Masting ontogeny: the largest masting benefits accrue to the largest trees

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Author contributions

MB, DK, JSz, AHP designed the study, AHP, PT, JL collected and curated the data, JSz analyzed the data, all authors interpreted the results, MB, DK wrote the first draft of the manuscript with contributions from all authors, all authors revised the draft.

Open research statement

The data supporting the results are archived and accessible at OSF.

Competing interests

The authors declare no competing interests.

Abstract

Background and Aims Both plants and animals display considerable variation in their phenotypic traits as they grow. This variation helps organisms to adapt to specific challenges at different stages of development. Masting, the variable and synchronized seed production across years by a population of plants, is a common reproductive strategy in perennial plants that can enhance reproductive efficiency through increasing pollination efficiency and decreasing seed predation. Masting represents a population-level phenomenon generated from individual plant behaviors. While the developmental trajectory of individual plants influences their masting behavior, the translation of such changes into benefits derived from masting remains unexplored.

Methods and Key Results We used 43 years of seed production monitoring in European beech (*Fagus sylvatica*) to address that gap. The largest improvements in reproductive efficiency from masting happen in the largest trees. Masting leads to a 48-fold reduction in seed predation in large, compared to 28-fold in small trees. Masting yields an 6-fold increase in pollination efficiency in large, compared to 2.5-fold in small trees. Paradoxically, although the largest trees show the biggest reproductive efficiency benefits from masting, large trees mast less strongly than small trees.

Conclusions That apparently suboptimal allocation of effort across years by large plants may be a consequence of anatomical constraints or bet-hedging. Ontogenetic shifts in individual masting behavior and associated variable benefits have implications for the reproductive potential of plant populations as their age distribution changes, with applications in plant conservation and management.

keywords: | economies of scale | fecundity | forest regeneration | geitonogamy | mast seeding | seed production | seed predation | pollen limitation | tree size | reproductive efficiency

Introduction

Both plants and animals display considerable variation in their phenotypic traits as they grow (Acosta *et al.*, 1997; Gagliano *et al.*, 2007; Ochoa-López *et al.*, 2020). This variation helps organisms to adapt to specific challenges at different stages of development and can be promoted by resource allocation needs to different functions (e.g. growth, reproduction, defense) and physiological and ecological costs inherent to developmental processes (Maherali *et al.*, 2009; Watson *et al.*, 2019; Ochoa-López *et al.*, 2020). Masting, a variable and synchronized variation in the reproductive effort is a prevalent strategy among perennial plants (Pearse *et al.*, 2016; Journé *et al.*, 2023). Masting can enhance reproductive efficiency through economies of scale (Pearse *et al.*, 2016; Bogdziewicz *et al.*, 2024). These benefits include decreased seed predation, achieved by subjecting seed consumer populations to cycles of scarcity in low-seeding years followed by satiation in high-seeding years (Zwolak *et al.*, 2022). Furthermore, the aggregation of flowering during substantial events increases pollination efficiency (Kelly *et al.*, 2001; Rapp *et al.*, 2013). Masting is a population-level phenomenon stemming from synchronized behavior among individuals of varying sizes (Pesendorfer *et al.*, 2021). Just as resource allocation between growth and reproduction shifts as plants grow (Kozłowski, 1992; Genet *et al.*, 2009), recent evidence points that masting behavior also changes (Minor & Kobe, 2017; Pesendorfer *et al.*, 2020; Bogdziewicz *et al.*, 2020c; Wion *et al.*, 2023), but consequences of these changes remain poorly studied.

Recent insights highlight two general patterns. First, very small plants do not mast; instead, they reproduce idiosyncratically with low synchrony and frequent reproductive failures, likely due to resource allocation favoring growth over reproduction (Bogdziewicz *et al.*, 2020c). Second, larger plants experience fewer failure years, a phenomenon speculated to relate to reduced resource constraints in larger individuals (Bogdziewicz *et al.*, 2020c; Wion *et al.*, 2023). The translation of these ontogenic shifts in individual masting behavior into corresponding population-level gains from economies of scale remains unexplored. This is an important gap, given that variations in synchrony or failure rates at the individual level correlate with seed predation rates and pollination efficiency (Bogdziewicz *et al.*, 2020a, 2021). Therefore, these ontogenic trajectories may influence the regenerative potential of populations in response to changes in stand age structure (Pesendorfer *et al.*, 2021).

The influence of plant size on the benefits derived from economies of scale is not necessarily aligned with the influence of plant size on seed crop variability and synchrony (i.e. the strength of mast seeding). Self-fertilization often increases with plant size as a consequence of stronger geitonogamy, i.e. self-fertilization resulting from the transfer of pollen within the same plant (de Jong *et al.*, 1993). In animal-pollinated plants, geitonogamy increases with size because pollinators visit more flowers in succession on large individuals (de Jong *et al.*, 1993; Fuchs *et al.*, 2003; Setsuko *et al.*, 2013). In the case of wind-pollinated plants, larger size can amplify the deposition of self-pollen onto stigmas, which even in self-incompatible species can reduce fertilization success when stigmas receive so much self-pollen there is less space for outcross pollen to land (Lloyd & Webb, 1986; de Jong *et al.*, 1993). Supporting this notion, pollination efficiency declines with tree size in European beech (*Fagus sylvatica*) (Bogdziewicz *et al.*, 2023). Furthermore, this decrease in pollination efficiency with size intensifies as masting synchrony diminishes amid climate warming (Bogdziewicz *et al.*, 2023). A hypothesis formulated by Bogdziewicz *et al.* (2023) proposes that the necessity for masting to increase pollination efficiency (i.e. the strength of selection pressure) is particularly pronounced in large individuals. This was attributed to the challenge of geitonogamy, which can potentially be mitigated through large and synchronized flowering events (Bogdziewicz *et al.*, 2023). However, this hypothesis remains untested.

Plant size-related variation in benefits linked to the satiation of specialist seed predators can be attributed to the propensity for less frequent failure years and the subsequent accumulation of seed consumer populations on larger individuals. Regular seeding reduces consumer starvation rates, rendering large trees a sanctuary for specialist seed predators (Bogdziewicz *et al.*, 2020c, 2021). Insect seed consumers tend to concentrate on individual plants that produce seeds when others do not (Bogdziewicz *et al.*, 2018a). Consequently, predation rates during periods of low seed production can be disproportionately elevated in large trees, resulting in a more pronounced reduction of seed predation rates during years of abundant seed production. However, whether the decline in seed predation rates associated with population-level seed production in a given year is more pronounced in larger individuals remains unexplored.

