No seed size–number trade-off in European beech: climate governs investment per seed

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Key words

| *Fagus sylvatica* | mast seeding | size–number trade-off | reproductive allocation | climatic gradients | nitrogen limitation | seed provisioning |

Abstract

- Mast seeding trees can vary seed output by orders of magnitude among years, but it remains unclear whether high seed production reduces per-seed investment, as predicted by fixed-budget allocation models.
- We quantified individual seed production with seed mass in European beech across 2,792 trees and 123 populations spanning the species' range and quantified seed protein and lipid content in 35 populations. Seed mass increased with seed production, with seeds from high-seeding years being 14% heavier than those from low-seeding years, providing no evidence for a seed size–number trade-off and instead supporting variable reproductive allocation. In contrast, protein content decreased by 31% with increasing seed production, whereas lipid content increased (by 14%), indicating that nitrogen becomes constraining at high reproductive output while carbon-based provisioning is maintained. Climate further structured provisioning: seed mass and protein content were the lowest at climatic range margins, being 28% and 32% lower, respectively, than at the center of the climatic range.
- European beech can increase seed output without reducing per-seed biomass, but that nitrogen limitation and climatic constraints may strengthen regeneration bottlenecks at both trailing and leading margins, especially as climate warming intensifies.

Introduction

The existence of trade-offs is a fundamental feature of ecological strategies (Stearns, 1989). Given finite resources, organisms must allocate them among growth, storage, and reproduction, and even within these domains, resources may be divided differentially (Genet *et al.*, 2009; Thomas, 2011; Hartmann *et al.*, 2020; Cope *et al.*, 2021). For plants, one important allocation problem lies in the balance between producing many small seeds or fewer large ones, the seed size–number trade-off (Smith & Fretwell, 1974; Muller-Landau, 2010). Life-history theory predicts that for a given reproductive effort, producing larger seeds necessarily reduces their number, generating a negative relationship between seed number and seed mass, as described by Smith-Fretwell model (Smith & Fretwell, 1974). Across species the trade-off is clearly observed, and small-seeded species clearly produce more seeds (Leishman & Leishman, 2001; Henery & Westoby, 2001; Muller-Landau *et al.*, 2008; Qiu *et al.*, 2022). Within species, however, empirical results are mixed (Guo *et al.*, 2010). This question is particularly relevant for mast-seeding trees, where seed output can vary by orders of magnitude among years (Bogdziewicz *et al.*, 2025), and the ecological consequences of such fluctuations depend not only on seed number but also on how seed size is maintained or altered across years. For example, a 30% decrease in seed mass in high-seeding years in the subtropical *Castanopsis fargesii* translated into a fivefold decrease in germination rate, canceling the benefits of masting such as reduced seed predation (Huang *et al.*, 2021).

Mast-seeding species pose an interesting case for the seed number–seed size trade-off because their reproductive effort varies enormously among years. For example, a single European beech (*Fagus sylvatica*) or white spruce (*Picea glauca*) individual may produce 250,000+ seeds in a high-seeding year, while a tussock of *Chionochloa* can produce >15,000 flowers, yet in failure years reproductive investment approaches zero (Hacket-Pain *et al.*, 2022; Bogdziewicz *et al.*, 2025). This fluctuation is interpreted as interannually variable reproductive allocation (Bogdziewicz *et al.*, 2024), with high-seeding years involving a larger fraction of resources devoted to reproduction, often at the expense of stored reserves, growth, or defense (Han *et al.*, 2011; Redmond *et al.*, 2019; Gonzalez *et al.*, 2023; Hacket-Pain *et al.*, 2025). If reproductive allocation indeed varies strongly across years, then increases in seed number do not need to come at the expense of seed size. Under the allocation theory, when the resource budget is limited, seed number is expected to fluctuate, whereas seed size is constrained by stabilizing selection on offspring survival (Smith & Fretwell, 1974; Sadras, 2007).

Importantly, in mast-seeding trees, initiation of reproductive allocation starts long before the optimal conditions for seed development are known. Floral initiation typically occurs in the year preceding seed maturation (Journé *et al.*, 2025; Hirsch *et al.*, 2025), and thus before the resource pool available for seed filling is realized. As a result, even when reproductive allocation increases in mast years, subsequent environmental constraints during seed development may limit the extent to which all initiated seeds can be fully provisioned (Espelta *et al.*, 2008; Pearse *et al.*, 2015). Under such circumstances, rather than aborting excess reproductive structures, trees may respond by reducing per-seed investment, allowing a larger fraction of initiated seeds to mature at smaller size. Indeed, while empirical tests in mast-seeding plants remain scarce, available evidence is partially consistent with this expectation. Seed mass declined with increasing seed production in *Pinus armandii* (Wang & Ives, 2017), *Castanopsis fargesii* (Huang *et al.*, 2021), and in high-crop individuals of *Quercus ilex* (Bonal *et al.*, 2007). In contrast, seed size did not decline with larger crops in *Quercus lobata* (Koenig *et al.*, 2009a). Taken together, the available evidence suggests that increases in seed number can coincide with reduced per-seed investment, potentially diminishing the ecological benefits typically attributed to mast seeding.

