predator satiation is thought to be particularly effective when the mast year is preceded by a low-reproduction year, and the demographic response by the predator reduces the population (Zwolak et al. 2022). Mast seeding has been shown to reduce insect seed predation in several temperate European forest trees, including *Fagus sylvatica* (Nilsson and Wastljung 1987, Bogdziewicz et al. 2020b), *Quercus robur* L. (Gurnell 1993, Crawley and Long 1995), *Larix decidua* Mill. (Poncet et al. 2009), and *Sorbus aucuparia* (Kobro et al. 2003, Żywiec et al. 2013). However, insect predators are not always satiated by mast seeding. For example, masting can result in a bottom up effect on the insect population that effectively cancels predator satiation (Bogdziewicz et al. 2018b). Similar responses were found for small mammals with fast increases of rodent densities largely driven by seed availability in mast years (Sachser et al. 2021) leading to low seed survival at experimental dishes and in natural populations (Nopp-Mayr et al. 2012).

Moreover, masting does not satiate insects if insect predators synchronize their life cycle with periodical seed production (Kelly et al. 2000, Maeto and Ozaki 2003). Mobile predators may even be attracted to large seed crops and consume relatively more seeds than they would otherwise, thereby selecting against

masting (Curran and Leighton 2000, Koenig et al. 2003). Some species can also sustain themselves on alternate food sources during low seed years, avoiding starvation and numerical reduction, and return to seeds of interest as they become increasingly available (Fletcher et al. 2010, Bogdziewicz et al. 2018a). Predator satiation benefits of EoS may therefore not be universal, but rather context- and species-dependent and thus need to be assessed case-by-case.

Here, we investigate how pollen limitation and predispersal predation vary with annual reproductive effort using a 10-year data set on seed production, seed predation, and pollen limitation in three forest-forming European species: European beech (*Fagus sylvatica*), Norway spruce (*Picea abies* (L.) H. Karst), and silver fir (*Abies alba* Mill.). While pollen limitation varies with annual flowering dynamics, predator satiation often shows lagged effects, detected by lower seed losses in years following a small seed crop, following a numerical response by insect populations (Silvertown 1980, Kelly & Sullivan 1997). Such sequence-dependence can thus result in very different levels of seed predation for two similarly-sized, intermediate reproductive efforts if one followed a high seed year and the other followed a low seed year. Furthermore, we test the hypothesis that interactions among the two mechanisms can dampen or amplify the EoS benefits of mast-seeding. Specifically, we predicted that pollen limitation, quantified by the proportion of hollow, non-viable seeds, would decrease the proportion of full, fertilized seeds depredated by insects, thereby reducing their density-dependent feeding rates. Finally, we test the hypothesis that EoS increase the temporal variability of viable seed densities that are subject to subsequent selection steps, such as vertebrate predation and dispersal.

Methods And Materials

The study was conducted in the Rothwald primeval forest, located in the Wilderness Area Dürrenstein in the northern Limestone Alps of Lower Austria (47°48' to 47°45'N, 15°01' to 15°07'E). The soils form a mosaic of Rendzinas and relictic loams, based on parent materials Dolomite and banked limestone (Zukrigl et al. 1963). Ranging from 900 to 1,350 m a.s.l., the site is dominated by European beech, particularly on slopes, with co-dominant Norway spruce and Silver fir (Zukrigl et al. 1963). The sub-maritime climate of the area is characterized by long winter periods and short, cool summers. Mean monthly temperatures range from -4.7°C in January to 12.8°C in July, with a mean annual temperature of 3.7°C. Precipitation, which can reach annual totals of 2,300 mm, follows a bimodal pattern with peaks in early summer and with wintertime snowfall, resulting in 200 days of continuous snow cover.