The potential size-related alterations in benefits gained from economies of scale could potentially drive selection for ontogenetic (size-dependent) shifts in individual masting behavior (Pesendorfer *et al.*, 2021). On the one hand, a positive correlation between the reproductive efficiency gained from masting and plant size might result in a more pronounced selection for masting in larger individuals. In support, population-level interannual variation in seed production increased with stand age across seven major forest-forming species in Central Europe (Pesendorfer *et al.*, 2020). Alternatively, there may be limitations on further concentrating reproduction in mast years for larger individuals due to constraints on maximum crop size. These constraints could be anatomical if most relevant branches are already bearing flowers in high-seeding years. Moreover, there are costs linked to the replacement of leaf buds with flower buds, impacting carbon acquisition (Innes, 1994; Vergotti *et al.*, 2019; Mund *et al.*, 2020). Furthermore, higher investment in seed crop size during mast years might result in elevated density-dependent seedling mortality (Visser *et al.*, 2011; Bogdziewicz *et al.*, 2024). Additionally, masting plants are predicted to incur substantial costs in terms of missed reproductive opportunities (Rees *et al.*, 2002; Tachiki & Iwasa, 2010). If further increases in seed production during mast years prove unfeasible, larger trees might opt to shift some reproduction to intermediate or low-seeding years—a strategy akin to bet-hedging (Koenig *et al.*, 2003; Qiu *et al.*, 2023).

Here, we used a 43-year-long monitoring of European beech (*Fagus sylvatica*) seed production to investigate the correlation between masting benefits and the size of individual trees. Firstly, we hypothesized that the observed decrease in pollination efficiency with increasing tree size (Bogdziewicz *et al.*, 2023) could be mitigated by extensive and synchronized reproduction. If this holds true, we anticipated a positive correlation between tree size and a proportional increase in pollination efficiency across varying flowering abundance within a given year. Secondly, we hypothesized that seed predation rates during years of low seed production would be higher in large trees compared to smaller ones, leading to more pronounced reductions in predation rates as the population-level seed crop size increases in larger trees. Subsequently, we examined alterations in masting behavior across different tree sizes. If the benefits stemming from economies of scale manifest most prominently in larger trees, we would anticipate larger trees allocate a greater proportion of their reproductive efforts during high-seeding years. Alternatively, the presence of limitations on maximum crop size could prompt a shift in the distribution of reproductive allocation towards years of intermediate and low seed production.

Methods

Study system and data European beech is a major forest-forming species in temperate Europe. Beech is a model masting species, with seed production characterized by large interannual variation and synchrony (Nilsson & Wastljung, 1987; Ascoli *et al.*, 2017; Mund *et al.*, 2020; Gratzer *et al.*, 2022). Pollination efficiency can be estimated from seed production data because fruit and seed coats develop if pollination occurs, while unpollinated fruits lack a seed (kernel) (Nilsson & Wastljung, 1987). We sampled seed production in beech trees located at 15 sites spaced across England annually between 1980 and 2022. Detailed descriptions of sites are given in Packham *et al.* (2008) and Bogdziewicz *et al.* (2023). The ground below each tree was searched for seeds for 7 minutes and seeds were later classified as viable, unpollinated (empty but with formed pericarps), or predated by *Cydia* sp. moth larvae.

In 2017, 2020, and 2022, we measured the tree diameter at the breast height (dbh) of all living trees within the network (n = 152). To estimate the past dbh, we cored 38 trees across 5 sites in 2022. The growth rate was ~2-4 cm diameter per tree per decade (Bogdziewicz *et al.*, 2023). Based on this estimate, we assumed that each tree grows an average of 0.3 cm per year, and reconstructed the size of trees in the past (Bogdziewicz *et al.*, 2023) (see Fig. S1 for median tree size distribution).

Analysis We first tested the hypothesis that masting gains associated with pollination efficiency are positively correlated with tree size. To this end, we examined the effects of conspecific flower abundance and tree size on individual-level pollination efficiency using a generalized linear mixed model (GLMM) with a binomial error structure and logit link. The model included the proportion of pollinated seeds as a response (empty vs. filled seeds; filled seeds also included those predated), while log-transformed population-level conspecific flower abundance, tree size (dbh), and their interaction were explanatory terms. To obtain population-level flower abundance in a particular year, we summed all seeds produced in trees at a focal site (filled and empty), excluding a focal individual. Because unpollinated flowers do not develop kernels, such a sum represents an index of flowering effort.

Next, we tested the hypothesis that masting gains associated with predator satiation are positively correlated with tree size. Using an analogous model, we examined the effects of population-level crop size and tree size on individual-level pre-dispersal seed predation rates. The model included the proportion of predated seeds as a response and annual, (log-transformed) population-level seed production (i.e. crop size) in interaction with tree size as explanatory terms. In that model, we summed filled seeds to obtain population-level crop size in a particular year (this time, including the focal tree). Both models included tree ID, site ID, and year as random intercepts.

We also examined how the distribution of reproductive allocation across varying levels of annual seed production depends on tree size using GLMMs. To this end, we ranked the annual seed production of each individual tree from the minimum to the maximum and normalized the ranks between 1 and 43 (i.e. the maximal length of a seed production series in our dataset) (see Fig. 2). The ranks were normalised as some trees entered the monitoring network later. Ranking allowed us to test whether most reproduction is concentrated in large years (high ranks) or is more evenly distributed (includes more seeding in lower-ranked years). In other words, we considered how each tree had allocated its reproduction between high-effort and low-effort years, ignoring the degree of synchrony with other trees. First, we examined absolute allocation across years. We fitted a model in which the response was focal-year annual seed counts per tree, fitted with a zero-inflated negative binomial error distribution and log-link. Zero inflation was included due to an excess of zeroes (22% of all observations), while the negative binomial error was used due to the response overdispersion. In a second model, we examined the relative reproductive allocation, i.e. the percentage of seeds produced by a tree in a given year in relation to the total number of seeds produced by that tree across the whole monitoring period. That model was fitted with a beta error distribution and logit link. Here, the beta error was used as the response was bounded between 0 and 1. Both models included normalized rank, tree size (median dbh), and their interactions as explanatory terms, while tree ID and site ID were included as random intercepts.

We conducted all analyses using R 4.2.2 and fitted the models using *glmmTMB* 1.1.5 (Brooks *et al.*, 2017).

