

Conspecific density enhances sound seed production during high-seed years in European beech

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Abstract

Climate change is reducing the supply of sound seeds available for forest regeneration, creating a need to identify management strategies that can counteract these losses. Managing local tree density offers one potential approach, as neighbouring trees can enhance pollination but also increase losses to seed predators. In masting species, which produce highly variable but synchronised seed crops, the balance between these benefits and costs may depend on annual reproductive effort. Here, using seeds collected beneath 314 European beech (*Fagus sylvatica*) trees across three stands in Poland and the United Kingdom over three years, we examined how conspecific density within 5–50 m buffers influenced pollination efficiency, pre-dispersal seed predation, sound seed production, and seed mass. During the high-seed year, predicted sound seed production increased almost 2-fold from low to high conspecific density, coinciding with a tendency for seed predation to decline with increasing density. In contrast, during low-seed years, seed predation increased with density, while pollination efficiency increased with density in one of two years. Mean seed mass decreased by approximately 9% with density in a high-seed year. These findings suggest that dense neighbourhoods can increase the number of sound seeds available for regeneration when their predation costs are weakened by high seed production. Future studies should determine whether greater seed supply outweighs reduced seed mass in its effects on seedling establishment and survival. Maintaining higher local densities of reproductive trees may therefore help sustain sound seed supply during mast events and partly buffer the consequences of masting breakdown for European beech regeneration.

Introduction

Mast seeding, or masting, is a widespread reproductive strategy among perennial plants (Kelly, 1994; Bogdziewicz *et al.*, 2024). Masting is a highly variable but strongly synchronised seed production among conspecifics and increases reproductive success through two positive density-dependent mechanisms: enhanced pollination efficiency and predator satiation (Kelly, 1994; Zwolak *et al.*, 2022; Pesendorfer *et al.*, 2024). Both mechanisms depend on the temporal pattern of reproduction: enhanced pollination requires synchronous flowering, while predator satiation relies on pronounced differences between low- and high-seed years. However, growing evidence suggests that climate change is altering the magnitude and temporal pattern of seed production across mast-seeding species, a change referred to as masting breakdown (Shibata *et al.*, 2020; Yukich Clendon *et al.*, 2023; Bogdziewicz *et al.*, 2023; Foest *et al.*, 2024).

These changes are expected to weaken both positive density-dependent processes, reducing pollination efficiency while increasing seed predation. Consequently, the production of sound seeds may decline, potentially limiting seed availability for forest regeneration and the trophic interactions supported by mast crops (Foest *et al.*, 2026). For example, declines in seed supply associated with masting disruptions in European beech can exceed 50% (Bogdziewicz *et al.*, 2023; Jantzen *et al.*, 2026). However, pollination and seed predation depend not only on temporal patterns of reproduction but also on the spatial distribution of reproductive trees. Local conspecific density may influence pollen availability (Nilsson & Wastljung, 1987; Knapp *et al.*, 2001) as well as the distribution and activity of seed predators (Jones & Comita, 2010; Xiao *et al.*, 2017; Bogdziewicz *et al.*, 2018). Unlike regional climatic conditions, local tree density can be modified through silvicultural practices. Whether maintaining denser neighbourhoods could buffer some of the consequences of masting breakdown therefore may depend on how local density affects successive stages of reproduction (Nilsson & Wastljung, 1987).

The first mechanism through which masting is thought to increase reproductive success is enhanced pollination efficiency. At the population level, synchronous flowering during mast years increases pollen availability and promotes outcrossing, as receptive flowers are more likely to receive compatible pollen when large quantities are released simultaneously (Satake & Iwasa, 2000; Kelly, 1994; Crone & Rapp, 2025; Bogdziewicz *et al.*, 2020). This mechanism is particularly important in wind-pollinated species (Kelly *et al.*, 2001). However, pollen dispersal ultimately occurs among neighbouring trees, suggesting that local conspecific density should also influence pollination success (Pearse *et al.*, 2026). Trees growing in denser neighbourhoods may therefore experience reduced pollen limitation and greater reproductive success than more isolated individuals (Knapp *et al.*, 2001). Consistent with this prediction, wind pollination is generally more efficient at higher conspecific densities (Kelly, 1994; Crone & Rapp, 2025), and studies of wind-pollinated oaks have shown that trees surrounded by more conspecifics produce larger acorn crops than isolated trees (Pearse *et al.*, 2026). Similar patterns have been reported in European beech, in which larger stands exhibit lower proportions of empty seeds (i.e. unpollinated flowers) than smaller stands (Nilsson & Wastljung, 1987).

The relationship between conspecific density and seed predation is more complicated because temporal and spatial density dependence can generate opposing effects. Predator satiation, one of the economies of scale proposed to explain masting, arises primarily from temporal variation in seed production: low-seed years limit predator populations, while subsequent large crops overwhelm the remaining predators and reduce the proportion of consumed seeds (Zwolak *et al.*, 2022). In contrast, the Janzen–Connell hy-

pothesis predicts lower seed and seedling survival near conspecific adults or in areas of high conspecific density because host-specific enemies are locally concentrated (Janzen, 1970; Connell, 1971; Comita *et al.*, 2014). Greater seed abundance can therefore reduce proportional predation through predator satiation, while greater local conspecific density may increase predation by concentrating specialised seed predators (Jones & Comita, 2010; Xiao *et al.*, 2017; Bogdziewicz *et al.*, 2018).