Beyond variation in seed mass, the orders-of-magnitude variation in seed number characteristic of mast seeding may also alter the storage compounds (e.g. protein and lipid content) of individual seeds. Increased plant biomass production is often associated with reduced concentrations of macro- and micronutrients (Kaspari & Welti, 2024). In mast-seeding trees, however, resource-budget models suggest that sufficient accumulation of reserves crucial for reproduction, particularly nitrogen, is required to initiate mass-flowering years (Miyazaki *et al.*, 2014; Sala *et al.*, 2012; Han & Kabeya, 2017). Such storage could buffer seed nutrient composition against large increases in reproductive output, maintaining protein content even when the biomass of produced seeds increases sharply. However, as for seed mass, this buffering is contingent on the temporal decoupling between reproductive commitment and seed development. Because flower initiation precedes seed maturation by a year (Journé *et al.*, 2025; Hirsch *et al.*, 2025), plants may commit to more seeds than can be fully provisioned if conditions during seed development are unfavorable, resulting in reduced per-seed investment. Which components of seed provisioning are reduced under such conditions depends on which resources constrain seed development. In contrast to nitrogenrich compounds such as proteins, lipid provisioning is less likely to be constrained, particularly if seed mass is maintained, as carbon supply is largely branch-autonomous and carbon limitation of reproduction is unlikely in temperate trees (Hoch, 2005; Han & Kabeya, 2017).

Beyond resource constraints associated with variable seed number, the environment in which seeds develop also shapes how much a tree invests per seed. The Smith–Fretwell model implies that environmental conditions can shift the optimal seed size, leading to adaptive differentiation among populations (Smith & Fretwell, 1974). For example, *Prunus virginiana* shows habitat-specific optima: plants in riparian sites produced many smaller seeds, where frugivore-mediated dispersal favored high seed number, whereas on dry slopes plants produced fewer but larger seeds, where seedling establishment was the limiting stage (Parciak, 2002). In contrast, broad-scale geographic patterns in seed mass are more often interpreted as responses to environmental constraints than as local adaptation. Across and within species, seed mass commonly declines toward colder climates, most frequently along latitudinal gradients (Moles *et al.*, 2007; Liu *et al.*, 2013; Frenne *et al.*, 2013). Because latitude covaries strongly with temperature, this pattern is generally attributed to thermal limitation. In a meta-analysis, De Frenne et al. (2013) showed that intraspecific seed mass increases with temperature, consistent with longer growing seasons, prolonged seed development, and reduced frost risk. In long-lived masting trees, these climatic effects on seed mass have rarely been evaluated together with variation in seed number, despite the potential for large fluctuations in fecundity to directly influence per-seed investment.

Here, we test whether European beech expresses a seed size–number trade-off, and how seed provisioning varies across climatic gradients. We quantified seed production and seed mass in 123 populations across the species' range and assessed protein and lipid composition in 35 of these populations. If high-seeding years reflect increased reproductive allocation rather than reallocation within a fixed resource budget, seed mass should be maintained even as seed output increases. Conversely, declines in seed mass in high-seeding years would indicate short-term constraints on per-seed provisioning, consistent with temporal decoupling between floral initiation and seed development. Such declines are expected to carry fitness costs, as heavier European beech seeds germinate more successfully and produce larger seedlings (Pawłowski *et al.*, 2024). Across climatic gradients, we expected seed mass, protein, and lipid content to reflect constraints on seed development, with heavier, better-provisioned seeds in regions with longer growing seasons and favorable thermal conditions, and reduced mass and nutrient concentrations toward climatic margins of the species' range, where growing seasons are shorter, temperatures are suboptimal, or heat and drought limit seed filling. With respect to protein and lipid content, we predicted contrasting responses of proteins and lipids. Protein content was expected to be maintained, or to decline in high-seeding years and toward climatic margins if nitrogen storage fails to buffer reproductive investment. In contrast, lipid concentrations were expected to show little variation with either seed number or climate, given that reproduction in temperate trees is unlikely to be carbon-limited.

Methods

Study species European beech is an economically and ecologically important forest-forming tree, distributed from the mountains of the Mediterranean to southern Scandinavia and eastwards to Poland and the Carpathians (Packham *et al.*, 2012). It is a wind-pollinated, masting species. Masting benefits European beech by enhancing pollination efficiency and reducing seed predation (Nilsson & Wästljung, 1987; Bogdziewicz *et al.*, 2020). Mast years are also characterized by a shift in allocation from radial growth towards reproduction (Hacket-Pain *et al.*, 2025). Seeds are dispersed mainly by scatter-hoarding animals such as rodents and jays (Zwolak *et al.*, 2016; Wróbel *et al.*, 2022). Storage materials of beech seeds include mainly fat and proteins, constituting up to 40 and 20% of dry weight, respectively (Prasad & Gülz, 1989; Kalemba *et al.*, 2019). Seeds lack long-term dormancy, germinate the following spring, and seed size and provisioning are crucial for seedling survival under shade and drought stress, with larger seeds translating into more vigorous seedlings (Pawłowski *et al.*, 2024). Among seed storage materials, proteins, the main nitrogen source are crucial for early seedling establishment (Kalemba *et al.*, 2019). Embryonic axes completely deplete proteins while elongating to a length of 15 mm, and seedlings with 20 mm and longer embryonic axes deplete proteins from cotyledon (Kalemba *et al.*, 2019).

Seed production and mass data We sampled seeds in 2023 and 2024, from 2,792 individual co-dominant to dominant trees, at 123 sites spanning the natural distribution of European beech across Europe (Fig. 1). At 30 of these sites, no viable seeds were recorded during the study, resulting in a final sample of 1,906 trees at 93 sites. Most sites included 20–30 dominant or co-dominant trees, while two plots, one in Poland and another two in the UK, contributed larger samples of 100 trees each. For each tree, we measured diameter breast height (DBH) and assigned a shading class on a five-level ordinal scale (1 = fully shaded, 5 = fully exposed) to describe canopy light exposure (Clark *et al.*, 2021).