Results

Large trees required a higher conspecific flower abundance to achieve comparable pollination efficiency as smaller individuals (Tree size × Flower abundance interaction term; Table 1, Fig. 1A, C). With a minor flowering effort, the estimated pollination efficiency for a large tree (~140 cm dbh) was approximately 7%, in contrast to the 17% observed in a relatively small tree (~60 cm dbh) (Fig. 1C). Notably, only during the largest mast flowering events did the pollination efficiency of larger individuals attain similar levels as that of their smaller counterparts, reaching 42% (Fig.1C). Consequently, a significant disparity emerged in the proportional benefits derived from economies of scale across various sizes. Masting resulted in a 2.5-fold increase in pollination efficiency for the small individuals, while the large individuals experienced a 6.1-fold increase (Fig. 1A).

Likewise, the decrease in pre-dispersal seed predation rates with increasing crop size was stronger in larger trees (Tree size × Crop size interaction term; Table 2, Fig. 1B,D). Larger trees experienced higher predation rates during years of low population-level crop sizes (Fig. 1B,D). Concurrently, estimated predation rates decreased substantially to their lowest levels in larger trees. This phenomenon gave rise to a large variation in the proportional benefits stemming from predator satiation across different tree sizes. Masting led to a predicted 28-fold decrease in seed predation rates for relatively small trees (60 cm dbh, from approximately 85% during low seed production years to 3% during peak seed production years), and an even more substantial 48-fold decrease in large trees (140 cm dbh, from 96% to 2%) (Fig. 1B).

The distribution of reproductive allocation across varying levels of annual seed production exhibited distinct variations among different tree sizes. For absolute reproductive effort, large individuals consistently produced a greater absolute quantity of seeds across all years (Fig. 2A,C, Table 2). Nevertheless, the difference was more pronounced in low and intermediate seed production years. For example, in a year characterized by minor seed investment (the lowest year for each plant), the absolute seed production by a large tree (140 cm DBH) was 4.1-fold higher than that of a small tree (60 cm DBH) (Fig. 2C). In a year characterized by intermediate seed investment (ranked as middle), the difference was 1.5-fold, whereas in years featuring maximum seed investment, seed production in such a large tree was 1.2-fold larger compared to a small tree (Fig. 2C).

Considering relative reproductive allocation, the shift in relative allocation towards years of lower and intermediate seed production in larger individuals is evident in Fig. 2B and D which illustrates the investment in reproduction for a specific year as a proportion of the total seeds produced by a tree throughout the entire monitoring period. For example, in a year characterized by minor seed investment (the lowest year for each plant), the predicted relative reproductive allocation for a large tree was 2.5-fold higher than that of a small tree (Fig. 2D). In a year characterized by intermediate seed investment (ranked 20th), the difference was 1.4-fold. In a year featuring maximum seed investment, the difference reversed, and relative investment was 1.2-fold higher in the small trees (20% of total reproductive effort in the biggest year, compared to 16% for large trees; Fig. 2B, D). Comparatively, smaller trees have more extreme masting: they allocate a higher proportion of their overall reproductive effort to years of abundant seed production, whereas larger trees invest proportionally more in years of lower and intermediate seed production (Fig. 2B).

Discussion

Our study reveals that patterns of reproductive allocation change as plants grow and so do the gains associated with masting-generated economies of scale. The largest trees get larger benefits with increasing crop size, primarily due to larger individuals having very high pollen limitation and seed predation rates during years of low seed production. In years characterized by minor flowering, larger trees experience pronounced pollen limitation, and their pollination efficiency rises when an ample supply of out-crossing pollen becomes available. Similarly, to facilitate a decline in seed predation rates in larger trees, a substantial population-level seed production becomes necessary.

Paradoxically, however, while large trees benefit most from the rare large reproductive events, their distribution of effort across years is less concentrated into large years than the comparable distribution of effort by small trees. While all sizes of trees have similar absolute seed densities in their biggest year (about 340 seeds per 7-minute count, which is not due to saturation of the count that can exceed 400, see Fig. S1 and Fig. S2), this is a much smaller percentage of their total reproductive output for large trees (14%) than for small trees (24%). Thus, instead of making larger mast years, the ontogenetic shift in masting behavior sees large trees putting more effort into years of intermediate seed production, and having fewer reproductive failures, relative to smaller trees. This is a paradox because, based on the pollination and predator satiation benefits listed above, any large tree that concentrated more of its reproductive effort into the largest mast years would produce more viable seeds.

We suggest three possible reasons for the apparently suboptimal allocation of reproduction effort across years in large trees. First, anatomical constraints may limit the maximum crop size. It could be that in a mast year, nearly all potential sites for flower buds already produce flowers, and further increases are not physically possible. Second, large trees may be practicing bet-hedging under imperfect synchrony. If a tree concentrated its flowering effort into a few very high years, but imperfect synchrony meant those years were not high years for neighboring trees, the focal tree would have relatively low pollination success and high seed predation. In European beech, synchrony among trees within a site (mean pairwise Pearson correlation) ranged between 0.85 and 0.60 over time (Bogdziewicz *et al.*, 2020b). Thus, under imperfect synchrony, there could be a selection to have multiple moderately high years rather than a few extremely high ones.

Third, benefits from economies of scale can plateau as mast years become very large, whereas the costs of masting probably do not. Pollination efficiency tends to reach an asymptote at about 70% of maximum flowering effort in species like *Pinus albicaulis* (Rapp *et al.*, 2013), *Dacrydium cupressinum* and *Nothofagus solandri* (Kelly *et al.*, 2001), and even earlier in *Fagus sylvatica* (Bogdziewicz *et al.*, 2020b). Therefore, two big years could get similar pollination efficiency as one massive year. Asymptotes have also been observed for reductions in seed predation with crop size, for example in *Chionochloa pallens* where predation never fell below 10% (Kelly *et al.*, 2008). But such asymptotes are less likely in predator satiation than in pollination due to the diversity of potential seed consumer communities (Curran & Webb, 2000; Gripenberg *et al.*, 2019; Xi *et al.*, 2020; Bogdziewicz *et al.*, 2022). If economies of scale plateau, the relative balance between economies of scale and opposing dis-economies of scale may shift into net disadvantage in very high-seed years. Dis-economies include factors like strong density-dependent seedling mortality (Hett, 1971; Visser *et al.*, 2011), which is likely to get stronger at very high seed crops rather than leveling out, and missed opportunities for reproduction. More regular seed production could increase the chances of reproduction in favorable years, such as after disturbance (Vacchiano *et al.*, 2021). Overall, the diminishing increases in pollination efficiency could mean the costs exceed the benefits in very high-seed years, favoring a greater reproductive allocation in intermediate years. A further factor could be that tree size might correlate with stand-level attributes such as stand density, which could influence competition and affect pollen supply. While we control for such factors using the site as a random effect in our models, such effects could also influence masting during stand development. Thus, the ontogenic trajectory of masting in the largest trees seems to be an outcome of the interplay between bet-hedging and variations in economies and dis-economies of scale, ultimately leading to changes in the relative allocation of reproduction across years as trees grow.