Seed production was monitored 2003-2018 on two 1-ha study plots (Mayer-Wegelin plot "MW", and Josef plot "JO") each equipped with 81 seed traps of 0.24 m² area, arranged in a geostatistical design (Gratzer et al. 2022). Starting in 2008, seeds collected in traps were sorted into sound, hollow, and infested by insects, as evidenced by chewing marks and exit holes. We present data for 2008 - 2018, when seed quality and predispersal predation data is available, but the period is representative in overall seed production patterns of the larger study (Gratzer et al. 2021).

Statistical Analysis

To characterize annual seed production patterns, we calculated annual plot-wide means of sound, hollow, and depredated seeds and summarized temporal patterns using the coefficient of variation (CV = standard deviation / mean), synchrony as measured by the mean pairwise Pearson correlation of seed production among individual seed traps in a plot through time, and lag-1 autocorrelation (Table 1) of the annual plot-level mean seed production.

To test the economies of scale hypotheses, we constructed a series of binomial generalized linear mixed models (GLMMs) of the proportion of sound, hollow, and depredated seeds per trap and year. The number of seeds of the relevant type (sound, hollow, depredated) was weighted by the total number of seeds of a species in a trap using the 'cbind' method (Zuur et al. 2009), thus leveraging the maximum amount of available information. Trap ID was used as a random intercept to account for repeated sampling, while the fixed effects of total seeds and lag-1 total seeds (both log-transformed) were scaled and centered to facilitate interspecific comparisons. For *P. abies*, seed rain density in one ("JO") of two plots was very low, which was therefore excluded from analyses.

All analyses were conducted in R version 4.0.2 (R Core Team, 2020). GLMMs were constructed in the package *glmmTMB* version 1.0.2.1 (Brooks et al. 2017) and model fit assessed using *performance* version 0.5.1 (Lüdtke et al. 2021). Model predictions were derived using the *ggeffects* package version 0.16.0 (Lüdtke 2018) and plotted with *ggplot2* version 3.3.2 (Wickham 2016) and *ggExtra* version 0.10 (Attali and Baker 2022).

Results

Seed production in all three species followed classic masting patterns: crops were highly variable between years, synchronized in space, and negatively autocorrelated to the previous year (Fig. 1). When considering sound seeds only, variability and autocorrelation remained unchanged in *A. alba* and *P. abies* (Table 1). In *F. sylvatica*, however, interannual variability increased in both plots by more than 25% for sound seeds when compared to all seeds (MW: 1.45 to 1.74; JO: 1.91 to 2.36). The extent of negative autocorrelation generally remained similar between seed types.

Table 1. Summary of population-level seed production A) *F. sylvatica*, B) *P. abies*, and C) *A. alba* in both study plots (JO, MW). Mean, annual variability (CVp), and lag-1 autocorrelation of all and sound seeds, as well as the mean percentage of hollow and infested seeds over all study years (2008 – 2018).

Species	Plot	All seeds [m ⁻²]			Sound seeds [m ⁻²]			Hollow seeds	Infested seeds
		Mean	CV _p	AR1	Mean	CV _p	AR1		
A) <i>F. sylvatica</i>	JO	109.1	1.45	-0.33	66.6	1.74	-0.32	22.6 %	35.9 %
	MW	57.0	1.91	-0.22	35.1	2.36	-0.19	18.9 %	42.6 %
B) <i>P. abies</i>	JO	5.6	1.71	-0.19	5.5	1.73	-0.18	-*	-*
	MW	22.0	1.51	-0.26	20.2	1.60	-0.25	1.5 %	14.2 %
C) <i>A. alba</i>	JO	9.0	1.41	-0.38	8.4	1.42	-0.37	3.2 %	6.2 %
	MW	18.4	1.12	-0.63	16.6	1.14	-0.58	2.8 %	10.1 %

* seed density too low

Pollination efficiency

The average proportion of unfertilized, hollow seeds in *F. sylvatica* was nearly an order of magnitude larger than in the two conifer species (Table 1). The proportion of hollow seeds declined significantly with the (log-transformed) number of seeds in a trap in *F. sylvatica* and *A. alba*, but not in *P. abies*. In *A. alba*, the significant interaction term between seeds per trap and plot illustrates that the effect was stronger in the plot of low conspecific density (JO: Table 2, Fig. 2).