Seeds were collected from the forest floor beneath the crown of each tree shortly after seedfall using a standardized 3.5-minute search (Foest *et al.*, 2025). The ground below each tree was searched for seeds for 3.5 min and seeds were later classified as sound, empty with formed pericarps (not pollinated), or damaged by Cydia sp. moth. Only filled (pollinated) seeds that were not infested/predated were retained for analysis presented in this study. All viable seeds from each tree were weighed individually to the nearest 0.001 g after air-drying at room temperature for four weeks. We chose air-drying rather than oven-drying in order to preserve samples for subsequent analyses of proteins and lipids. To verify that this approach did not bias seed mass estimates, we oven-dried a subset of seeds for 24 hours at 80 °C and compared mass before and after drying. Seed mass decreased by 7% on average after oven-drying, and this percentage loss was consistent across sites and years (SD of the % decline = 0.0055).

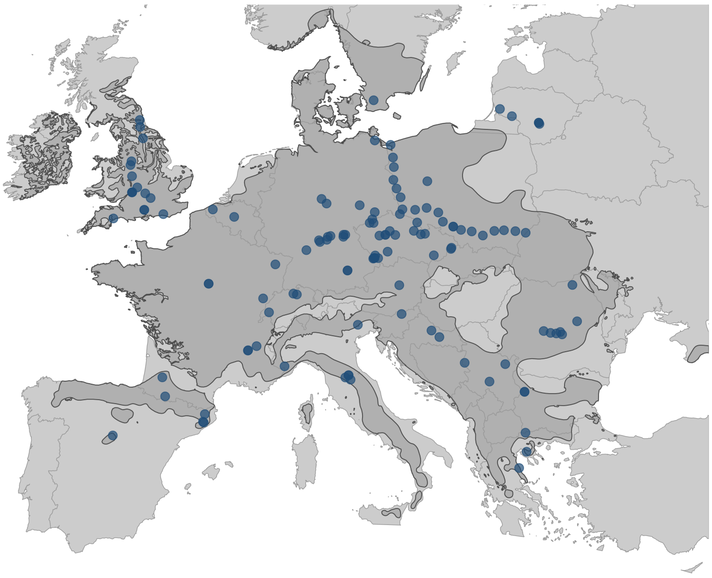

Figure 1: Map of the 123 study sites where European beech seed production was measured in 2023–2024. Each point represents one study site (N trees = 2,792). The darker gray area indicates the natural distribution of European beech. The climate space covered by our sample is shown in Fig. S1.

Climate data and growing season metrics Daily weather data for each site were obtained from the corresponding 0.1° grid cell of the E-OBS dataset (Cornes *et al.*, 2018). To determine growing season length, we first averaged daily minimum temperature across all years from 1950 to 2024 to obtain long-term daily means for each site (Körner & Basler, 2010). The start and end of the growing season were then defined as the first and last day of the year when long-term daily means exceed 5 °C and growing-season length was calculated as the number of days between them (Körner & Hiltbrunner, 2018; Körner, 2021). The 5 °C threshold is based on Körner (2021) and follows from the cessation of cambial activity below 5 °C (Cabon *et al.*, 2020). Within the site-specific growing season length, we calculated mean-growing season temperature and mean-growing season precipitation for our observation period using weather data from 1950 to 2024. We used long-term climate data to characterize site-level climatic conditions rather than interannual variation during the sampling years.

Seed nutrient content Protein and lipid content were determined for 4830 seeds collected in 2023 from a subset of randomly selected 35 sites, where at least 10 viable seeds were available for protein and lipid content analyses.

Ten whole seeds per tree (N = 483) were extracted from the pericarp and seed coat and ground in liquid nitrogen. Samples of 100 mg were used for protein determination, and samples of 200 mg were used for lipid determination.

To extract proteins, samples were extracted in 0.5 mL of 60 mM Tris–HCl buffer (pH 6.8) containing 10% (v/v) glycerol and 2% (w/v) SDS, following the protocol of Stone and Gifford (Stone & Gifford, 1997). The homogenate was centrifuged at 18,000 × *g* for 20 min. Protein content was determined using the 2-D Quant Kit, with bovine serum albumin used as a standard.

Lipids were extracted using chloroform:methanol [2:1 (v/v)] supplemented with 0.05% butylated hydroxytoluene (BHT), according to Freeman *et al.* 1966. The homogenate was mixed with an aqueous phase containing 1 M potassium chloride and left overnight at 4 °C to allow phase separation. The lower phase (chloroform containing lipids) was collected, dried by vacuum distillation, and the resulting oil was weighed.

Analysis To examine the relationship between individual seed mass, seed production, and climate, we fitted a generalized linear mixed model (GLMM) with seed mass as the response variable, while tree ID nested with site ID were included as random intercepts. This allowed the seed size–number relationship to be estimated from within-tree variation across years, accounting for differences in resource acquisition among individuals (van Noordwijk & de Jong, 1986; Pease & Bull, 1988; Reznick *et al.*, 2000). The model was fitted with a Gamma error distribution and a log link, as seed mass is a continuous, positive variable. Fixed effects included annual, tree-level seed production, shading class, DBH and climatic predictors, i.e., the long-term averages of growing season length, mean growing-season temperature, and mean-growing season precipitation. In addition, we included interaction terms between growing season length and growing season climate (temperature and precipitation). All predictors were standardized to a zero mean and unit variance prior to analysis to facilitate comparison of effect sizes.

To analyze variation in seed protein and lipid content, we fitted two additional GLMMs with seed protein content or seed lipid content (both expressed as percentage of dry mass) as response variables. The fixed-effects structure was the same as in the seed-mass model. Because protein and lipid cont t data were available for a single year only, year was not included as a random effect. These models were fitted using a Beta error distribution with a logit link.

