No refuge at the edge for European beech as climate warming disproportionately reduces masting at colder margins

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Key words

climate change, masting, fecundity, forest resilience, tree demography

Abstract

Reproduction is vital for forest resilience to climate change, as tree populations depend on adequate seed production to recover demographically from disturbances and migrate to more suitable sites. Neglecting reproduction in projections of habitat suitability and range shifts risks overestimating forest resilience to climate change. For many tree species, including European beech (*Fagus sylvatica*), producing viable seeds depends on the variability of seed production from year to year (CVp), known as masting. Analysing data from 341 sites (average record length: 31.7 years), we find that rising summer temperatures in Central Europe are associated with declines in masting. Crucially, declines are more pronounced in sites with lower mean annual temperatures, indicating that higher latitudes and elevations may offer no refuge. Using the identified relationship between masting and climate, we project changes in masting across the species range under contemporary and future climates. The risk of masting decline is predicted to be widespread throughout the species range, due to ubiquitous summer warming, but the risk is highest in colder areas (up to ~54% decline in CVp). Large masting disruptions are expected to become the norm in future climates, especially at the cold margins, with declines of up to ~83%. With masting crucial for tree regeneration, and wider consequences including on seed consumer populations, its disruption under climate change could have far-reaching ecological impacts. To mitigate the impacts of masting disruptions, monitoring recruitment in vulnerable areas is vital, combined with testing forest management strategies to mitigate the effects of masting decline.

Significance statement

Forest resilience depends on successful tree reproduction, yet viable seed availability is often assumed to remain unchanged under climate change. We show that climate warming reduces masting (inter–annual variability in seed production linked to seed viability) particularly at the cold margins of European beech. Using data from 341 sites of >30 years, we show rising summer temperatures drive masting declines most strongly in sites with lower mean annual temperatures. This challenges the view that higher latitudes and elevations will serve as climate refugia for this important European forest tree. Projections under historic and future scenarios indicate widespread reproductive disruption, likely threatening forest regeneration and altering ecosystem dynamics. Incorporating reproductive processes into climate resilience frameworks and management is crucial.

Introduction

Under climate change, forests and their carbon sequestering services have become vital in global policies (1; 2; 3). Consequently, the impacts of climate change on forest ecosystems have attracted significant attention, highlighting accelerated disturbance rates, increased mortality, and altered growth patterns (4; 5; 6; 7; 8). These efforts have advanced our understanding of how changing climates alter forest dynamics (9; 10; 11). However, due to logistical challenges in measuring seed production over sufficient timescales, the reproductive capacity of trees in response to climate change remains understudied (12; 13). Yet, tree reproduction underpins the persistence and resilience of forest ecosystems (14; 15).

Current range projections under changing climate are typically based on climate suitability for adult trees, neglecting whether new climates allow successful reproduction (16; 17; 18). Seed availability is essential for the resilience and regeneration of existing forests, as well as to support their migration in response to climate change (19; 20; 21; 15). All these processes depend on successful reproduction and collectively determine the nature of future forests. Therefore, integrating reproductive dynamics into climate-based forest management strategies is essential to ensure the sustainability of forest ecosystems (22).

Importantly, for most temperate tree species, viable seed supply is not a simple function of total seed production (Box 1). Instead, viable seed production is linked to masting, a common reproductive strategy in temperate and boreal forest trees (23; 24; 25). Masting refers to the phenomenon where long-lived plants produce large seed crops at irregular, multi-year intervals, synchronised across individuals and populations (26; 27). Masting enhances pollination efficiency and reduces pre-dispersal seed predation (Box 1), thereby maximising viable seed production and increasing the chances of successful seedling establishment (28; 29; 30). Thus, understanding how masting is affected by climate change is essential for predicting tree reproduction and forest regeneration success (31).