Predispersal seed predation

The proportion of depredated seeds declined with the number of (non-hollow, non-depredated) sound seeds per trap in *F. sylvatica* and *P. abies*, but not in *A. alba* (Table 3). In both species with predator satiation, there was also a significant interaction between current-year seeds and the number of seeds in the previous year, indicating that preceding predator starvation enhances satiation (Table 3A, B). Furthermore, we found a significant effect of the proportion of hollow seeds, i.e. the extent of pollination efficiency, on seed predation rates in *F. sylvatica* (Table 3A).

Table 2: Pollination efficiency: the relationship between seed production and the proportion of hollow (unfertilized) seeds in A) *F. sylvatica*, B) *P. abies*, and C) *A. alba*. Estimates, associated standard errors, z-values, and P-values for generalized linear mixed models with binomial error distribution and seed trap ID as random intercepts. Sample sizes (trap years with at least one seed in trap; *Fs* N = 1404; *Pa*: N = 431 (only MW plot) and *Aa*: N = 901.

A) <i>F. sylvatica</i>	Estimate	Std. Error	z value	
(Intercept)	-1.304	0.077	-16.9	***
log(seeds)	-0.161	0.017	- 9.5	***
area (mw)	-0.425	0.127	- 3.3	***
log(seeds):area	0.043	0.029	1.5	n.s.
B) <i>P. abies</i>				
(Intercept)	-6.984	1.068	- 6.5	***
log(seeds)	-0.338	0.242	- 1.4	n.s.
C) <i>A. alba</i>				
(Intercept)	-1.971	0.422	- 4.7	***
log(seeds)	-1.064	0.235	- 4.5	***
area (mw)	-0.799	0.557	- 1.4	n.s.
log(seeds):area (mw)	0.802	0.279	2.9	**

Table 3. The effect of seed production and pollination efficiency on predispersal seed predation in A) *F. sylvatica*, B) *P. abies*, and C) *A. alba*.

A) <i>F. sylvatica</i>	Estimate	Std. Error	z value	
(Intercept)	0.339	0.077	4.380	***
log(non-hollow seeds)	-0.459	0.020	-23.012	***
log(seeds T ₋₁)	-0.042	0.033	- 1.273	n.s.
proportion hollow seeds	-0.684	0.104	- 6.553	***
log(seeds T ₋₁):log(seeds)	0.033	0.009	3.671	***
B) <i>P. abies</i>				
(Intercept)	-2.071	0.359	-5.772	***
log(seeds)	-0.408	0.121	-3.370	***
log(seeds T ₋₁)	-0.579	0.267	-2.164	*
log(seeds):log(seeds T ₋₁)	0.371	0.098	3.771	***
C) <i>A. alba</i>				
(Intercept)	-3.311	0.384	-8.618	***
log(seeds)	0.208	0.151	1.378	n.s.
log(seeds T ₋₁)	-0.504	0.810	-0.622	n.s.
proportion hollow seeds	-0.403	1.109	-0.363	n.s.
log(seeds):log(seeds T ₋₁)	-0.095	0.315	-0.301	n.s.