Temporal predator satiation and spatial Janzen–Connell effects may also interact, causing the effect of conspecific density to vary with annual seed production. In *Quercus serrata*, for example, the direction and magnitude of density-dependent pre-dispersal seed predation differed between high- and low-seed years (Xiao *et al.*, 2017). A high density of reproductive trees reduced insect attack at the population scale during the high-seed year, while greater seed production by individual trees was associated with increased predation during the low-seed year (Xiao *et al.*, 2017). In *Quercus ilex*, temporal variation in acorn production affected predation differently depending on local conspecific density. Predator satiation was evident in isolated trees but weakened in dense oak patches (Bogdziewicz *et al.*, 2018).

Conspecific density may consequently affect successive stages of reproduction in opposing directions. Greater conspecific density may improve pollination while simultaneously increasing losses to seed predators, particularly during low-seed years, making its net effect on sound seed production difficult to predict. The advantages arising early in reproduction may be offset during later stages and therefore fail to increase final reproductive output. For example, Fedriani *et al.* (2015) found that greater local conspecific density increased fruit initiation but reduced subsequent fruit development, effectively neutralizing the initial positive density effect in *Pyrus bourgaeana*. However, effects operating at successive reproductive stages do not always offset one another. In *Jacaranda copaia*, the positive effect of conspecific density on fruit set persisted through fruit development, and the number of mature fruits increased with local conspecific density (Jones & Comita, 2010).

Seed mass represents an additional component of reproductive success, alongside the number of sound seeds produced, as it can also influence regeneration. In European beech, heavier seeds produce larger seedlings, and early differences in seedling size are associated with long-term seedling survival (Pawłowski *et al.*, 2024; Ammer *et al.*, 2026). Local conspecific density may affect seed mass by intensifying competition among adult trees for resources required during seed development. It may also influence the genetic composition of received pollen. Because European beech exhibits fine-scale spatial genetic structure, nearby pollen donors may be closely related, meaning that high local pollen availability does not necessarily ensure genetically diverse or compatible pollen (Chybicki *et al.*, 2009). Mating

among related individuals can reduce offspring quality and has been associated with lower seed mass in wind-pollinated trees (Seltmann *et al.*, 2009). Conversely, a larger number of neighbouring trees could increase the diversity of potential pollen donors. Seed mass may therefore capture neighbourhood effects on reproduction that are not reflected in the number of sound seeds alone.

Here, we investigated whether local conspecific density — a component of stand structure that can be modified through silvicultural practices — could help buffer declines in sound seed supply associated with masting breakdown. This question is increasingly relevant because masting breakdown is occurring across the geographical range of European beech and is projected to intensify, including at colder range margins of the species (Foest *et al.*, 2024, 2025b). Long-term studies in the United Kingdom indicate associated declines in sound seed production of approximately 50–80% owing to reduced pollination efficiency and increased seed predation (Bogdziewicz *et al.*, 2021b, 2023). Similarly, following masting breakdown in a Dutch beech population, seed predation increased from approximately 6% to 20%, while pollination efficiency declined by 30% (Jantzen *et al.*, 2026). To determine whether denser neighbourhoods could mitigate these losses, we quantified how conspecific density affected pollination success, pre-dispersal seed predation, sound seed production, and seed mass across spatial scales and over three years differing markedly in seed production. We expected pollination success to increase with neighbourhood density because of greater local pollen availability. In contrast, we expected the effect of conspecific density on seed predation to depend on annual seed production: dense neighbourhoods could concentrate seed predators during low-seed years, whereas predator satiation could weaken or reverse this relationship during high-seed years. Consequently, we expected the net effect of conspecific density on sound seed production to depend on the balance between its effects on pollination and seed predation. We additionally explored whether conspecific density was associated with mean seed mass, either negatively due to increased competition in denser stands or positively due to greater diversity of potential pollen donors.

Methods

Study species European beech (*Fagus sylvatica* L.) is one of the dominant forest tree species in Europe. It is a wind-pollinated masting species that reproduces predominantly through outcrossing (Wang, 2003; Packham *et al.*, 2012). Flower buds are initiated during the growing season preceding seed production, while flowering and pollination occur the following spring. Female flowers become receptive before

male flowers release pollen, promoting cross-pollination (Packham *et al.*, 2012). Although beech pollen can be dispersed over long distances (Sjölund *et al.*, 2019), parentage analyses indicate that successful mating is predominantly mediated by nearby trees, with mean pollen dispersal distances ranging from approximately 24 to 184 m depending on stand structure (Chybicki *et al.*, 2009; Piotti *et al.*, 2012). Following pollination, developing beech seeds are dispersed by a range of vertebrates but are also subject to pre-dispersal seed predation, primarily by a moth, *Cydia fagiglandana* Z.(Tortricidae), whose larvae consume the seed contents before dispersal. Pre-dispersal infestation can remove a substantial proportion of the seed crop, especially in low-seeding years (Bogdziewicz *et al.*, 2021b; Jantzen *et al.*, 2026).

Study sites and data collection The study was conducted at three mature, beech-dominated forest stands in Europe: one in Wielkopolski National Park, Poland, and two in Buckholt Woods, United Kingdom (Fig. S1). Data were collected over three consecutive reproductive seasons (2023–2025) at two sites (Poland, Buckholt Woods I), and over two years (2024–2025) at the second Buckholt Woods site. We monitored 314 focal trees across the three sites: 114 in Wielkopolski National Park, 101 in Buckholt Woods I, and 99 in Buckholt Woods II. Trees were selected from among dominant or co-dominant canopy individuals, with a DBH (diameter at breast height) of ≥ 20 cm to ensure reproductive maturity.