Weather variation plays a central role in driving masting (27; 31). This occurs via weather cues which regulate and synchronise year-to-year variation in reproduction (31). Changes in temperature and precipitation regimes can alter the frequency of cues, thereby dampening variability, and desynchronising reproductive effort (32; 31). This reduces the efficiency benefits derived from masting, leading to substantially decreased reproductive success (Box 1) (31). Therefore, understanding masting drivers can help identify regions at risk of declining viable seed production and subsequent recruitment failure, enabling management actions and guiding research to develop solutions.

Advances in understanding masting mechanisms have identified drivers and consequences of its disruption under climate change (31). However, these studies are limited due to the logistical challenges of monitoring seed production over decades (43; 12; 44; 45). Long-term research on European beech (*Fagus sylvatica*) in England has revealed that increasing summer temperatures during flower primordia differentiation (June-July) change the frequency of weather cues triggering high seeding (37; 46), leading to reduced inter-annual variation and synchrony in seed production. This ultimately caused a $\sim 50 - 80\%$ reduction in viable seed supply (41) (Box 1). European beech is an important forest-forming species in Europe, providing numerous ecosystem services and serving as the continent's third-largest carbon sink (47; 11). The growth of beech is declining under warming and drying conditions (48; 49). Nevertheless, beech is considered a potential "winner" of climate change, as projections suggest relatively small range contractions compared to other major forest-forming species, with the potential for colonisation eastward and northward (17; 50; 51). However, these forecasts overlook the risks associated with warming effects on beech reproduction.

Here, we analysed an unprecedented dataset of annual seed production from European beech across Poland, covering 341 sites monitored for over 30 years (1988–2020). The dataset is based on harvest records and includes information on annual seed demand, enabling us to account for variations in harvesting effort. Building on previous research suggesting that warming summer temperatures disrupt masting behaviour (37; 46), we expected that increasing temperatures would be associated with a decline in inter-annual variation in masting (measured as

Box 1: Declining inter-annual variation (CVp) in masting leads to a strong decline in viable seed supply.

A four-decade-long monitoring study of 130 European beech (*Fagus sylvatica*) trees in England has revealed that increasing summer temperatures lead to decreased tree-level inter-annual variation (CVi) and reduced synchrony (S) in seed production among trees (33). Combined, this results in a decline in population-level inter-annual variation in masting (CVp) (34; 33), with severe consequences for viable seed production (Fig. IB-D; for methodology, see Note .1)).

Mechanism. Years of high seed production in European beech are triggered by a sequence of temperature cues: a cold summer two years before, and a warm summer one year before seeding (35; 36). This sequence initiates the development of large numbers of flower buds and sets the stage for a large seeding event. However, as summers have warmed, the frequency of warm summer cues has changed fivefold (37). Trees are now experiencing shorter intervals between the environmental signals triggering large reproductive efforts. This depletes tree resources (38; 39), leading to a diminished response to cues and greater variability in individual tree responses (37). The result is less pronounced inter-annual variation and reduced seed production synchrony (37).

Consequences for viable seed supply. This shift in seed production patterns has two major consequences. Firstly, it results in the **disruption of predator satiation**. Masting reduces seed predation by alternating low-seed years, which starve seed predators, and high-seed years, where an overabundance of seeds overwhelms the reduced predator populations (29). As seeds are being produced more consistently each year, the more stable food supply leads to a higher abundance of seed predators. This led to increased pre-dispersal seed predation, from an efficient average of ~8% predation during the 1980s, to ~ 43% in recent years (Fig. I)(33). Secondly, it results in a **decline in pollination efficiency**. Synchronised mass flowering enhances cross-pollination among trees (40; 28). Reduced synchrony and smaller flowering events have led to a decline in pollination rates—from 52% at the start of monitoring to 38% in recent years (Fig. I) (33).

The combined impact of increased seed predation and decreased pollination efficiency results in a ~66% reduction in viable seed supply (Fig. I) (33; 41). Importantly, at the population level, years of peak seed production correspond to pulses of seedling recruitment (42), and masting translates to seedling recruitment success at the individual level: individuals characterized by large inter-annual variation and synchrony of seed production produce more seedlings (30).