Discussion

Our results demonstrate that spatiotemporal variation in seed production in three mast-seeding species, *A. alba*, *F. sylvatica*, and *P. abies*, results in economy-of-scale impacts on early seed fate. Specifically, we found that in years of high seed production, *A. alba* showed increased pollination efficiency (Fig. 2B), *P. abies* reduced pre-dispersal predation (Fig. 3B), and *F. sylvatica* benefitted from both mechanisms (Fig. 2A, 3A). Furthermore, our results show that the effect of pollen limitation in years of low *F. sylvatica* seed production further reduced the extent of seed predation by insects, evidence that sequential EoS mechanisms can interact to determine early seed fate (Table 3A). Similar to Nilsson & Wästljung's (1987) seminal study, we found that pre-dispersal insect predator satiation provided stronger EoS benefits to *F. sylvatica* than pollen limitation (Tables 2 & 3). Importantly, our temporal analysis, which contrasts with their space-for-time substitution, further revealed a strong lag effect (Fig. 3A), illustrating the crucial effect

of the sequence of predator starvation followed by satiation, an effect that we also found in *P. abies* (3B; Zwolak et al. 2022).

Pollination efficiency increased strongly with increasing number of seeds per trap for *F. sylvatica* and *A. alba*. Both species showed a threshold, below which the proportion of full seeds increased rapidly before reaching an asymptote well beyond 80% of viable seeds (Fig 2). Pollination efficiency at mean seed production values was high for both species, indicating moderate to low benefits from masting in terms of pollination efficiency according to the conceptual model on benefits of masting for wind-pollinated species (Kelly et al. 2001). However, in contrast to the model, the proportion of filled seeds in seed traps does not directly reflect the proportion of flowering trees, as traps far from mother trees may receive fewer seeds even in years of high seed production (Gratzer et al. 2022). Nonetheless, means for filled *F. sylvatica* seeds for the two study plots (representing 81 seed traps ha⁻¹) show that all but one year had more than 50% of full seeds, even during low average seed production in the plots. This suggests either clumped distributions of flowering trees in years of low overall seed production or a low per-tree seed production of many trees. Gratzer et al. (2022) found spatially distinct hotspots of seed densities in such years, making the first explanation more plausible.

Similar to pollination efficiency, pre-dispersal seed predation of *F. sylvatica* showed a steep decrease up to seed densities of around 50 seeds per trap (~25%) and a further decrease to around 10% at very high seed densities (150+ seeds per trap). Overall levels of pre-dispersal predation were low, however, highlighting the important role of post-dispersal predator satiation in determining overall EoS effects of masting in our study system. This corroborates previous work, which showed that populations of seed-eating rodents keep up with seed abundance and depredate nearly all seeds, even in years of bumper crops (Nopp-Mayr et al. 2012; Sachser et al. 2021).

The sequence of individual and population-level processes that culminate in seed production, dispersal, and establishment provide opportunities for selection on the synchrony and variability of plant reproduction (Pearse et al. 2016; Dale et al. 2021; Pesendorfer et al. 2021). Certain steps, such as the timing and extent of the floral transition - the switch from vegetative to reproductive growth - are triggered by internal and external cues that are not directly associated with economies of scale, but rather with internal resource dynamics of a plant (Lalonde & Roitberg 1992; Kozłowski 1992; Crone & Rapp 2014). In contrast, density-dependent processes, such as pollination, seed predation, and dispersal, have all been shown to result from emergent properties of population-level effects, the hallmark of economies of scale (Norton & Kelly 1988; Kelly 1994; Seget et al. 2022). In fact, selection pressure from the latter stages of the phenological sequence are likely strong enough to affect the sensitivity of individuals to internal or external cues that affect floral transition and other individual aspects of reproduction (Kelly & Sork 2002; Pearse et al. 2016). The two EoS mechanisms considered here also differ fundamentally in their sensitivity to the temporal sequence of years of high and low seed production. While predator satiation only works in combination with a certain degree of predator starvation (Zwolak et al. 2022), pollen limitation is likely insensitive to flowering efficiency in the previous year, other than due to indirect effects mediated by individual resource limitation (Pesendorfer et al. 2016; Abe et al. 2016). As evidence is

increasing that species and populations vary in the mechanisms by which masting emerges from the interactions between internal resource dynamics and external (synchronizing) mechanisms (Bogdziewicz et al. 2017; Nussbaumer et al. 2018), a general framework which captures the sequential thresholds that have to be surpassed to achieve synchronized, temporally-variable seed production in plant populations would be essential (Pesendorfer et al. 2021). This framework could also provide the necessary foundation to advance our understanding of selection pressures, as well as potential historical and future scenarios, as environmental conditions change on a global scale.