Collinearity among predictors was assessed using variance inflation factors (VIF) calculated with the `car` package, and all predictors showed low collinearity (VIF < 1.6) (Fox *et al.*, 2024). Mean growing season precipitation and its interaction with growing-season length had no significant effect in the models, and were excluded from further analyses. All analyses were conducted in R version 4.2.3 (R Core Team, 2023), and the models were fitted using the glmmTMB package version 1.1.7 (Brooks *et al.*, 2017).

Results

Seed number relationship with seed mass, protein, and lipid content

Seed mass varied substantially across the 52,861 seeds measured from 1,906 trees, ranging from 0.012 g to 0.709 g. Seed production per tree had a positive relationship with seed mass (Table 1, Fig. 2). The estimated seed mass for low seed production (10 seeds per tree $^{-1}$ yr^{-1}, based on a standardized 3.5-minute ground collection) was 0.23 g, while it increased to 0.26 g (~14%) for high seed production (200 seeds per tree^{-1} yr^{-1} per ground collection). Lipid content also increased with higher seed production. For instance, the estimated lipid content for low seed production (10 seeds tree^{-1} yr^{-1}) was 34.8% and it increased to 39.7% (i.e. by 14%) for high seed production (200 seeds tree^{-1} yr^{-1}). In contrast, the protein content declined with increasing seed production (Table 1, Fig. 2). For example, the estimated proportion of protein in seed dry mass for low seed production (10 seeds tree^{-1} yr^{-1}) was 0.24, while it decreased to 0.16 (by ~31%) for high seed production (200 seeds tree^{-1} yr^{-1}). Tree size (DBH) and shading class had a weak, but significant negative effect on lipid content, but not on seed mass or protein content. For example, the estimated lipid content for small trees (32 cm DBH) was 38.4%, decreasing by 4.9% to 33.5% in large trees (75 cm DBH) (Table 1). Tree size categories correspond to the 10th and 90th percentiles of the observed diameter at breast hight (DBH) distribution (Fig. S2.

Table 1: Models summary. Predictors were z-standardized prior to the analysis. Generalized linear mixed models were fitted with a log link (Gamma for seed mass; Beta for protein and lipid content). Significant effects (p <0.05) are shown in bold. GS stands for growing season. Coefficients are shown on the link scale; standard errors in parentheses. Models included tree-ID nested within site-ID random intercepts. N_{tree} = 1,906, N_{site} = 93.

Predictor	Model A: Seed mass		Model B: Protein %		Model C: Lipid %	
	Estimate (SE)	*p*	Estimate (SE)	*p*	Estimate (SE)	*p*
Intercept	−1.413 (0.019)	< 0.001	1.285 (0.038)	< 0.001	−0.562 (0.032)	< 0.001
Seed number	**0.036** (**0.003**)	< 0.001	**−0.052** (**0.019**)	0.007	**0.079** (**0.029**)	0.006
Shading class	0.001 (0.004)	0.803	0.011 (0.015)	0.498	**−0.049** (**0.022**)	0.027
DBH	0.003 (0.004)	0.549	−0.005 (0.018)	0.785	**−0.060** (**0.026**)	0.021
Temperature (GS)	−0.018 (0.021)	0.405	**−0.119** (**0.0469**)	0.011	−0.034 (0.040)	0.402
Growing season length	0.027 (0.023)	0.239	0.010 (0.049)	0.839	−0.005 (0.042)	0.905
Precipitation (GS)	−0.012 (0.015)	0.438	0.044 (0.031)	0.147	0.021 (0.029)	0.460
Temp (GS) × GS length	**−0.025** (**0.011**)	0.026	**−0.104** (**0.0323**)	< 0.001	−0.026 (0.028)	0.368

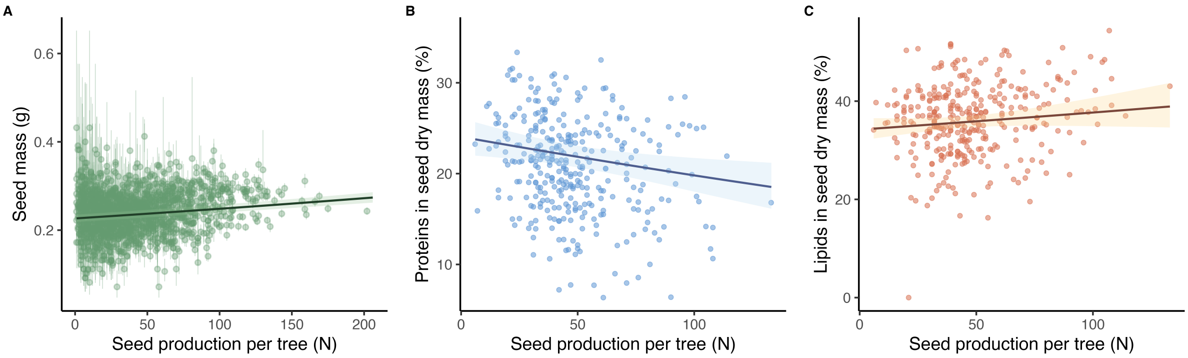

Figure 2: Seed mass and lipid content increase, while protein content decreases with increasing seed production. (A) Relationship between seed production per tree and individual seed mass. Seed production represents the number of seeds collected per tree during a standardized 3.5-minute ground search (Foest *et al.*, 2025). (B) Relationship between annual seed production per tree and seed protein content. (C) Relationship between annual seed production per tree and seed lipid content. Points represent tree-level mean seed mass with 95% confidence intervals (A) or tree-level measurements of protein and lipid content (B, C), and solid lines show the generalized linear mixed-model predictions with 95% confidence intervals. Models included tree ID and site ID as random intercepts (seed mass: N_{tree} = 1,906, N_{site} = 93; protein and lipid content: N_{tree} = 419, N_{site} = 35).