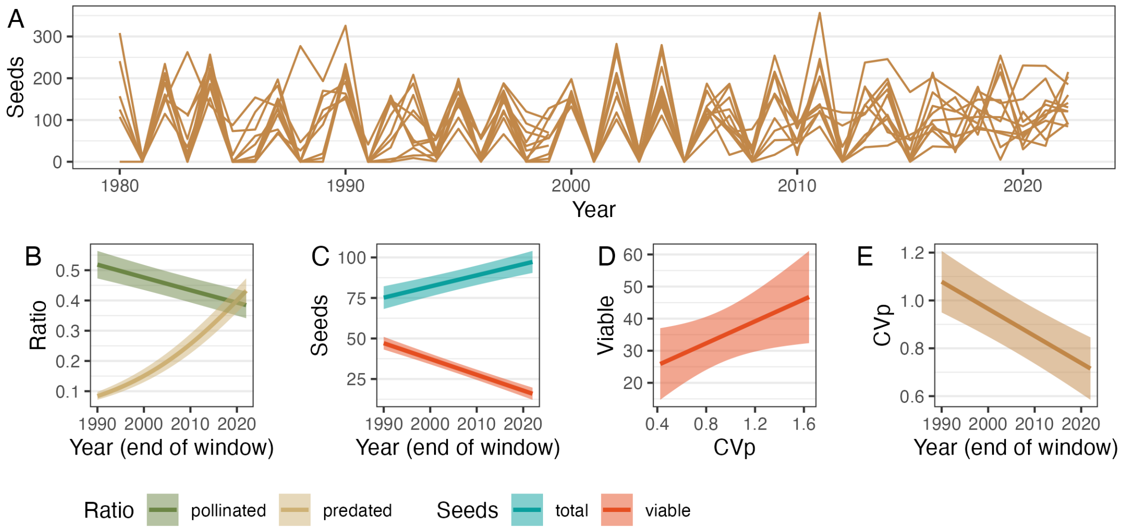

Figure I: A) population-level seed production in European beech measured across 15 sites and 130 trees in England. Temporal changes in B) pollination and pre-dispersal seed predation rates, and C) seed production: total (all seeds), and viable (pollinated and not predated). D) Relationship between population-level inter-annual variability in seed production (masting, CVp) and viable seed production. E) temporal decline in CVp. B-E were calculated with moving window approaches (10 years, step of 5). B-C is based on individual-level data, while D-E on population-level data. For individual-level data, Site and TreeID were used as random (nested) intercepts, and for population-level data, only Site was used as a random intercept.

the coefficient of variation, CVp) and a reduction in synchrony among populations. Moreover, we hypothesised that the sensitivity of CVp to summer warming would vary with baseline climate. In contrast to previous studies on the effects of climate change on European beech masting, our extensive and unified sampling enabled us to establish a quantitative link between masting trends and summer temperatures across large climatic gradients, while also examining how these relationships vary across space. As a next step, we predicted how the observed pace of warming translates into masting changes throughout the species range. Furthermore, we projected future masting dynamics under the intermediate (RCP4.5) and more pessimistic (SSP2.45) IPCC climate scenarios.

While European beech has been highlighted as one of the few native species with a continued potential to continue to provide timber, carbon uptake and storage, as well as high habitat value (52), our work indicates that we may need to reassess these projections. That is, beech is experiencing strong disruptions to its reproductive strategy, particularly in the colder regions which are usually thought of as buffers or climate refugia with continued growth and persistence (49; 52) . If, as the literature suggests (33; 41), the observed declines in CVp are linked to strong reductions in supply of viable seeds, this poses significant concerns for European beech regeneration and calls for urgent attention.

Results

Rising summer temperatures disrupt masting. We found a temporal decline in CVp of 21.81%, from an estimated 2.15 (95% CI = 2.09 – 2.21) in the earliest decade (1988-1997) to 1.68 (95% CI = 1.63 – 1.72) in the last decade of monitoring (2012-2020) (Fig. 1A). Annually, CVp declined by 1.06% (95% CI = -0.89 – -1.23%, $p < 0.001$). Spatially, the decrease in CVp was near-ubiquitous, with the strongest CVp declines occurring in the south of Poland where summer temperature increase was most rapid, and at higher elevations (Fig. 2A).