The spatial position of study trees was determined using a Leica total station in the Polish stand and one Buckholt stand, whereas a 1×1 m grid was used in the second Buckholt stand. To avoid underestimating neighbourhood density near the study site boundaries, all European beech trees within each study site and an additional 50-m buffer surrounding its boundaries were mapped. This distance encompasses the local reproductive neighbourhood expected to contribute most strongly to effective pollination (Chybicki *et al.*, 2009; Piotti *et al.*, 2012). Across the three study sites, 965 beech trees were mapped, including 314 focal trees monitored for seed production and DBH, as well as 651 additional trees included in the neighbourhood analyses (trees in the buffer zone). Within a 10-m radius, focal trees had a median of 6 neighbouring beech trees (25th–75th percentile: 4–8). This increased to 13 neighbours (range: 10–17) within 15 m and 23 neighbours (range: 19–28) within 20 m. Other measurements, including DBH and seed collection, were restricted to the study trees.

Seeds were collected from the forest floor beneath the crown of each tree shortly after seed fall using a standardised 3.5-minute search (Foest *et al.*, 2025a; Kondrat *et al.*, 2026a). Timed counts are strongly related to seed density (seeds m^{-2}) rather than total seed production per tree, allowing comparisons of seed production that are less dependent on differences in crown size (Foest *et al.*, 2025a). Following collection, seeds were classified as sound, empty with fully formed pericarps (not pollinated), or damaged

by *Cydia fagiglandana*. For seed mass measurements, only sound (pollinated) seeds that were not infested by *C. fagiglandana* were retained. All retained seeds were air-dried at room temperature for four weeks and weighed individually to the nearest 0.001 g, following a protocol previously validated against oven drying (Kondrat *et al.*, 2026a). Because only 67 sound seeds were available for weighing in 2025, seed mass analyses were restricted to 2023 and 2024. Pollination, seed predation, and sound seed analyses included data from all three years and were based on all collected seeds (2023: N = 3,714; 2024: N = 14,223; 2025: N = 1,487; total N = 19,424).

Analysis To investigate the spatial scale over which conspecific density influenced reproduction, we quantified conspecific density as the number of reproductive beech trees within buffers ranging from 5 to 50 m around each focal tree (5-m increments). Generalized linear mixed models (GLMMs) were fitted separately for each buffer radius to examine how the effects of conspecific density varied across spatial scales. Based on these analyses (Fig. 1), the 10-, 15-, and 20-m buffers were selected for subsequent analyses.

For each buffer, pollination success, seed predation, sound seed production, and mean seed mass were analysed separately using GLMMs. Conspecific density was included in interaction with seed collection year to test whether neighbourhood effects varied among years. DBH was included in each model as a fixed effect. Tree ID and site ID were included as random intercepts in all models. Within-year effects of conspecific density were tested using year-specific slopes estimated with the `emtrends()` function from the `emmeans` package (Lenth & Piaskowski, 2026).

Pollination success was modelled using a binomial error distribution based on the numbers of pollinated and empty seeds. The model included conspecific density and population-level flowering as fixed effects. Population-level flowering was calculated as the total seed production of all other focal trees within the same site and year, excluding the focal tree, and was included as a proxy for population-level masting intensity and associated pollen availability, accounting for differences in reproductive effort among sites and years.

Seed predation was analysed using binomial error distributions including conspecific density and log-transformed total (i.e. including empty, predated, and sound) seed production of the focal tree as fixed effects. Focal-tree seed production was included to account for the effect of local seed abundance on predation rates independently of conspecific density.

Sound seed production was modelled as the number of sound seeds using a negative binomial error distribution with a log link. The model included conspecific density and population-level flowering as

fixed effects.

Mean seed mass was analysed using a Gaussian distribution and included conspecific density and population-level flowering as fixed effects.

DBH, population-level flowering and total seed production of the focal tree were fitted using natural spline functions. We assessed potential multicollinearity using variance inflation factors (VIFs) and found no evidence of problematic collinearity (all VIFs < 4). All analyses were conducted in R version 4.6.1 (R Core Team, 2025), and the models were implemented using the glmmTMB package version 1.9.23 (Brooks *et al.*, 2017).

Results

Overall effects of conspecific density Greater local conspecific density increased sound seed production in the high-seed year (2024), with predicted seed production rising 1.78-fold, from 9 to 16 seeds, between trees with two and ten neighbours within 10 m. During this year, mean seed mass decreased by approximately 9% with increasing neighbourhood density, while seed predation tended to decrease with density (Fig.1). In contrast, predation increased with conspecific density during both low-seed years, when no corresponding increase in sound seed production was detected. Pollination efficiency increased with conspecific density only in 2023.

Seed production varied markedly among sites and years (Fig. S2). Production was particularly high in Wielkopolski National Park in 2024, while 2025 was characterised by relatively low production across sites.

Pollination success only locally moderated by density in low seeding year Conspecific density had a weak effect on pollination success (Fig.1A). In 2023 (a low-seeding year, Fig. S2), pollination success increased with conspecific density within the 5- and 10-m buffers, but no significant relationship was detected beyond the 10-m buffer (Fig.1A). Within the 10-m buffer, predicted pollination success increased from 66.5% to 74.5% between trees with 2 and 10 neighbouring trees, respectively, corresponding to an increase of 8.05 percentage points (Fig. 1A). No significant relationship between conspecific density and pollination success was observed in 2024 or 2025 (Table S1). Population-level flowering was consistently and positively associated with pollination success across the retained 10-, 15-, and 20-m buffers, whereas tree DBH had no detectable effect (Table 1, S2).