The presence of economies of scale across all three species points towards a potential sensitivity of Central European forests to climate warming. In masting plants, recruitment depends both on mean seed production and on the interannual variability and among-plant synchrony in seed production (Hackett-Pain & Bogdziewicz 2021). On a proximate level, masting is triggered by species-specific climate cues that usually involve deviations from mean temperature or precipitation (Pearse et al. 2016, LaMontagne et al. 2021, Wion et al. 2021). The dependence on weather makes masting sensitive to climate change, as warming changes the cueing phenology (Bogdziewicz et al. 2021) and consequently can erode interannual variation and synchrony on which sound seed production depends (Pesendorfer et al. 2020, Shibata et al. 2020). In that context, the importance of temporal trends in interannual variation and synchrony matter only if the fitness of affected trees is linked to the degree of variation and synchrony through economies of scale. The results presented here indicate that all three major forest-forming species we studied benefit from masting through decreased predation, increased pollination efficiency, or both. Such dependence on EoS may bring the risk that their recruitment potential or proportional representation will shift as the climate changes. Long-term monitoring is therefore required to establish whether masting breakdown happens and the degree to which it may hamper recruitment.

Declarations

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Conflicts of interest: The authors declare no conflicts of interest.

Availability of data and materials: The datasets used during the current study are available from the corresponding author on reasonable request.

Author contributions: MBP and GG conceived the study, MBP, GG, UNP, and IO collected the data, MBP and IO analyzed the data, MBP, MB, IO, and GG wrote the first draft, all authors provided editorial input.

Ethics approval: Ethics approval was not required for this study according to local legislation