Other seed production patterns revealed that this decrease in CVp was the result of decreased variability, not increasing mean seed crop size. That is, the long-term mean seed production (smoothed data; $p = 0.06$) as well as the annual seed crop size (yearly fluctuations) showed negative ($p = 0.24$), yet statistically insignificant trends. We did observe an increase in seed production during low seeding years ($\beta = 0.16$ ln(kg/year) ± 0.03 SE, $p < 0.001$).

The decline in CVp was associated with rising summer (June–July) temperatures, with an estimated average decline of 0.27 per 1°C at mean seed demand and MAT levels (SEM = 0.002, $p > 0.001$, Fig. 1B). The interaction between summer temperature and MAT was significant, with a larger sensitivity of CVp to summer temperatures in colder sites ($p < 0.001$). At average baseline MAT levels (7.57 °C), a summer temperature increase of 2.20°C above the baseline period (1960 - 1979) led to a CVp decline of 25.98% relative to its estimated baseline value (i.e. CVp when the summer temperature anomaly is zero). In colder sites (10th percentile of MAT = 6.83°C), this decrease was 32.74%, whereas it was 18.82% in warmer sites (90th percentile of MAT = 8.28 °C) for the same level of summer warming. The temporal decline in masting (i.e. slopes of ln(CVp) over time) was also associated with local baseline climate, i.e. at lower MAT, the decline was stronger (MAT, $p = 0.01$), and the temporal slopes did not vary with mean annual precipitation (MAP, $p = 0.32$). Congruently, temporal CVp declines tended to be larger at higher elevations ($p < 0.001$).

The temporal decline in among-site synchrony of masting, calculated as mean cross-correlation of a site with all other sites in the dataset, was of an even greater magnitude: a 57.24% decline from 0.53 (95% CI = 0.52 – 0.55) in the earliest decade to 0.23 (95% CI = 0.21 - 0.25) (Fig. 1C) to the most recent decade. We observed an average annual decrease in synchrony of -0.01 ± 2.02 $\times 10^{-4}$ SEM ($p < 0.001$). Synchrony declines over time were observed in all but a few sites (Fig. 2B).

As in the case of CVp, the decline in synchrony was associated with rising summer temperatures, and the effect of summer temperatures on synchrony depended on MAT ($p = 0.03$; 1B). Synchrony declined on average by -0.17 per 1°C for mean levels of demand and MAT (± 0.002 SEM, $p < 0.001$; Fig. 1D). For the warmest summer temperature anomalies (2.65 °C) at mean MAT levels, almost complete desynchronisation (mean synchrony = 0.09, CI = 0.06 - 0.12) was observed, translating into a 84.09% decline compared to baseline (i.e. anomaly of zero) (Fig. 1D). In cold sites (10th percentile MAT), this decline was stronger (90.23%) than in warm sites (90th percentile MAT), where it was 78.20%.

Near-ubiquitous disruptions in masting across the species range. Based on 1) summer temperature trends across the European beech range, and 2) the identified interaction between MAT and summer temperatures on CVp, we projected zones at risk of masting disruption under both contemporary and future climate scenarios (Fig. 3).

The risk of masting disruption is extensive, reflecting widespread recent summer warming. The largest reductions are projected to result in reductions of up to ~54% in CVp, and are concentrated in the more mountainous parts of the species range (Fig. 3). The high-elevation sites in the southern-central belt of the species range are at the highest risk (-30 – -54 % CVp; ~20% of grid cell predictions) due to strong temperature increases, and colder mean annual climates. Regions with a projected 20–30% decrease in CVp (36% of grid cells), are scattered across the range. Relatively safer zones which are still associated with a projected -4—20% decrease in CVp (44% of grid cells), have been predominantly concentrated in the northern regions of the distribution during the recent past (Fig. 3). No grid cells show projected increases in CVp.