Seed predation strongly interacts with conspecific density

Conspecific density had the strongest effect on seed predation, with positive relationships extending across the full range of spatial scales examined (Fig. 1B). In both 2023 and 2025 (poor seeding years, Fig. S2), the proportion of predated seeds increased with conspecific density. For example, within the 10-m buffer, predicted seed predation doubled from 31.9% to 63.1% between trees with 2 and 10 neighbouring trees in 2023. In 2025, predicted seed predation increased from 59.3% to 81.1% (Fig. 1B, 2B). In contrast, seed predation tended to decrease with conspecific density in 2024, when seed production was particularly high in the Polish stand ($p = 0.088$), declining from 45% to 38.4% between trees with 2 and 10 conspecifics at 10 m range. Total seed production by focal tree and tree DBH were positively associated with seed predation across 10-, 15-, and 20-m buffers (Table 1, S2).

Denser plots have more sound seeds

Conspecific density had strong effects on the number of sound seeds, and these effects differed among years (Fig. 1C). In 2024 (high-seeding year), the number of sound seeds increased with conspecific density, whereas no significant relationship was observed in 2023 and 2025. Within the 10-m buffer in 2024, the estimated number of sound seeds increased 1.78-fold, from 9 seeds (per 3.5 min search) for a tree with two neighbouring trees to 16 seeds for a tree with 10 neighbouring trees (Fig. 2C). Population-level flowering and tree DBH were consistently and positively associated with the number of sound seeds across the retained 10-, 15-, and 20-m models. (Tables 1, S2).

Flowering promotes seed mass, but high density constrains it in high seeding years

Conspecific density had modest and year-dependent effects on seed mass (Fig. 1D). In 2024, seed mass decreased with conspecific density within the 5- and 10-m buffers, whereas no significant relationship was detected in 2023 at these scales. Within the 10-m buffer in 2024, predicted mean seed mass decreased from 0.265 g for trees with two neighbouring trees to 0.241 g for trees with 10 neighbouring trees, corresponding to a decrease of 9.2% (Fig. 2D). Population-level flowering was consistently and positively associated with seed mass across the retained 10-, 15-, and 20-m models, whereas tree DBH had no detectable effect (Tables 1, S2).