Climate relationship with seed mass, protein, and lipid content

Growing season length and mean annual temperature jointly influenced seed mass (Table 1). In consequence, seed mass was estimated to be lowest (~0.18-0.20 g) at the sampled climatic range margins, i.e., sites characterized by short growing seasons (less than 150 days) and low growing season temperatures (less than 14 °C), as well as at sites with very long growing seasons (above 210 days) and high temperatures (above 17 °C) (Fig. 3A). Seed mass peaked (~0.25 g) at sites characterized by intermediate conditions, i.e., either long growing seasons (180-210 days) and mild temperatures (~14 °C), or shorter growing seasons (150-160 days) and warm temperatures (16–17 °C) (Fig. 3A).

These joint climatic effects translated into a clear spatial structure across the European range (Fig. 4). Predicted seed mass was high (~0.24 g) across large parts of western and central Europe, with particularly high values (~0.26 g) in the British Isles and along Atlantic-influenced regions of western Europe, where mild temperatures coincide with extended but not extreme growing seasons. In contrast, lower seed mass (~0.20-0.22 g) was predicted toward northern (Scandinavia) and high-elevation margins characterized by short and cool growing seasons, as well as toward southern and southeastern margins (Balkans) where very long growing seasons coincide with high temperatures.

Growing season length and growing season temperature jointly influenced protein proportion in seed dry mass (Table 1). Protein proportion was highest (~0.24-0.25 %) at sites characterized by long growing seasons (180-210 days) and intermediate growing season temperatures (approximately 13-14 °C) (Fig. 3B). In contrast, protein proportion declined toward warmer conditions, reaching lowest values (~0.17-0.18) at sites with high growing season temperatures (above 16-17 °C) and long growing season length (Fig. 3B). Generally, the effects of temperature and growing seasons length on protein content of seeds largely mirrored the effects of climate on seed mass.

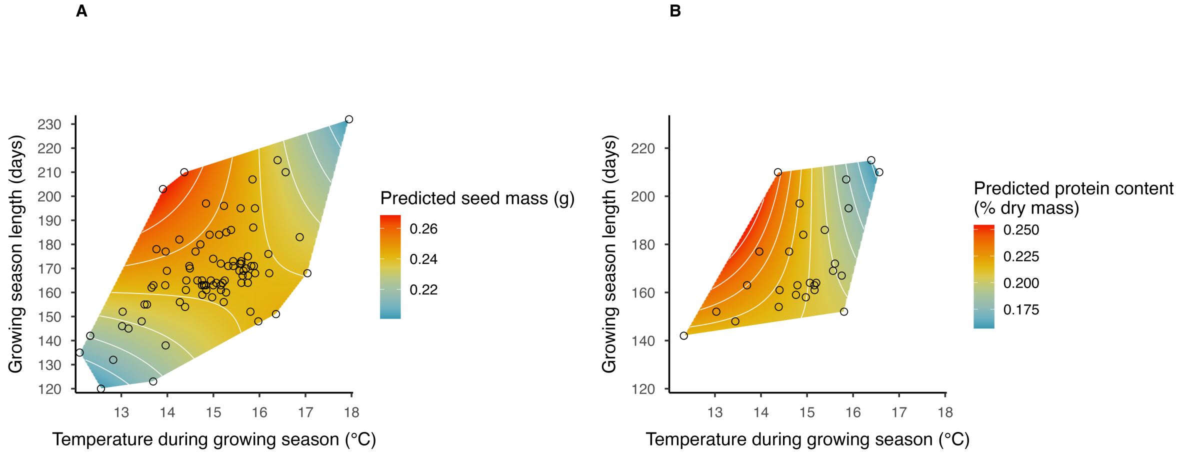

Figure 3: **Seed mass peaks under intermediate growing-season conditions, whereas seed protein proportion decreases toward warmer and longer growing seasons.** The color surface represents model-estimated A) seed mass, and B) % protein in seed dry mass, with warmer colors indicating higher values. Black circles show observed site-level combinations of mean growing-season temperature and growing-season length, which define the convex hull of the data. Note that the axes range in panel B were adjusted to match that in panel A, as the range of values in panel B was narrower;the climate conditions represent the long-term norms, not annual variation.