In 2070, according to the RCP4.5 and SSP2.45 projections, the summer temperatures will be higher by >3°C compared to the baseline across the species range (range RCP 4.5: 1.29–4.84

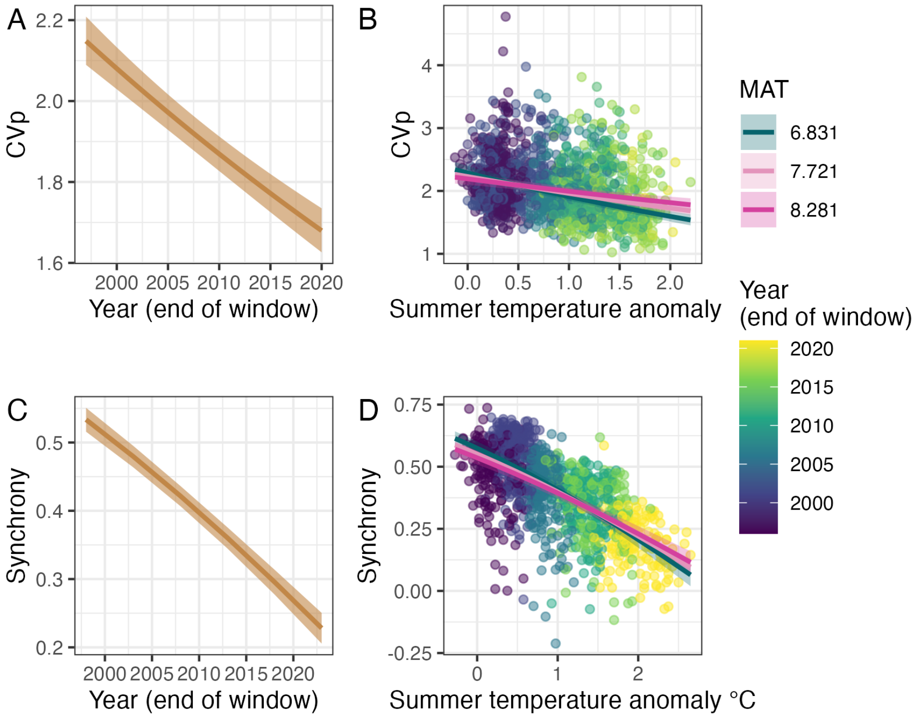

Figure 1: Temporal declines in masting (CVp) and seed production synchrony in European beech, measured across 341 sites, are associated with increasing summer temperatures. Temporal trend in A) masting (CVp) and C) masting regional synchrony. The relationship between B) CVp and D) synchrony and summer temperature (June-July average daily temperature) anomaly, where the effects of summer temperatures on CVp and synchrony vary with baseline MAT (average during 1960-1979). Line colour in B) shows the 10th, 50th and 90th percentile of baseline MAT. CVp and synchrony are calculated in moving windows (10 years, step size of 5 years), and trend lines and associated 95% confidence intervals are derived from GLMMs (see Methods). The start years for the moving windows were determined differently for CVp and synchrony: they were set at the individual time series level for CVp, while for synchrony, they were determined across all time series. Points at B) and D) are residuals coloured according to the end year of the given window. Summer temperature anomaly is defined as a difference in average summer temperature in a particular window vs baseline, i.e. average maximum summer temperature in 1960-1979. CVp is the coefficient of variation (SD/mean), while synchrony is calculated as the mean Spearman cross-correlation of a site with all other sites.