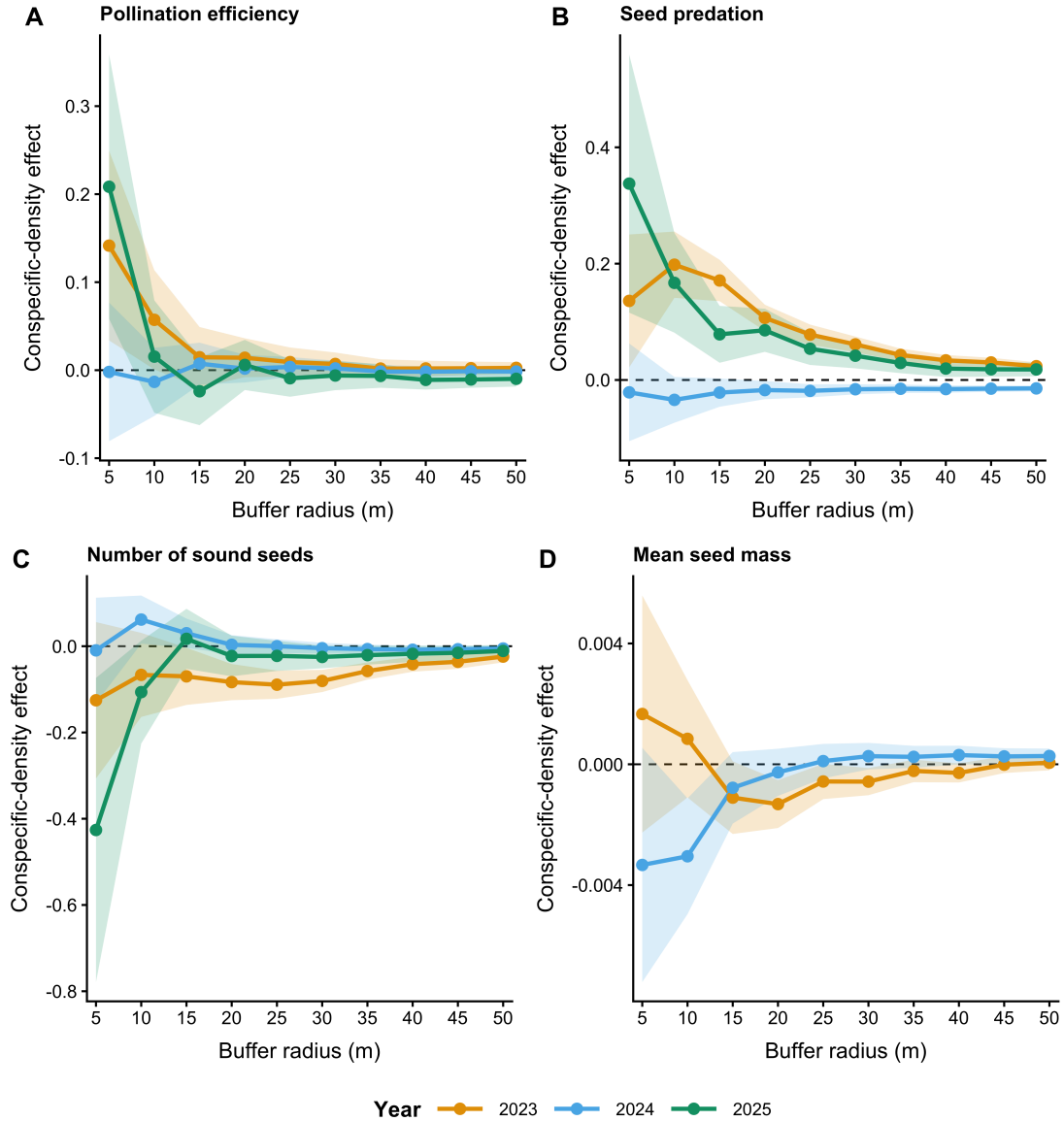


Figure 1: Conspecific density has the strongest effect on seed predation, with weaker effects on pollination, sound seed production, and seed mass. Panels show the estimated effect of conspecific density on (A) pollination efficiency, (B) seed predation, (C) number of sound seeds, and (D) mean seed mass across buffer radii (5–50 m) in 2023, 2024, and 2025 (2024: high-seed year; 2023 and 2025: low-seed years). The horizontal dashed line highlights 0. Estimates were obtained from generalized linear mixed models fitted separately for each buffer radius and included an interaction between conspecific density and year. All models included tree ID and site ID as random intercepts.

Table 1: Type II Wald χ^2 tests for the models fitted using the 10-m conspecific buffer. Population-level flowering refers to the number of pollinated seeds in the population, whereas total seed production refers to the total number of seeds collected from the focal tree, including empty, predated, and sound seeds, and was included in the predation model. Results for 15-, and 20-m buffers can be found in Table S2.

Response	Predictor	df	χ^2	<i>p</i>
Pollination	Population-level flowering	1	578.64	< 0.001
	DBH	1	1.44	0.230
	Conspecific density (10 m)	1	0.02	0.896
	Year	2	57.34	< 0.001
	Conspecific density $\times$ Year	2	7.00	0.030
Predation	Total seed production	1	300.18	< 0.001
	DBH	1	9.11	0.003
	Conspecific density (10 m)	1	3.42	0.064
	Year	2	137.50	< 0.001
	Conspecific density $\times$ Year	2	77.95	< 0.001
Sound seed count	Population-level flowering	1	370.28	< 0.001
	DBH	1	10.41	0.001
	Conspecific density (10 m)	1	0.55	0.456
	Year	2	103.40	< 0.001
	Conspecific density $\times$ Year	2	10.86	0.004
Seed mass	Population-level flowering	1	16.88	< 0.001
	DBH	1	1.68	0.195
	Conspecific density (10 m)	1	5.60	0.018
	Year	1	5.16	0.023
	Conspecific density $\times$ Year	1	1.49	0.222