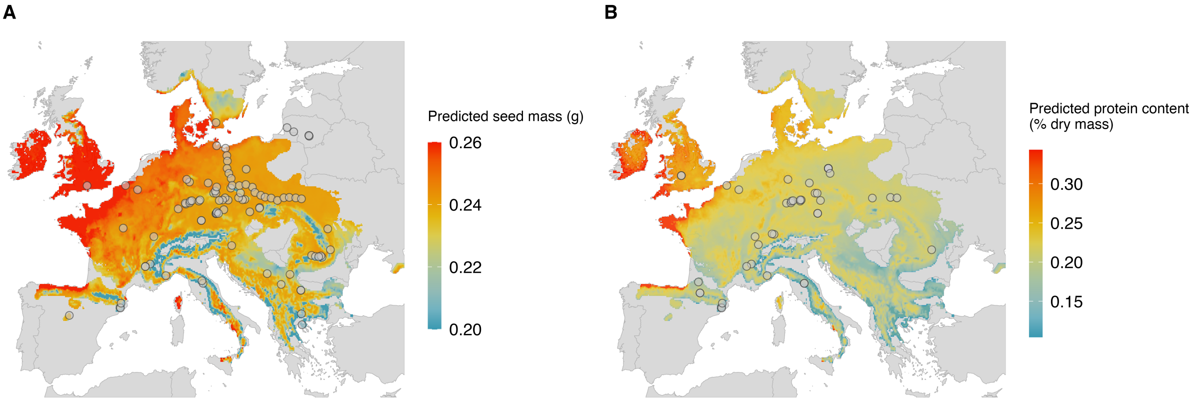

Figure 4: **Seed mass and seed protein content peak in Atlantic and Atlantic-temperate regions of western Europe**. Predicted individual seed mass (g) (panel A) and % protein in seed dry mass (panel B) values are shown across the European distribution of European beech based on the fitted GLMM. Predictions were generated for each grid cell within the beech distribution using site-level mean growing-season temperature and mean growing-season length. Other co-variates were held constant at their reference values, with total seed production and DBH fixed at its median value across sites and shading class fixed at its most frequent level. Study sites at which seeds mass (panel A, N = 93 sites) and protein content (B, N = 35 sites) were measured are shown as gray points. Color scale indicates predicted seed mass or protein content, with warmer colors representing higher values.

Discussion

Our results show that European beech can increase seed output without reducing seed mass, while revealing nitrogen availability and climate as key constraints on seed provisioning. Contrary to predictions of fixed-budget allocation models (Smith & Fretwell, 1974), individual seed mass increased with higher seed output, indicating that high-seeding years involve an increase in reproductive allocation rather than redistribution within a constant resource pool allocated to reproduction. This provides rare, range-wide empirical support for a long-standing assumption that has been difficult to quantify in long-lived trees (Kelly, 1994; Bogdziewicz *et al.*, 2025). In contrast to seed mass, increased seed production was associated with reduced protein content but higher lipid concentrations, implying that carbon supply for seed filling is not limiting, whereas nitrogen becomes constraining at high reproductive output. This is consistent with the view that nitrogen is a key resource limiting reproduction in temperate trees (Pearse *et al.*, 2016; Abe *et al.*, 2016; Han & Kabeya, 2017). Finally, seed mass and protein content declined toward the climatic margins of the species' range, a pattern with asymmetric demographic consequences: reduced provisioning is expected to exacerbate regeneration failure at the trailing edge while constraining establishment and spread at the leading edge.

Our results demonstrate that European beech does not exhibit a seed size–number trade-off. Allocation models predict that, under a fixed reproductive budget, increasing seed number must come at the cost of reduced seed size (Smith & Fretwell, 1974). Instead, we observed a positive association between seed output and seed mass, consistent with a scenario in which reproductive allocation increases in high-seeding years. Similar patterns have been reported in other mast-fruiting trees, including *Quercus lobata*, where seed size was also maintained across large variation in crop size (Koenig *et al.*, 2009a). In contrast, declining seed mass with increasing seed production has been documented in several other masting species (e.g. Bonal *et al.*, 2007; Wang & Ives, 2017; Huang *et al.*, 2021), indicating that mast seeding does not universally relax size–number trade-offs. This heterogeneity suggests that species differ in the extent to which reproductive investment can be increased during high-seeding years. Although the small number of available studies precludes generalization, plausible drivers include differences in nutrient storage capacity, particularly nitrogen (Miyazaki *et al.*, 2014; Han *et al.*, 2025), the degree of temporal decoupling between floral initiation and seed development (Hirsch *et al.*, 2025), and life-history strategies governing abortion versus provisioning of initiated seeds (Pearse *et al.*, 2016). In addition, masting species differ in how flexibly resources can be diverted away from other functions, such as growth or defense, during high-reproductive years (Barczyk *et al.*, 2025; Hirsch *et al.*, 2026). Comparative analyses across masting species will be required to determine which of these mechanisms explains why some species maintain seed size under high reproductive output while others do not.

While variable reproductive allocation explains why seed mass is maintained in high-seeding years, our results also show spatial structuring of seed provisioning across the species' climatic range. Seed mass and protein content increased with growing-season temperature and growing-season length, but only up to intermediate values of both, resulting in a climatic optimum characterized by moderately warm summers and long growing seasons. This is consistent with intraspecific syntheses showing larger seeds in warmer environments, where longer seasons and reduced frost risk allow more complete seed filling (Frenne *et al.*, 2013), but it also indicates that high temperatures constrain provisioning.Similar responses have been reported in temperate and Mediterranean oaks, including *Q. robur*, *Q. ilex* and *Q.macrocarpa*, in which seed mass increases toward warmer regions (Koenig *et al.*, 2009b; Bogdziewicz *et al.*, 2019; Moreira *et al.*, 2021). Variation in seed size of this magnitude (30% in our study across climates) can have substantial fitness consequences: experimental and comparative studies show that a 5-11% difference in seed mass is associated with 0.5-2% increase in germination success, establishment, or early survival, particularly under stressful conditions (Gómez, 2004). Importantly, seeds produced at climatic margins in our study were both smaller and poorer in protein, a combination that is likely to further reduce germination capacity and early seedling performance, as nitrogen content directly constrains enzymatic activity during germination and early growth (Milberg & Lamont, 1997; Leishman & Leishman, 2001; Muffler *et al.*, 2021; Pawłowski *et al.*, 2024). Beyond direct effects on provisioning, seed size also mediates biotic interactions (Lichti *et al.*, 2017; Wróbel *et al.*, 2022). Smaller seeds are less likely to be cached and buried by small mammals (Lichti *et al.*, 2017), a process that enhances germination and seedling establishment (Zwolak *et al.*, 2016). Thus, the climate-driven reductions in seed mass and nitrogen content could potentially lower effective dispersal and establishment at range margins, possibly tightening regeneration bottlenecks. Whether such variation translates into demographic constraints at the trailing edge or limits northward advance remains to be tested experimentally, as other factors such as competition, local adaptation, and biotic interactions also vary across the range.