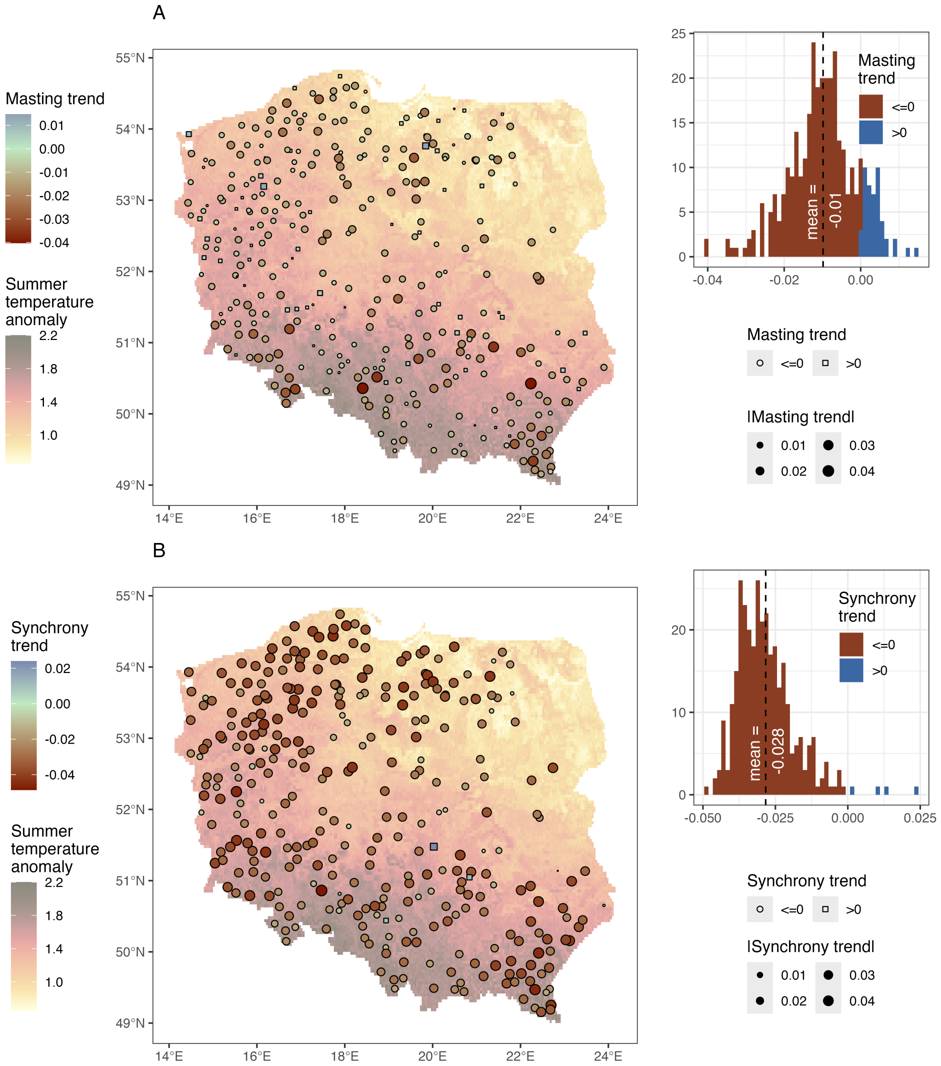

Figure 2: Pervasive decreases in masting (CVp) and seed production synchrony in the context of summer warming. Temporal trends in A) masting (natural logarithm of CVp, where CVp is the coefficient of variation (SD/mean)), and B) masting regional synchrony (mean Spearman cross-correlation) across our sites (points) in Poland. Trends in masting and synchrony were obtained from mixed models using moving window estimates (window size = 10 years, step size of 5 years), with random slopes for sites. Point shape indicates the direction of the trend, and point size is the absolute effect size (i.e. |effect|). Histograms of the random slopes are given next to the maps, with colour showing the direction of the trend. Spatial variation in warming (background colour) is shown as the temperature difference between the last window (window size 10, end-year = 2017) and the baseline summer temperature (average from 1960-1979). See Materials and Methods for details.