Together with a few recent studies exploring how masting changes with plant size (Minor & Kobe, 2017; Pesendorfer *et al.*, 2020; Bogdziewicz *et al.*, 2020c; Wion *et al.*, 2023), our study sheds new light into the overall ontogenetic development of mast seeding (Pesendorfer *et al.*, 2021). Three stages of masting across different sizes emerge (Table 3). The first stage (Stage 1) includes very small individuals, not covered by our data. These very small plants reproduce infrequently: over 70% of years have no seed set (Bogdziewicz *et al.*, 2020c). In trees, these could correspond to small individuals racing to reach the canopy, prioritizing growth over reproduction (Suzuki *et al.*, 2019). These small trees sporadically reproduce as resource availability increases, being under selection against delayed reproduction due to elevated mortality rates. Consequently, their involvement in reproduction is idiosyncratic, failing to achieve synchrony in which years have high seed crops — an attribute contrasting with synchronized masting failures shared among larger trees (Pesendorfer *et al.*, 2016; Bogdziewicz *et al.*, 2018b).

In Stage 2, the trees reach canopy status. These trees experience reduced yet still frequent reproductive failures, but these are shared among other individuals, fostering synchrony (Pesendorfer *et al.*, 2016; Bogdziewicz *et al.*, 2018b; Wion *et al.*, 2023). During Stage 2, limitations on maximum seed crop size in mast years have yet to take effect, leading intermediate-sized trees to predominantly allocate their reproductive efforts to years of large seed production when economies of scale ensure efficient reproduction. The third stage (Stage 3) is when large trees have similar high-seed years as plants in Stage 2, but these trees have a larger total resource for reproduction, so they also increase investment in years of lower and intermediate seed production as discussed above.

In summary, the increase in reproductive efficiency linked to masting exhibits a positive correlation with tree size. Large trees can only achieve high pollination efficiency by flowering when conspecifics flower heavily, yet this does not translate into large trees concentrating relatively more effort into their biggest reproduction events. Instead, compared to small trees, the larger trees allocate relatively more of their efforts toward years of intermediate and lower seed production. Further research will be needed to clarify the roles of size-related selection (such as asymptotes in benefits and costs of very high-seed years) versus constraints (anatomical limits on flower density) in shaping the ontogenetic effects described here.

The implications resulting from the ontogenic trajectories described here are diverse and encompass effects on regeneration potential and the resilience of forest ecosystems to climate change. On one hand, forests dominated by older or larger trees may exhibit robust regeneration potential due to their efficient reproduction during mast years and bet-hedging during other periods. On the flip side, dominance by regularly seeding large trees might lead to increased seed losses to seed consumers (Soler *et al.*, 2017; Ruiz-Carbayo *et al.*, 2018). Additionally, our results have implications for the climate change resilience of forests dominated by masting trees. Large trees need synchronized, population-level flowering to achieve efficient pollination and mitigate seed predation. If increasing temperatures associated with global warming decrease interannual variation and synchrony of masting, as observed in European beech (Bogdziewicz *et al.*, 2020b) or *Quercus crispula* (Shibata *et al.*, 2020), then large trees suffer the most (Bogdziewicz *et al.*, 2023). Consequently, the examination of the interactive effects of stand size structure and masting on recruitment potential, in the context of masting alterations driven by climate warming, becomes warranted.

References

Acosta, F.J., Delgado, J.A., López, F. & Serrano, J.M. (1997). Functional features and ontogenetic changes in reproductive allocation and partitioning strategies of plant modules. *Ecology*, 132, 71–76.

Ascoli, D., Vacchiano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J. *et al.* (2017). Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications 2017 8:1*, 8, 1–9.

Bogdziewicz, M., Kelly, D., Ascoli, D., Caignard, T., Chianucci, F., Crone, E.E. *et al.* (2024). Evolutionary ecology of masting: mechanisms, models, and climate change. *Trends in Ecology Evolution*, 39, 851–862.

Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P., Foest, J., Lageard, J. *et al.* (2023). Reproductive collapse in european beech results from declining pollination efficiency in large trees. *Global Change Biology*, 29, 4595–4604.

Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P.A., Lageard, J.G. & Hacket-Pain, A. (2020a). Climate change strengthens selection for mast seeding in european beech. *Current Biology*, 30, 3477–3483.e2.

Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A. & Hacket-Pain, A. (2020b). Climate warming disrupts mast seeding and its fitness benefits in european beech. *Nature Plants*, 6, 88–94.

Bogdziewicz, M., Kuijper, D., Zwolak, R., Churski, M., drzejewska, B.J., Wysocka-Fijorek, E. *et al.* (2022). Emerging infectious disease triggered a trophic cascade and enhanced recruitment of a masting tree. *Proceedings of the Royal Society B: Biological Sciences*, 289.

Bogdziewicz, M., Marino, S., Bonal, R., Zwolak, R. & Steele, M. (2018a). Rapid aggregative and reproductive responses of weevils to masting of north american oaks counteract predator satiation. *Ecology*, 99, 2575–2582.

Bogdziewicz, M., Steele, M.A., Marino, S. & Crone, E.E. (2018b). Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytologist*, 219, 98–108.

Bogdziewicz, M., Szymkowiak, J., Calama, R., Crone, E., Espelta, J., Lesica, P. *et al.* (2020c). Does masting scale with plant size? high reproductive variability and low synchrony in small and unproductive individuals. *Annals of Botany*, 126, 971–979.

Bogdziewicz, M., Szymkowiak, J., Tanentzap, A.J., Calama, R., Marino, S., Steele, M.A. *et al.* (2021). Seed predation selects for reproductive variability and synchrony in perennial plants. *New Phytologist*, 229, 2357–2364.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. *et al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Curran, L.M. & Webb, C.O. (2000). Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting dipterocarpaceae. *Ecological Monographs*, 70, 129.

Fuchs, E.J., Lobo, J.A. & Quesada, M. (2003). Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree pachira quinata. *Conservation Biology*, 17, 149–157.

Gagliano, M., McCormick, M.I. & Meekan, M.G. (2007). Survival against the odds: Ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1575–1582.