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Figures

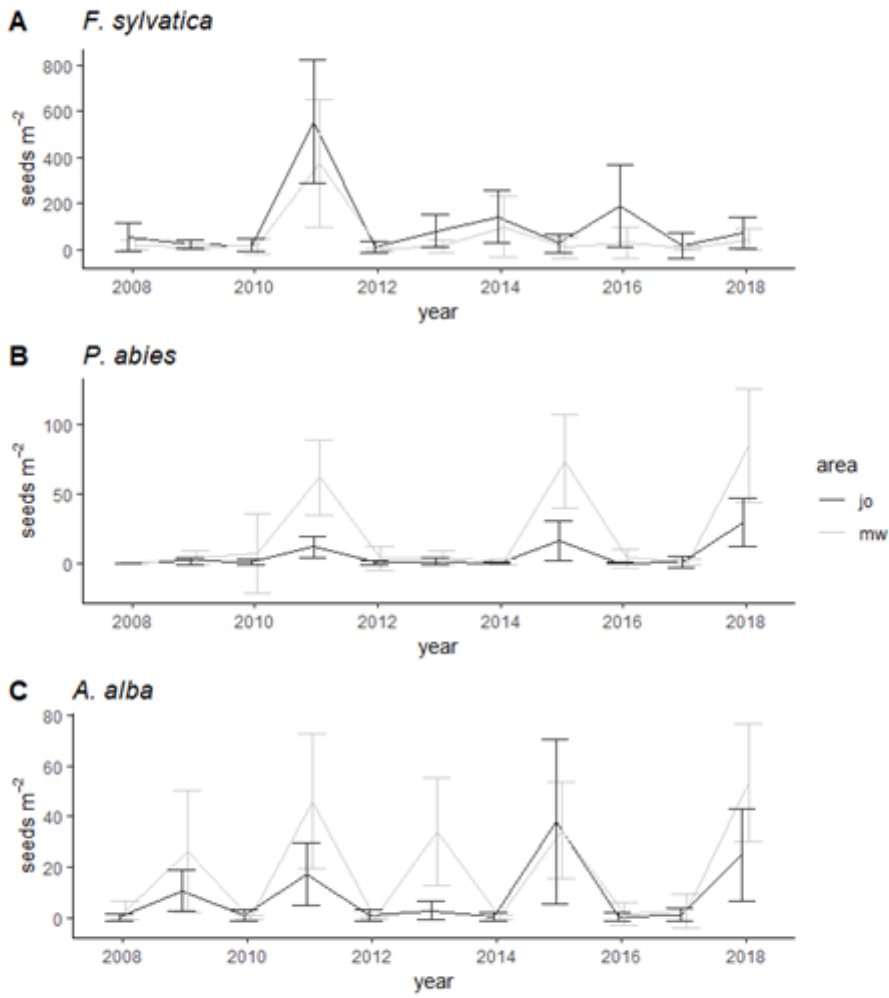


Figure 1

Interannual variation in seed production of A) *F. sylvatica*, B) *P. abies*, and C) *A. alba* in the two study areas. Lines denote annual means for 81 traps, whiskers denote standard deviation