Protein content declined as seed output increased, whereas lipid content and seed mass increased. This pattern supports the view that carbon rarely limits seed filling in temperate trees, whereas nitrogen can (Hoch, 2005; Pearse *et al.*, 2016; Han & Kabeya, 2017). Experimental source–sink manipulations show that fruiting branchlets in temperate trees can sustain fruit development without importing carbon from the rest of the tree, consistent with branch-level carbon autonomy (Hoch, 2005). Stable carbon supply during reproduction is further supported by isotope and seasonal non-structural carbohydrates evidence, indicating that fruit production in masting broadleaves does not rely on mobilizing stored carbon reserves (Hoch *et al.*, 2013). By contrast, multiple studies point to stronger constraints on mineral nutrients: in a masting pine, large crop production caused measurable depletion of stored N and P, demonstrating that reproduction can deplete nutrient pools over timescales longer than the seed-filling season (Sala *et al.*, 2012). In *Fagus crenata*, masting is linked to large N investment into reproductive organs and to N-limitation for subsequent reproductive commitment, such as reduced N status of winter buds and constraints on flower primordia formation (Han *et al.*, 2008; Miyazaki *et al.*, 2014; Abe *et al.*, 2016). Experimental fruit removal in *Quercus ilex* similarly prevented seasonal depletion of leaf N, while starch dynamics did not indicate carbohydrate depletion in fruiting trees, again separating nutrient limitation from carbon limitation (Roncé *et al.*, 2020, 2023). In this context, our observation that protein (N-rich) provisioning declines with high fecundity, while lipid provisioning (largely carbon-based) is maintained, is consistent with a scenario in which beech can sustain carbon supply for seed biomass and lipid deposition, but progressively dilutes N allocation per seed as reproductive demand increases.

Several aspects of our study design should be considered when interpreting these results. Our inference is based on extensive spatial replication rather than long time series: seed production and seed mass were measured over two years, and seed nutrient composition in a single year. While this limits direct inference about temporal dynamics within individual populations, the broad geographic coverage encompassed the full range of interannual variation in seed production documented in a 45-year beech monitoring study using comparable count methods (Bogdziewicz *et al.*, 2020; Hacket-Pain *et al.*, 2025). This indicates that the variation required to detect seed size–number relationships and provisioning patterns was captured at the species level. Furthermore, spatial variation in seed protein content may also reflect long-term differences in nitrogen availability across Europe. Atmospheric nitrogen deposition is highly heterogeneous, with consistently higher inputs in Western and parts of Central Europe than in Northern and Eastern regions, broadly overlapping with the geographic patterns of seed mass and protein content observed here (Sanczuk *et al.*, 2024). Although seed filling in European beech is primarily governed by internal nitrogen storage and remobilization and is largely decoupled from short-term soil nitrogen dynamics (Han & Kabeya, 2017), sustained nitrogen inputs may influence the size of internal nitrogen pools over longer timescales. Testing this hypothesis would require integrating spatially explicit nitrogen deposition data with multi-year measurements of seed provisioning. Moreover, while our spatial coverage spanned most of the European range of beech, some regions were underrepresented, including the southernmost parts of the species' range in southern Italy and Sicily, where climatic stress may be strongest. These limitations highlight the need for multi-year studies combining seed production, provisioning, and experimental assessments of seedling performance to fully resolve the demographic consequences of variation in seed mass and nutrient composition across space and time. Finally, the interpretation of geographic variation in seed provisioning as direct evidence for range-limiting processes requires caution. Within a site, seed mass is positively associated with germination success and seedling performance (Muffler *et al.*, 2021; Pawłowski *et al.*, 2024). Among sites, however, seed size covaries with multiple environmental factors, making it difficult to infer fitness consequences from spatial patterns alone. Thus, while our results reveal geographic variation in seed provisioning, the demographic consequences of this variation remain to be tested directly.

In summary, our study indicate that the large interannual variation in seed production in European beech is accommodated through changes in reproductive allocation rather than through a trade-off between seed number and seed mass. By increasing seed mass at high seed output, beech departs from predictions of fixed-budget allocation models, while declining protein content reveals nitrogen, rather than carbon, as the principal constraint on seed provisioning. Importantly, the absence of a seed size–number trade-off implies that the ecological benefits of masting in beech are not reduced by diminished per-seed biomass, but post-germination growth can be reduced by lower protein provisioning. Germination trials with diverse seed provenances across a range of seed production investment are thus an important next research step. The decline in seed mass and nitrogen content toward climatic margins identifies a pathway through which climate can constrain regeneration at climatic range edges, as well as migration in response to climate change.

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Author Contributions Statement

MB, AHP, KK, PJ, and JSz designed the study. KK, PJ, UE, JSz, and EMK conducted the analysis. KK and MB co-wrote the first draft of the manuscript. All other authors contributed to data collection. All authors contributed to the interpretation of the analysis, revised the draft, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data Availability Statement

The data and code supporting this study are available in Figshare (https://doi.org/10.6084/m9.figshare.31331731).

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Supporting Information

Authors: Kondrat et al.