Genet, H., Bréda, N. & Dufrêne, E. (2009). Age-related variation in carbon allocation at tree and stand scales in beech (fagus sylvatica l.) and sessile oak (quercus petraea (matt.) liebl.) using a chronosequence approach. *Tree Physiology*, 30, 177–192.

Gratzer, G., Pesendorfer, M.B., Sachser, F., Wachtveitl, L., Nopp-Mayr, U., Szwagrzyk, J. *et al.* (2022). Does fine scale spatiotemporal variation in seed rain translate into plant population structure? *Oikos*, 2022, e08826.

Gripenberg, S., Basset, Y., Lewis, O.T., Terry, J.C.D., Wright, S.J., Simón, I. *et al.* (2019). A highly resolved food web for insect seed predators in a species-rich tropical forest. *Ecology Letters*, 22, 1638–1649.

Hett, J.M. (1971). A dynamic analysis of age in sugar maple seedlings.

Innes, J.L. (1994). The occurrence of flowering and fruiting on individual trees over 3 years and their effects on subsequent crown condition. *Trees*, 8, 139–150.

de Jong, T.J., Waser, N.M. & Klinkhamer, P.G. (1993). Geitonogamy: The neglected side of selfing. *Trends in Ecology Evolution*, 8, 321–325.

Journé, V., Hacket-Pain, A. & Bogdziewicz, M. (2023). Evolution of masting in plants is linked to investment in low tissue mortality. *Nature Communications*, 14, 7998.

Kelly, D., Hart, D.E. & Allen, R.B. (2001). Evaluating the wind pollination benefits of mast seeding. *Ecology*, 82, 117–126.

Kelly, D., Turnbull, M.H., Pharis, R.P. & Sarfati, M.S. (2008). Mast seeding, predator satiation, and temperature cues in chionochloa (poaceae). *Population Ecology*, 50, 343–355.

Koenig, W.D., Kelly, D., Sork, V.L., Duncan, R.P., Elkinton, J.S., Peltonen, M.S. *et al.* (2003). Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos*, 102, 581–591.

Kozłowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology Evolution*, 7, 15–19.

Lloyd, D.G. & Webb, C.J. (1986). The avoidance of interference between the presentation of pollen and stigmas in angiosperms i. dichogamy. *New Zealand Journal of Botany*, 24, 135–162.

Maherali, H., Caruso, C.M. & Sherrard, M.E. (2009). The adaptive significance of ontogenetic changes in physiology: A test in avena barbata. *New Phytologist*, 183, 908–918.

Minor, D.M. & Kobe, R.K. (2017). Masting synchrony in northern hardwood forests: super-producers govern population fruit production. *Journal of Ecology*, 105, 987–998.

Mund, M., Herbst, M., Knohl, A., Matthäus, B., Schumacher, J., Schall, P. *et al.* (2020). It is not just a 'trade-off': indications for sink- and source-limitation to vegetative and regenerative growth in an old-growth beech forest. *New Phytologist*, 226, 111–125.

Nilsson, S.G. & Wastljung, U. (1987). Seed predation and cross-pollination in mast-seeding beech (fagus sylvatica) patches. *Ecology*, 68, 260–265.

Ochoa-López, S., Damián, X., Rebollo, R., Fornoni, J., Domínguez, C.A. & Boege, K. (2020). Ontogenetic changes in the targets of natural selection in three plant defenses. *New Phytologist*, 226, 1480–1491.

Packham, J.R., Thomas, P.A., Lageard, J.G. & Hilton, G.M. (2008). The english beech masting survey 1980–2007: Variation in the fruiting of the common beech (fagus sylvatica l.) and its effects on woodland ecosystems. *Arboricultural Journal*, 31, 189–214.

Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212, 546–562.

Pesendorfer, M.B., Ascoli, D., Bogdziewicz, M., Hacket-Pain, A., Pearse, I.S. & Vacchiano, G. (2021). The ecology and evolution of synchronized reproduction in long-lived plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200369.

Pesendorfer, M.B., Bogdziewicz, M., Szymkowiak, J., Borowski, Z., Kantorowicz, W., Espelta, J.M. *et al.* (2020). Investigating the relationship between climate, stand age, and temporal trends in masting behavior of european forest trees. *Global Change Biology*, 26, 1654–1667.

Pesendorfer, M.B., Koenig, W.D., Pearse, I.S., Knops, J.M. & Funk, K.A. (2016). Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (quercus lobata). *Journal of Ecology*, 104, 637–645.

Qiu, T., Aravena, M.C., Ascoli, D., Bergeron, Y., Bogdziewicz, M., Boivin, T. *et al.* (2023). Masting is uncommon in trees that depend on mutualist dispersers in the context of global climate and fertility gradients. *Nature Plants*, 9, 1044–1056.

Rapp, J.M., Mcintire, E.J. & Crone, E.E. (2013). Sex allocation, pollen limitation and masting in whitebark pine. *Journal of Ecology*, 101, 1345–1352.

Rees, M., Kelly, D. & Bjørnstad, O.N. (2002). Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist*, 160, 44–59.

Ruiz-Carbayo, H., Bonal, R., Pino, J. & Espelta, J.M. (2018). Zero-sum landscape effects on acorn predation associated with shifts in granivore insect community in new holm oak (quercus ilex) forests. *Diversity and Distributions*, 24, 521–534.

Setsuko, S., Nagamitsu, T. & Tomaru, N. (2013). Pollen flow and effects of population structure on selfing rates and female and male reproductive success in fragmented magnolia stellata populations. *BMC Ecology*, 13, 1–12.

Shibata, M., Masaki, T., Yagihashi, T., Shimada, T. & Saitoh, T. (2020). Decadal changes in masting behaviour of oak trees with rising temperature. *Journal of Ecology*, 108, 1088–1100.

Soler, R., Espelta, J.M., Lencinas, M.V., Peri, P.L. & Pastur, G.M. (2017). Masting has different effects on seed predation by insects and birds in antarctic beech forests with no influence of forest management. *Forest Ecology and Management*, 400, 173–180.

Suzuki, M., Umeki, K., Orman, O., Shibata, M., Tanaka, H., Iida, S. *et al.* (2019). When and why do trees begin to decrease their resource allocation to apical growth? the importance of the reproductive onset. *Oecologia*, 191, 39–49.

Tachiki, Y. & Iwasa, Y. (2010). Both seedling banks and specialist seed predators promote the evolution of synchronized and intermittent reproduction (masting) in trees. *Journal of Ecology*, 98, 1398–1408.