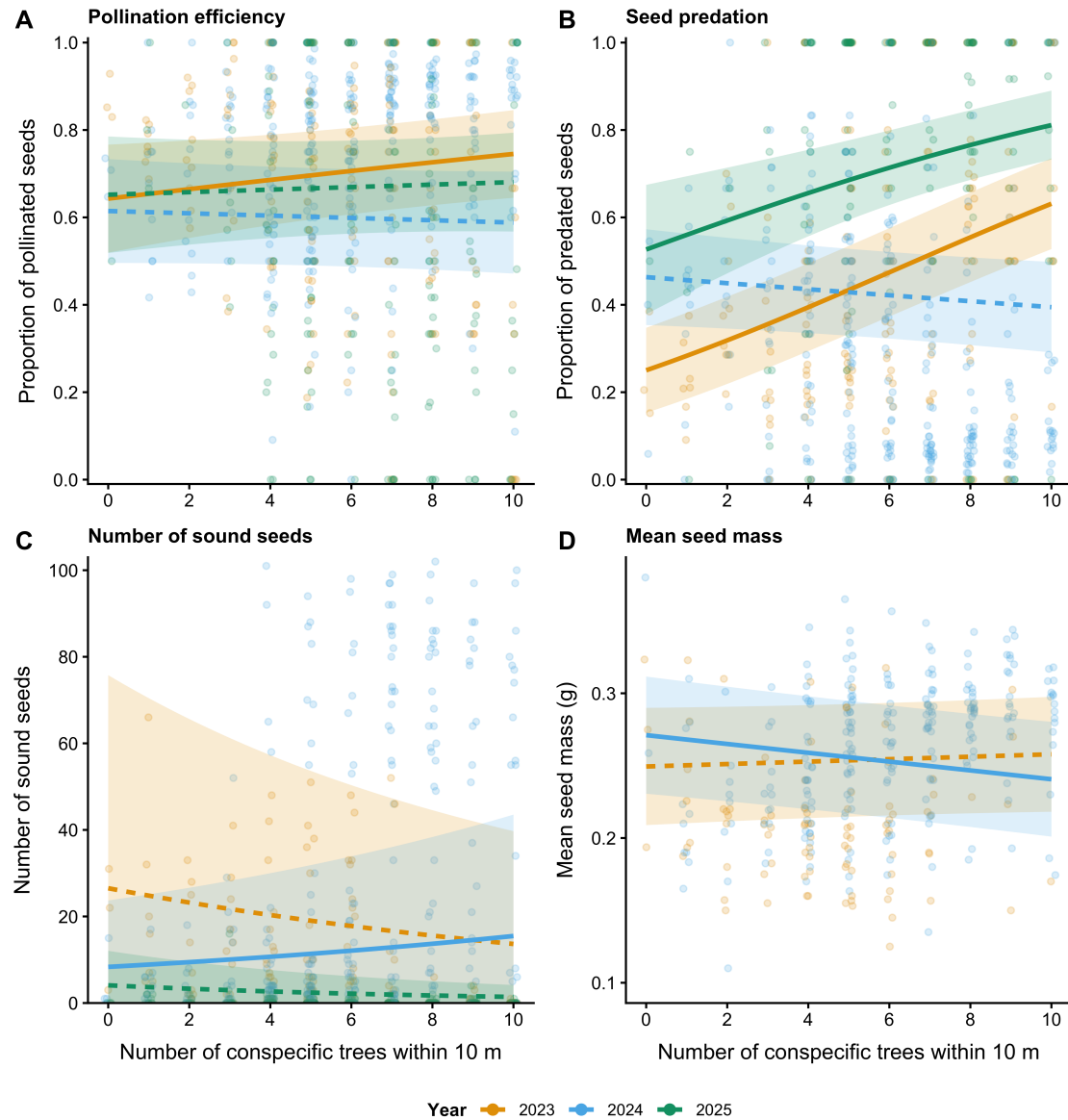


Figure 2: Higher conspecific density increased sound seed production but reduced seed mass in the high-seed year, while increasing seed predation in low-seed years. Panels show the relationships between conspecific density within a 10-m radius and (A) the proportion of pollinated seeds, (B) the proportion of predated seeds, (C) the number of sound seeds, and (D) mean seed mass in 2023, 2024, and 2025. Lines and shaded ribbons show mixed-model predictions and their 95% confidence intervals. Solid lines indicate significant year-specific effects of conspecific density, whereas dashed lines indicate non-significant effects. Seed-mass results are shown only for 2023 and 2024. We monitored 100 trees at each site.

Discussion

Higher conspecific density increased sound seed production during the high-seed year. Within 10 m, predicted production increased from 9 to 16 sound seeds between trees with two and ten neighbours, representing a 78% increase. This benefit emerged only during the high-seed year, when the seed

predation rates tended to decrease with higher conspecific density. Thus, the reproductive consequences of conspecific density depended on annual seed production, with dense neighbourhoods increasing final sound seed output when their associated predation costs were weakened. This 78% increase is notable given that mast seeding breakdown has been associated with declines in sound seed production of 50–83% in UK beech populations (Bogdziewicz *et al.*, 2021b, 2023). Although these estimates are not directly equivalent, they suggest that maintaining higher local densities of reproductive trees could partly offset declining sound seed supply during high-seeding years.

Pollination in our study stands appears to depend primarily on pollen availability across the wider population, with immediate conspecifics providing an additional benefit only in 2023. In that low-seed year, reduced flowering may have made pollen from nearby trees relatively more important, resulting in higher pollination efficiency in denser neighbourhoods. During the high-seed year of 2024, widespread and synchronised flowering likely generated abundant pollen across the population, reducing the importance of immediate neighbours for pollination success (Bogdziewicz *et al.*, 2021a). However, conspecific density also had no effect in the low-seed year of 2025, showing that low annual seed production does not necessarily imply insufficient local pollen. This may reflect the spatial scale over which beech pollen is exchanged. Mean effective pollen-dispersal distances range from approximately 24 to 184 m (Chybicki *et al.*, 2009; Piotti *et al.*, 2012), so trees with few conspecifics within our maximum 50-m buffer could still receive pollen from more distant conspecifics. Pearse *et al.* similarly found that isolation affected seed production in wind-pollinated oaks over distances of approximately 100 m (Pearse *et al.*, 2026). Conspecific density within 50 m may therefore capture only part of the pollen pool contributing to fertilisation.

Seed predation increased with conspecific density during both low-seed years, but this relationship disappeared during the high-seed year. Our results suggest that pre-dispersal seed predation depends on the interaction between spatial and temporal density dependence. During low-seed years, greater local conspecific density was associated with higher seed predation by *Cydia fagiglandana*, consistent with the negative density dependence in seed survival predicted by the Janzen–Connell hypothesis (Janzen, 1970; Connell, 1971). During the high-seed year, however, the positive relationship between conspecific density and seed predation disappeared, probably because the abundant seed crop satiated seed predators and reduced proportional seed losses. A similar weakening of density-dependent predation during a high-seed year was observed in *Quercus serrata* (Xiao *et al.*, 2017), while positive local density dependence in pre-dispersal seed predation has also been reported in the tropical tree *Jacaranda copaia* (Jones & Comita,

2010). This supports the prediction that predator satiation can weaken the effect of local conspecific density on seed predation when seeds are abundant.

Sound seed production increased with conspecific density during the high-seed year, showing that the balance between pollination and seed predation favoured greater final seed output in denser neighbourhoods. Because sound seeds constitute the pool of seeds potentially available for germination, their greater production in denser neighbourhoods could increase seed supply for regeneration. For European beech, the concentration of the sound-seed benefit in the high-seed year is particularly relevant because high seeding events can generate pulses of seedling establishment (Gratzer *et al.*, 2022). Maintaining denser reproductive neighbourhoods may therefore increase the regeneration potential of high-seed years, and partly compensate for the seed supply decline associated with climate change.