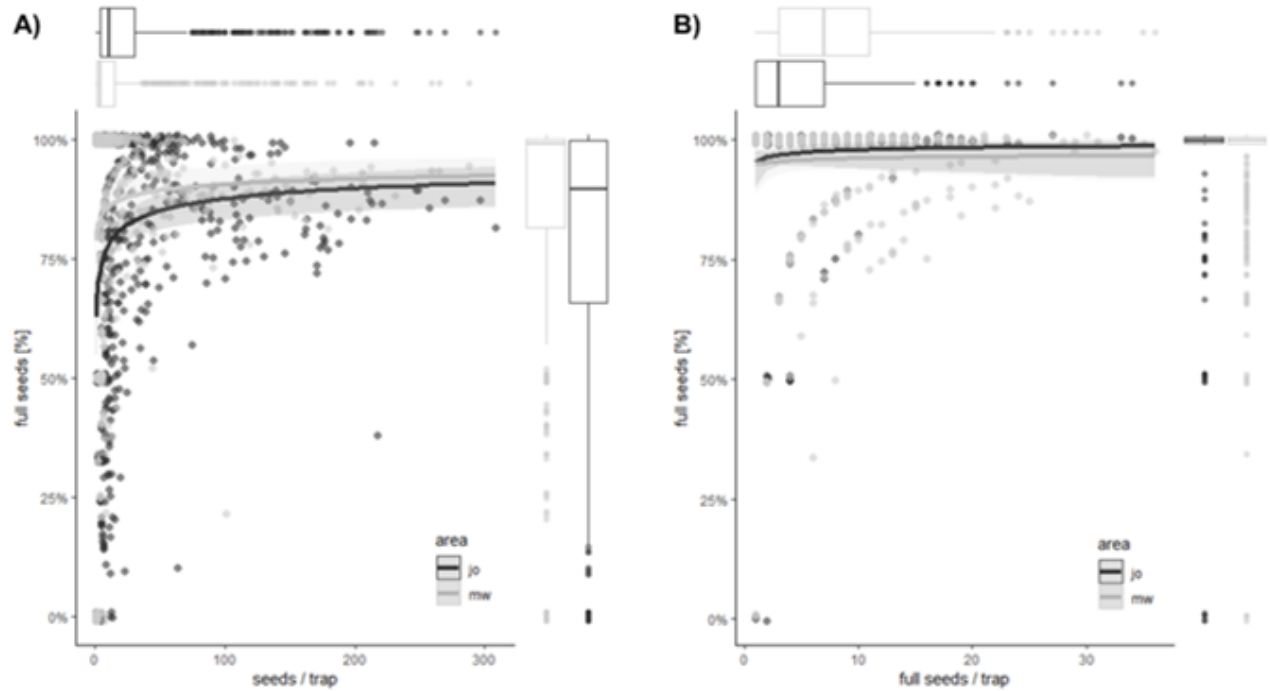


Figure 2

Pollination efficiency in A) *F. sylvatica* and B) *A. alba*. Percentage of pollinated seeds detected in seed traps as a function of the total number of seeds in a 0.24 m² trap. Lines indicate model predicted relationships for each plot, shaded areas 95 % C.I. N(beech) = 1404 trap years and N(fir) = 901 trap years with at least 1 seed (of 1782 possible).

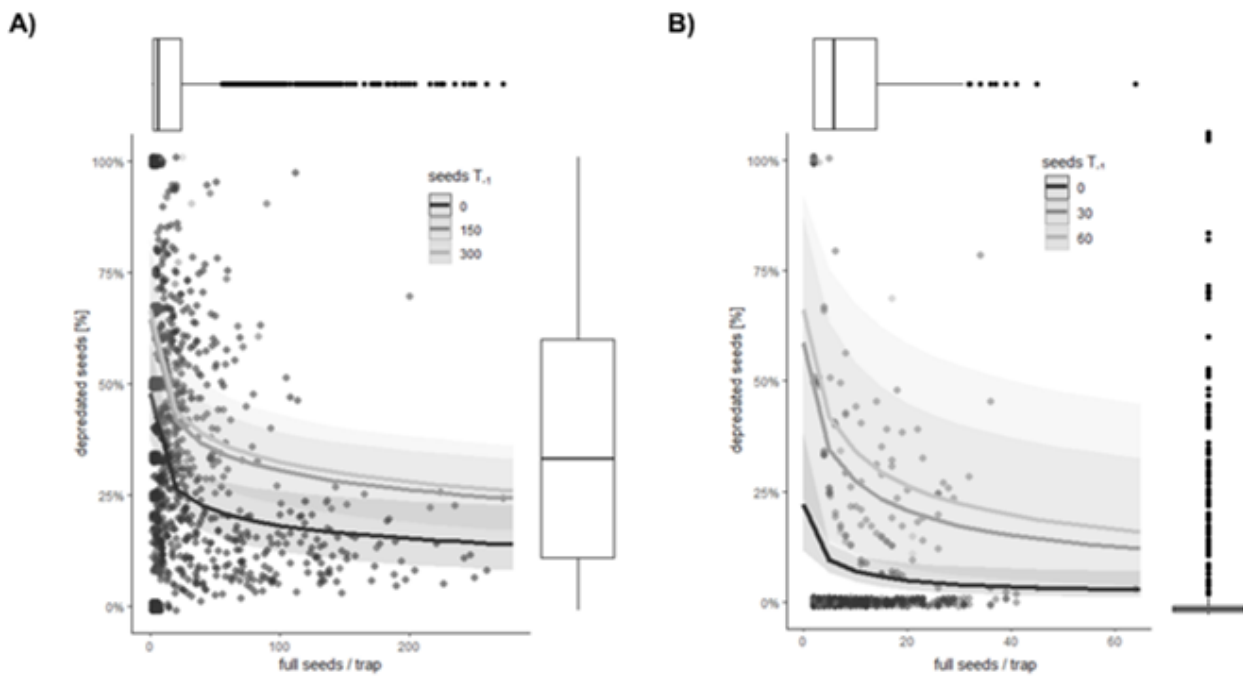


Figure 3

Predator starvation and satiation in *F. sylvatica* (left) and *P. abies* (right). Proportion of insect-damaged seeds as a function of number of (non-hollow) seeds per trap. Colored lines indicate model-predicted relationship for interaction with seeds per trap in the previous year (T-1), shaded areas 95 % C.I. N(beech) = 1325 trap years; N(spruce) = 704 trap years with at least 1 non-hollow seed (of 1782 possible).