Vacchiano, G., Pesendorfer, M.B., Conedera, M., Gratzer, G., Rossi, L. & Ascoli, D. (2021).

Natural disturbances and masting: from mechanisms to fitness consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200384.

Vergotti, M.J., Fernández-Martínez, M., Kefauver, S.C., Janssens, I.A. & Peñuelas, J. (2019). Weather and trade-offs between growth and reproduction regulate fruit production in european forests. *Agricultural and Forest Meteorology*, 279, 107711.

Visser, M.D., Jongejans, E., van Breugel, M., Zuidema, P.A., Chen, Y.Y., Kassim, A.R. *et al.* (2011). Strict mast fruiting for a tropical dipterocarp tree: a demographic cost–benefit analysis of delayed reproduction and seed predation. *Journal of Ecology*, 99, 1033–1044.

Watson, C.M., Degon, Z., Krogman, W. & Cox, C.L. (2019). Evolutionary and ecological forces underlying ontogenetic loss of decoy coloration. *Biological Journal of the Linnean Society*, 128, 138–148.

Wion, A.P., Pearse, I.S., Rodman, K.C., Veblen, T.T. & Redmond, M.D. (2023). Masting is shaped by tree-level attributes and stand structure, more than climate, in a rocky mountain conifer species. *Forest Ecology and Management*, 531, 120794.

Xi, X., Yang, Y., Tylianakis, J.M., Yang, S., Dong, Y. & Sun, S. (2020). Asymmetric interactions of seed-predation network contribute to rare-species advantage. *Ecology*, 101, 1–10.

Zwolak, R., Celebias, P. & Bogdziewicz, M. (2022). Global patterns in the predator satiation effect of masting: A meta-analysis. *Proceedings of the National Academy of Sciences of the United States of America*, 119, e2105655119.

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Table 1: Results of generalized linear mixed models testing the effects of tree size and conspecific flower abundance on individual-level pollination efficiency and crop size on seed predation rate. These are binomial family models with tree ID (N = 152), site ID (N = 16), and year (N = 43) used as random intercepts. The year was used as a random intercept to allow testing for within-year, among tree differences in reproductive efficiency.

Predictor	β	SE	z	p
Pollination efficiency				
Intercept	-0.899	0.472	-1.91	0.057
Tree size	-0.012	0.003	-3.44	<0.001
Flower abundance	0.079	0.024	3.35	<0.001
Tree size * Flower abundance	0.001	0.0003	5.23	<0.001
Random effects				Variance
Tree ID				0.31
Site ID				1.86
Tree ID				0.92
Pre-dispersal seed predation rate				
Intercept	0.757	0.657	1.51	0.250
Tree size	0.017	0.005	3.49	<0.001
Crop size	-0.472	0.041	-11.48	<0.001
Tree size * Crop size	-0.003	0.001	-6.29	<0.001
Random effects				Variance
Tree ID				0.48
Site ID				3.53
Tree ID				1.92

Table 2: Results of generalized linear mixed models testing the effects of tree size on tree-level seed production and reproductive allocation across years. These were zero-inflated negative binomial and beta family generalized linear mixed models, respectively, both including tree identity and site as random intercepts (N trees = 96, N sites = 11, N years = 43). Only trees observed for at least 10 years were included in that analysis. Seed production rank is based on annual seed production of each individual tree, ranked from the minimum to the maximum.

Predictor	β	SE	z	p
Tree-level annual seed production				
Intercept	0.894	0.257	3.47	<0.001
Seed production rank	0.115	0.004	26.93	<0.001
Tree size	0.015	0.003	5.12	<0.001
Tree size * Seed production rank	0.0003	4.7e-05	-6.99	<0.001
Random effects				Variance
Tree ID				2.45e-08
Site ID				0.15
Reproductive allocation				
Intercept	-6.049	0.198	-30.59	<0.001
Seed production rank	0.115	0.003	39.94	<0.001
Tree size	0.009	0.002	4.48	<0.001
Tree size * Seed production rank	-3.2e-04	3.2e-05	-9.88	<0.001
Random effects				Variance
Tree ID				0.11
Site ID				0.04

Table 3: Summary of proposed ontogenic stages of masting development. Stage 1 follows from past studies, whereas Stage 2 and 3 are from the results presented here. Note that the particular stages are defined by the tree status and behavior, and thus we have not assigned specific dbh of trees to each stage.

Stage	Seeding patterns	Comment
Stage 1: sub-canopy trees	Very frequent, idiosyncratic failures	Growth prioritized over reproduction
Stage 2: canopy trees of intermediate size	Frequent, but synchronized failures; reproductive allocation concentrated in large-seeding years	Dis-economies of scale or anatomical constraints of limited importance
Stage 3: canopy trees of large size	Infrequent failures; reproductive allocation shifts towards low- and intermediate-seeding years	Dis-economies of scale or anatomical constraints substantial; regular reproduction allows bet-hedging