Mean seed mass decreased with conspecific density during the high-seed year. Trees in denser neighbourhoods produced more sound seeds, but these seeds were approximately 9% lighter than those produced in less dense neighbourhoods. Nevertheless, mean seed mass was higher overall in 2024 than in 2023, consistent with previous evidence that European beech generally produces heavier seeds in high-seed years (Kondrat *et al.*, 2026a). Thus, the negative relationship with conspecific density occurred within a year in which seeds were comparatively large overall. It may still partly reduce the regeneration benefit of greater sound seed production in dense neighbourhoods, as heavier beech seeds produce larger seedlings and early size advantages are associated with higher subsequent survival (Pawłowski *et al.*, 2024; Ammer *et al.*, 2026). Competition among neighbouring adult trees for light, water, and nutrients may limit resource allocation to seed development and explain the within-year decline in seed mass. In European beech, competition effects can be strongest in dense stands, although their magnitude depends on tree size and site-level resource availability (Fichtner *et al.*, 2012). Whether this relationship recurs during other high-seed years remains unclear, as seed mass was measured in only two years and the effect was detected only in 2024.

Our findings have implications for thinning practices intended to increase seed production. By reducing competition, thinning can increase seed production by retained trees, as reported in oaks and Korean pine (Healy *et al.*, 1999; Nguyen *et al.*, 2019). However, higher production per tree does not necessarily mean higher production per hectare, because fewer trees remain. In Korean pine, the strongest thinning produced the highest cumulative cone yield per tree, whereas moderate thinning produced the highest yield per hectare (Nguyen *et al.*, 2019). In a Norway spruce seed orchard, thinning did not increase cone production per tree and consequently reduced production per hectare (Almqvist, 2024). Benefits

may also differ across regeneration stages: thinning in European beech reduced seedling emergence and only temporarily improved seedling survival (Toranj *et al.*, 2026). In our study, trees with more reproductive neighbours produced more sound seeds during the high-seed year. This suggests that removing reproductive trees could affect seed supply both by reducing their number and by altering the reproductive success of those remaining. Thinning decisions should therefore consider the retention of reproductive neighbours alongside the potential benefits of reduced competition. Because we did not manipulate tree density, the consequences of thinning for sound seed supply remain to be tested. Since thinning also alters light availability and soil moisture, its effects on seed production should be considered alongside those on seedling establishment and survival when planning stand management.

The temporal and spatial extent of our study should be considered when interpreting these findings. The three study years included both low- and high-seed conditions and span the typical 2–3-year masting period reported for European beech (Kondrat *et al.*, 2026b). Thus, the dataset contained only one high-seed event, largely restricted to the Polish site, preventing us from determining whether the year-specific conspecific effects recur during subsequent high-seeding events. Long-term declines in masting have been documented in both English and Polish beech populations (Bogdziewicz *et al.*, 2021b; Foest *et al.*, 2026). However, seed production at our Polish site varied markedly over the three study years, with a pronounced high-seed event in 2024. We therefore interpret the observed effects of conspecific density as evidence that stand structure can influence sound seed supply under contrasting reproductive conditions, but further monitoring will be important.

In summary, our results demonstrate that conspecific density influences final seed output through its effects on predation and pollination rates. Higher local densities of reproductive beech within 10 m supported greater sound seed production during the high-seed year, with the highest seed supply observed at approximately ten neighbours within this radius. This finding has management implications: retaining groups of reproductive beech at high densities may help maximise sound seed supply during high seeding events. Maintaining such dense reproductive neighbourhoods could therefore support forest regeneration and partly buffer the negative effects of masting breakdown in European beech.

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Author Contributions Statement

KK, AHP, and MB designed the study; all authors collected the data; KK analyzed the data; KK wrote the first draft of the manuscript. All authors interpreted the data and revised the paper.

Declaration of interests

No competing interests to declare.

Data availability statement

The data supporting the results are archived in the Open Science Framework and are available at: .

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Supporting Information

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Title: Conspecific density enhances sound seed production during high-seed years in European beech

Table S1: Year-specific effects of conspecific density on pollination efficiency, seed predation, number of sound seeds, and mean seed mass at the 10-m conspecific buffer. Estimates represent the slope of each response with increasing conspecific density within each year. SE denotes the standard error and CI the 95% confidence interval.

Response	Year	Estimate	SE	Lower 95% CI	Upper 95% CI	<i>p</i>
Pollination efficiency	2023	0.057	0.029	0.001	0.114	0.047
	2024	-0.013	0.020	-0.052	0.025	0.500
	2025	0.015	0.033	-0.048	0.079	0.636
Seed predation	2023	0.198	0.029	0.141	0.255	< 0.001
	2024	-0.034	0.020	-0.073	0.005	0.088
	2025	0.167	0.044	0.081	0.253	< 0.001
Number of sound seeds	2023	-0.066	0.050	-0.164	0.031	0.181
	2024	0.062	0.028	0.006	0.118	0.030
	2025	-0.106	0.061	-0.225	0.013	0.080
Mean seed mass	2023	0.001	0.001	-0.001	0.003	0.394
	2024	-0.003	0.001	-0.005	-0.001	0.002

Table S2: Type II Wald χ^2 tests for the final models fitted using the retained 15- and 20-m conspecific buffers. Population-level flowering refers to the number of pollinated seeds produced by all other focal trees within the same site and year. Total seed production refers to the total number of seeds collected from the focal tree, including empty, predated, and sound seeds, and was included in the predation model.