No seed size–number trade-off in European beech: climate governs investment per seed

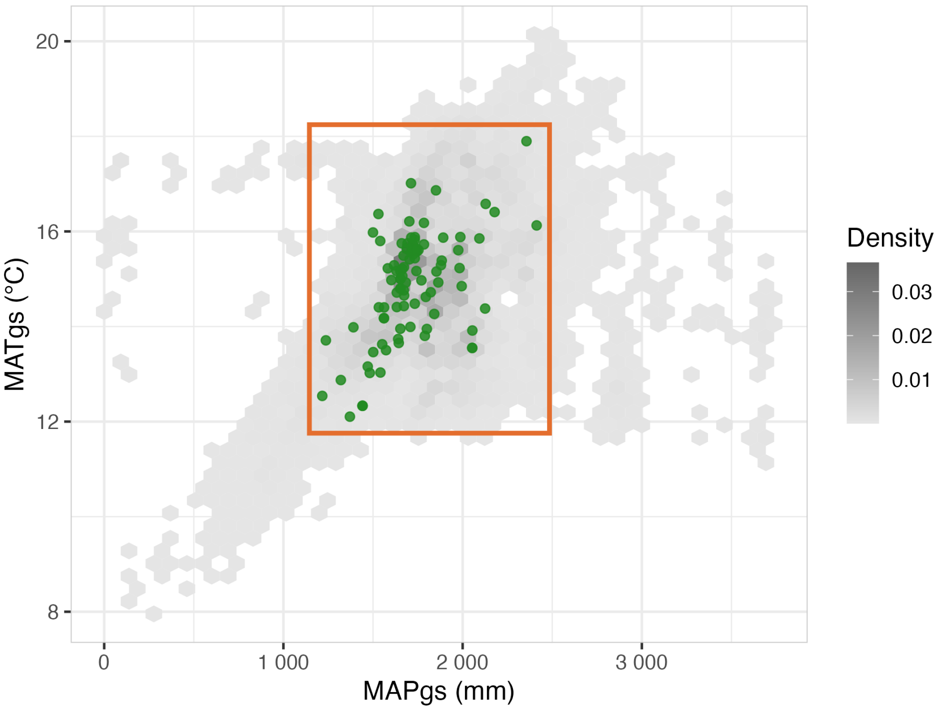

Figure S1: Climate coverage of sampled sites within the European beech climatic distribution. Each green point represents one population and the orange rectangle denotes the climatic envelope spanned by the sampled sites. Grey hexagons show the density of grid cells across the European beech range derived from E-OBS climate data, plotted as mean growing-season temperature (MATgs) against mean growing-season precipitation (MAPgs).

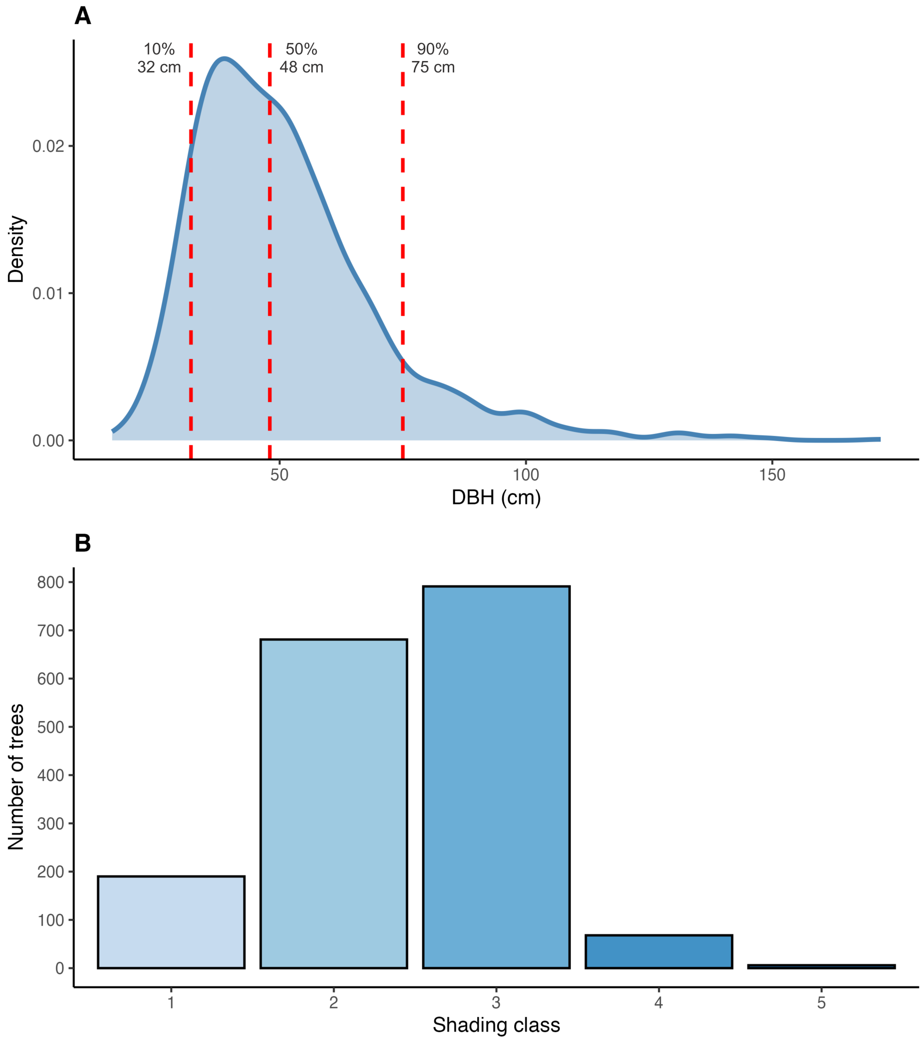

Figure S2: Distribution of tree size and shading conditions across the study dataset (A) Density distribution of diameter at breast height (DBH) for all sampled trees. Dashed vertical lines indicate the 10th, 50th (median), and 90th percentiles. (B) Frequency distribution of trees across shading classes.