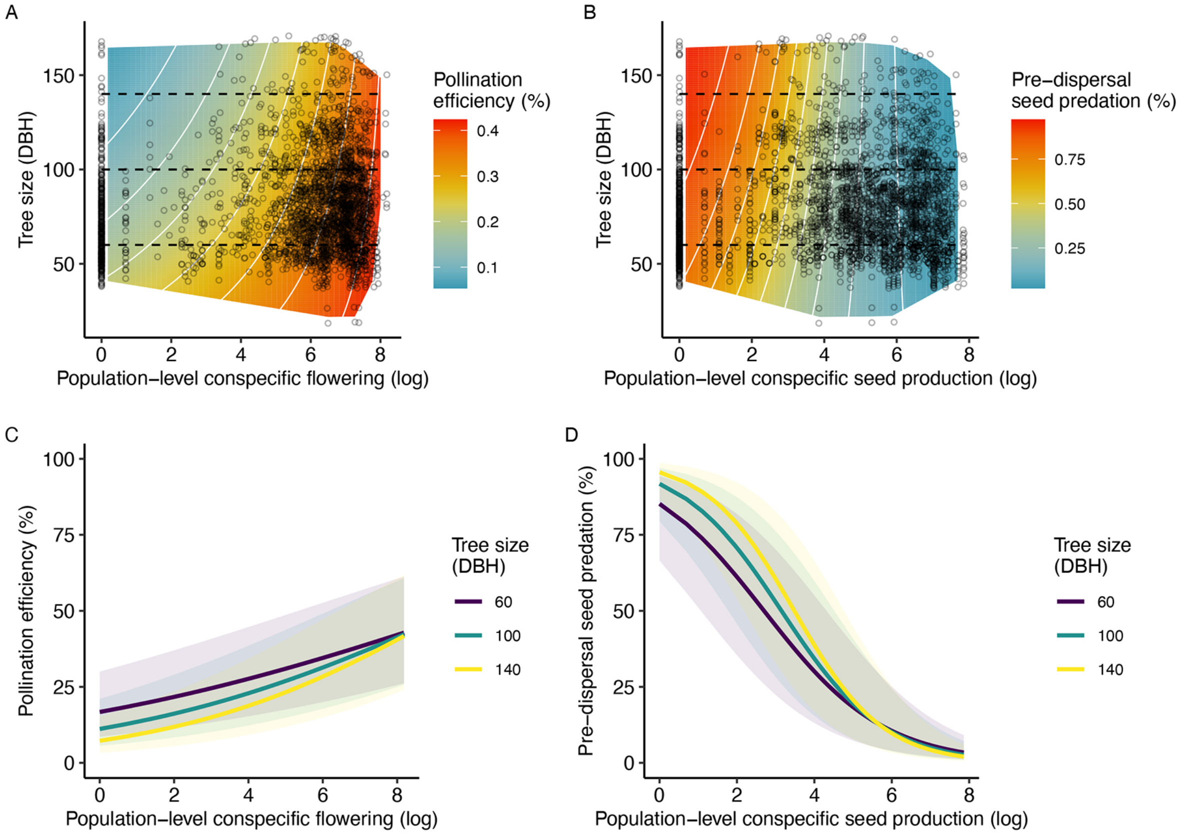

Figure 1: The relationship between (A, C) conspecific flower abundance and individual-level pollination efficiency and (B, D) between crop size and pre-dispersal seed predation rate. Surface plots show estimated (A) pollination efficiency and (B) pre-dispersal seed predation rates across combinations of population-level reproductive effort and tree size, with the convex hulls defined by observations (black points). Black dashed lines at A) and B) indicate the transects plotted in C) and D), i.e., the conditional relationship between pollination efficiency/seed predation and reproductive effort for selected tree sizes. Prediction lines at C) and D) are sections through surfaces highlighted by transects at A) and B). The predictions and corresponding 95% confidence intervals are derived from binomial generalized linear mixed models that included tree identity (N = 152), site (N = 16), and year (N = 43) as random intercepts. Pollination efficiency is the % of total seeds that are filled; seed predation is the % of seeds destroyed by pre-dispersal seed predators. The x-axis on (A, C) is log(e) of overall conspecific flowering (i.e. pollinated plus unpollinated seeds) at the population level in a particular year. The x-axis on (B, D) is log(e) seed production at the population level in a particular year (excludes unpollinated seeds).

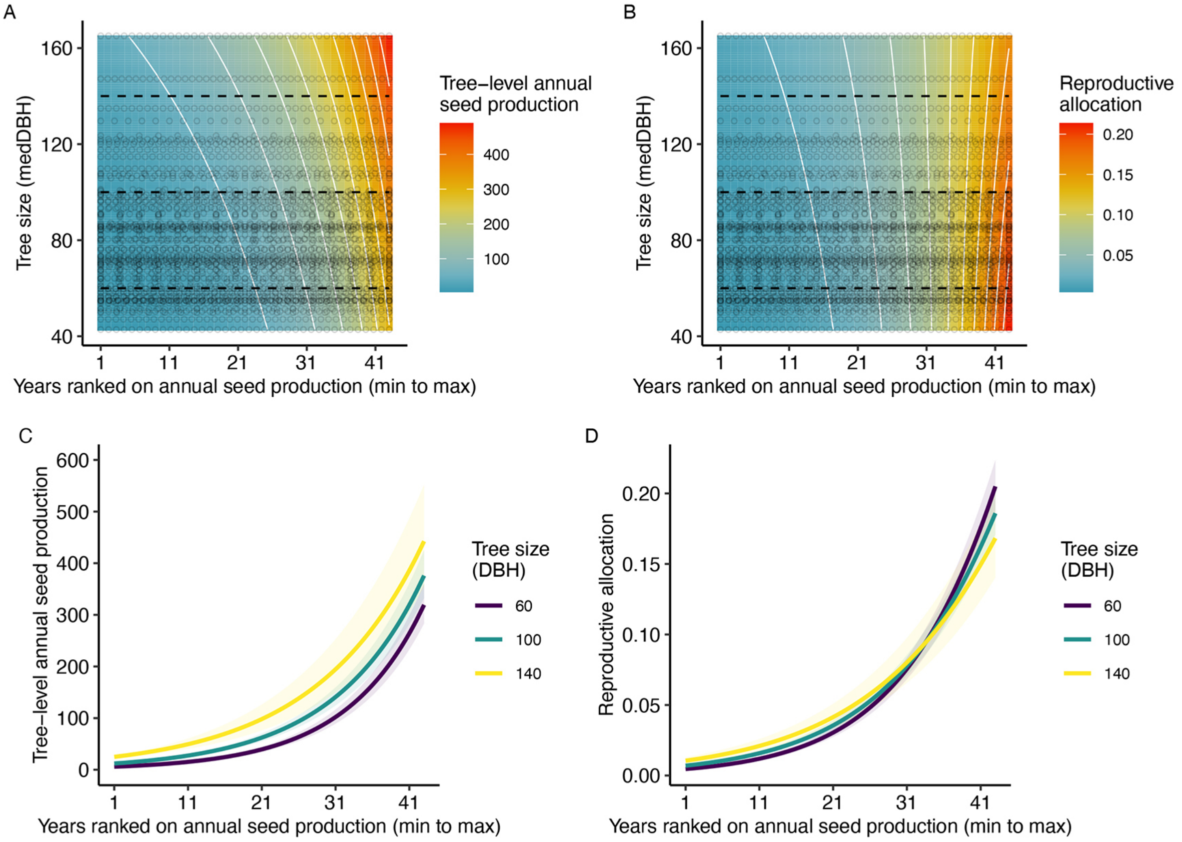

Figure 2: Reproductive allocation across years and tree sizes. Relationship between (A, C) tree-level annual seed production (unpollinated and pollinated) and year rank, (B, D) and relative reproductive allocation (% investment in a particular year based on the sum of all seeds produced by a tree across the whole monitoring period) and year rank. Surface plots show estimated (A) tree-level annual seed production and (B) relative reproductive allocation across combinations of tree size and year rank, with the convex hulls defined by observations (black points). Black dashed lines at A) and B) indicate the transects plotted in C) and D), i.e., the conditional relationship between seed production/relative reproductive allocation and year rank for selected tree sizes. The year rank is based on the annual seed production for each tree, sorted from the minimum to the maximum. The lines are predictions and corresponding 95% confidence intervals derived from (A, C) zero-inflated negative binomial or (B, D) beta family generalized linear mixed models that included tree identity (N = 96) and site (N = 11) as random intercepts. Colors show predictions for trees of different sizes. These models included only trees that were monitored for at least 10 years, thus the smaller sample size compared to Fig. 1.