Response	Buffer	Predictor	df	χ^2	<i>p</i>
Pollination	15 m	Population-level flowering	1	403.61	< 0.001
		DBH	1	1.36	0.243
		Conspecific density	1	0.12	0.734
		Year	2	57.67	< 0.001
		Conspecific density $\times$ Year	2	3.61	0.164
	20 m	Population-level flowering	1	427.56	< 0.001
		DBH	1	1.28	0.259
		Conspecific density	1	0.30	0.582
		Year	2	57.82	< 0.001
		Conspecific density $\times$ Year	2	1.45	0.484
Predation	15 m	Total seed production	1	214.70	< 0.001
		DBH	1	7.17	0.007
		Conspecific density	1	3.63	0.057
		Year	2	141.32	< 0.001
		Conspecific density $\times$ Year	2	136.92	< 0.001
	20 m	Total seed production	1	192.02	< 0.001
		DBH	1	6.37	0.012
		Conspecific density	1	3.15	0.076
		Year	2	137.34	< 0.001
		Conspecific density $\times$ Year	2	148.15	< 0.001
Sound seed count	15 m	Population-level flowering	1	308.68	< 0.001
		DBH	1	10.28	0.001
		Conspecific density	1	0.74	0.391
		Year	2	104.48	< 0.001
		Conspecific density $\times$ Year	2	7.81	0.020
	20 m	Population-level flowering	1	301.88	< 0.001
		DBH	1	6.97	0.008
		Conspecific density	1	2.03	0.154
		Year	2	106.14	< 0.001
		Conspecific density $\times$ Year	2	14.44	< 0.001
Seed mass	15 m	Population-level flowering	1	12.03	< 0.001
		DBH	1	1.30	0.254
		Conspecific density	1	2.23	0.135
		Year	1	5.40	0.020
		Conspecific density $\times$ Year	1	3.75	0.053
	20 m	Population-level flowering	1	14.90	< 0.001
		DBH	1	1.12	0.291
		Conspecific density	1	1.29	0.256
		Year	1	5.49	0.019
		Conspecific density $\times$ Year	1	3.97	0.046



Figure S1: Location of the three study stands within the European beech distribution. Study stands were located in Wielkopolski National Park, Poland, and Buckholt Woods, United Kingdom. Two stands were sampled at Buckholt Woods; their markers were displaced slightly to prevent overlap at the geographical scale shown. Grey shading indicates the natural distribution of *Fagus sylvatica*.

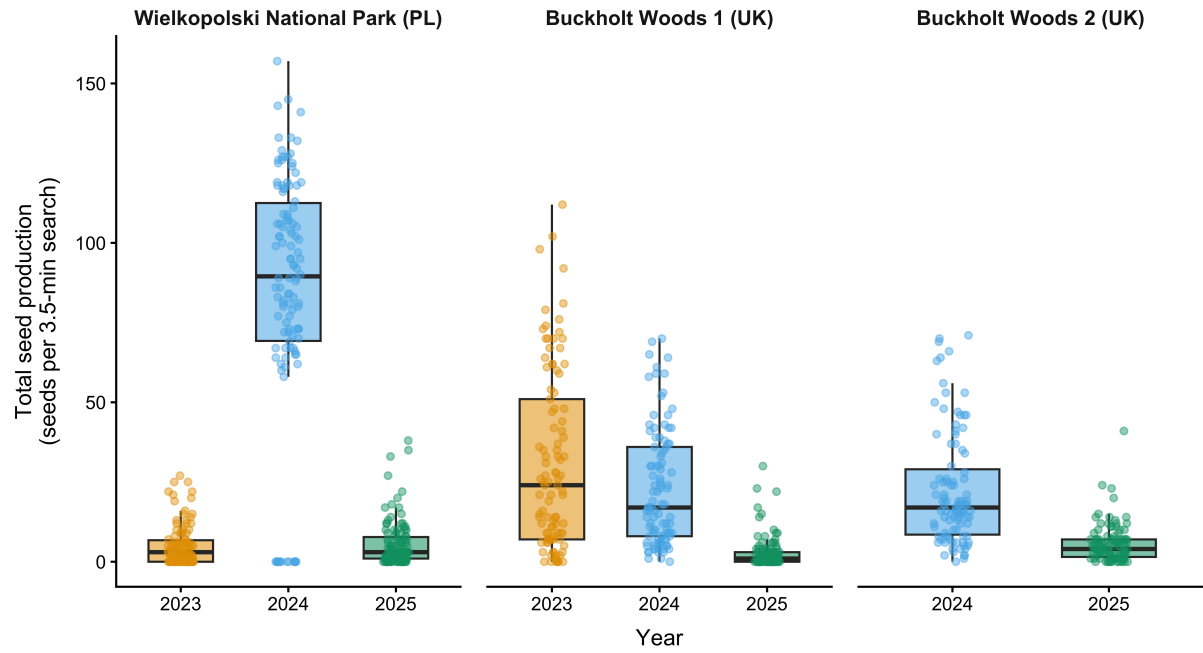


Figure S2: Annual variation in seed production across study sites. Boxes denote the 25th, 50th, and 75th percentiles, whiskers extend to the most extreme observations within 1.5 times the interquartile range, and points represent seed production by individual trees. Total seed production refers to the total number of seeds collected from the focal tree, including empty, predated, and sound seeds during 3.5 minute search. No seed data were collected at Buckholt Woods 2 in 2023. 100 trees were monitored at each site.