Supporting Information

Article title: Masting ontogeny: the largest masting benefits accrue to the largest trees

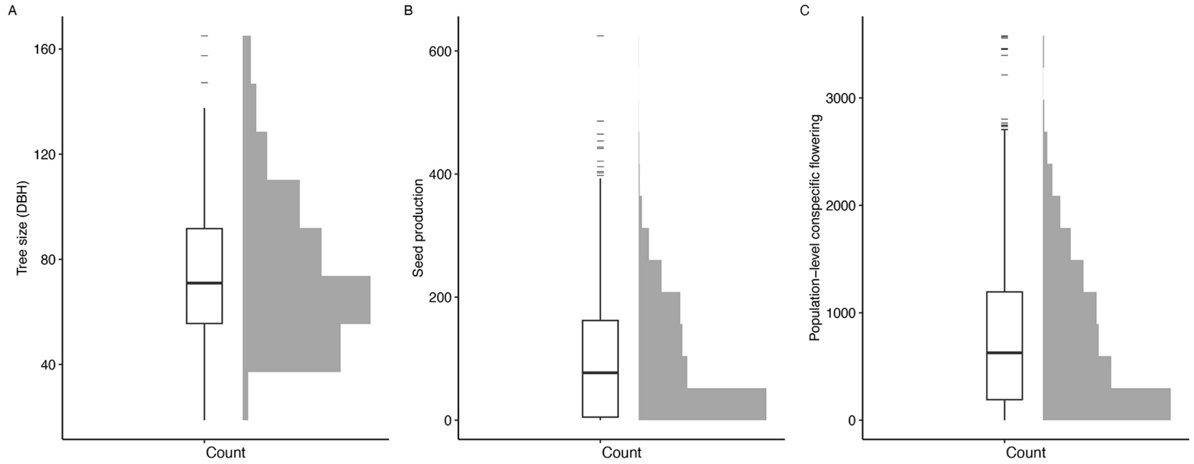

Figure S1: The distributions of median tree size (A), seed production (B) and population-level conspecific flowering (C) data used in this study.

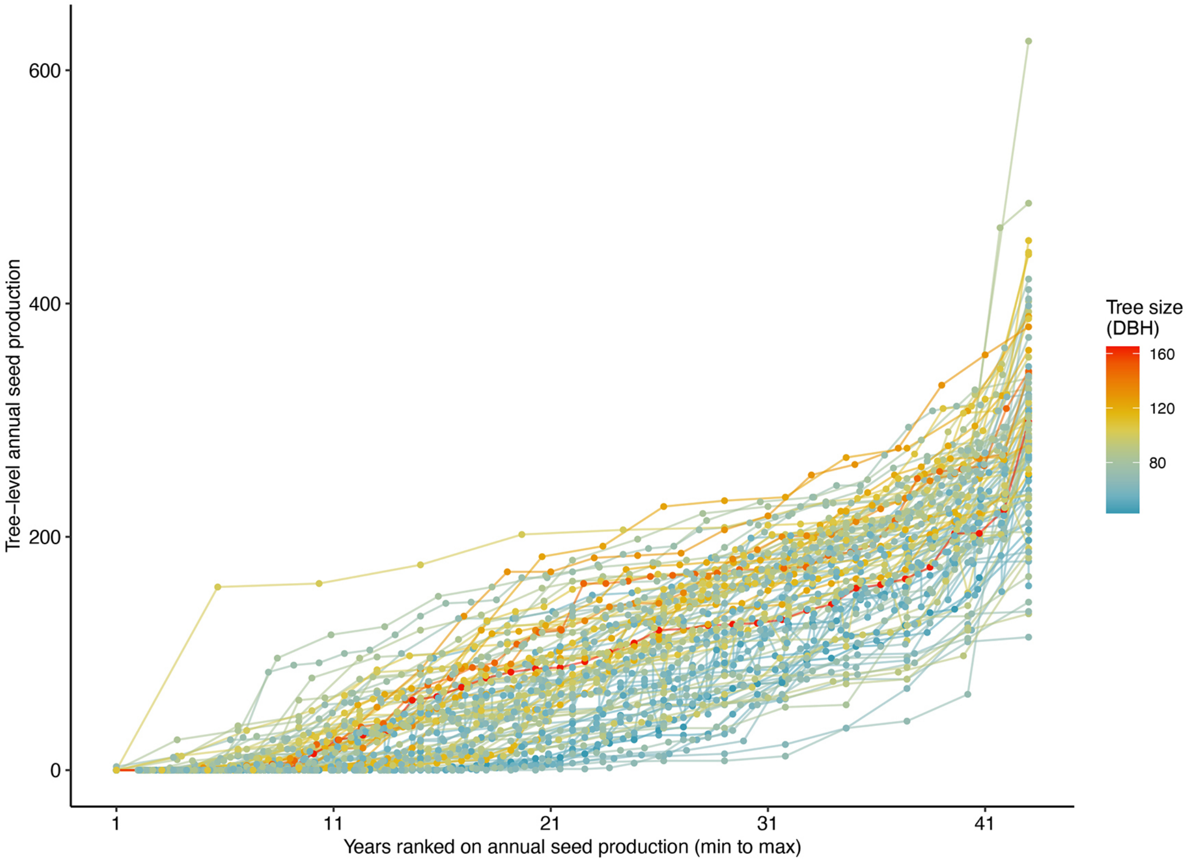

Figure S2: The relationship between tree-level annual seed production and ranked years. Points are observations (per tree per year) linked by the ID of the tree. The color shows the tree's size. For the analysis that examined how reproductive allocation changes across years (e.g. whether larger trees invest a similar proportion of their overall reproductive effort into large-seeding years as smaller trees), we ranked the annual seed production of each tree from the minimum to maximum. Some trees were monitored for less than 43 years (they entered monitoring later or died). Therefore, the ranks were normalized between 1 and 43, to allow comparisons among trees. Thus, for example, rank 43 is the rank for a year when seed production was the largest, irrespective of how many years the tree was monitored. We excluded trees monitored for less than 10 years in that analysis (see Methods).