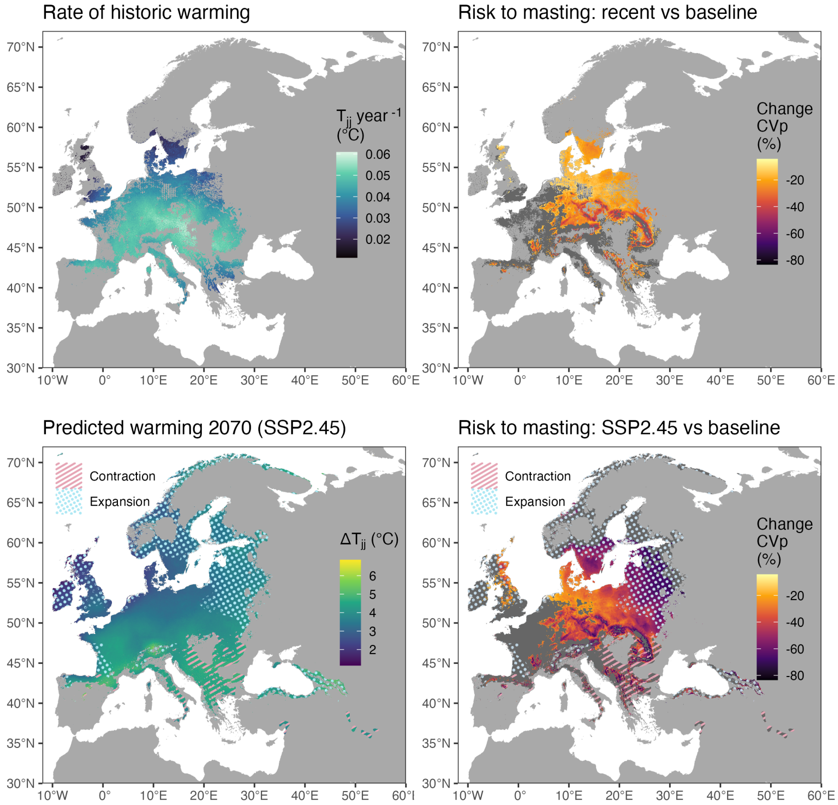

Figure 3: Maps projecting the warming-related change in European beech masting (CVp) across the species range. Left-side panels show summer temperature changes; top: historic warming (the temporal trend in temperature from the baseline (1960-1979) until the most recent time window (end-year 2021). Bottom: Warming as predicted for 2070 in the SSP2.45 scenario, compared to the baseline. Right-side panels show predicted decreases in CVp derived from the summer temperature anomalies and local mean temperatures (Fig. 1B). The current range (coloured region, top panels) was derived from (53). Overlay symbols in the bottom panels show European beech range changes derived from (17), with hashed lines highlighting predicted range contractions, dots marking range expansions, and a transparent symbol overlay indicating range stability. Dark grey regions indicate areas within the projected species range for which no prediction was generated as they fall outside the MAT range of the observational data. See Fig. S2 for the RCP4.5 results.

°C, range SSP2.4: 1.14–6.83 °C). As is evident from Fig. 3 and Fig.S2, the regions where beech is projected to expand its range (dotted regions) overlap with regions of high risk of masting disruptions. For the RCP4.5 and SSP2.45 scenarios, 74.70% and 80.87% of grid cells show decreases of ≥ 30% respectively.

Discussion

Using a spatio-temporally extensive dataset, we show that masting in European beech has decreased over time in response to rising summer temperatures, and that colder sites experience the strongest declines. Our projections suggest the most pronounced CVp declines are currently concentrated in the mountainous regions across the species distribution range. In both the RCP4.5 and SSP2.45 climate change projections — i.e. the ’intermediate’ climate change scenarios by the IPCC (54) — the entire species range and projected future range would face a high risk of large reductions in masting, particularly in the north. Therefore, the reproductive strategy of this key forest-forming species appears extensively compromised by climate change, posing risks to its long-term persistence and migration ability. We believe this warrants urgent attention, and we outline a roadmap for research and management to support European beech forest resilience (Box 2).

The observed decrease of 21.81% in the inter-annual variation of seed production and 57.24% in seed production synchrony in European beech in Poland over the past three decades serves as a warning of a potential decline in viable seed supply (Fig. 1, S3). Crucially, UK studies link a comparable decline in masting to a reduction in viable seed production of over 60% (Box 1) (33; 41). Similarly, a recent analysis detected a general decline in masting in Europe using data from 50 sites, though without assessing spatial variation (46). These findings underscore the urgent need for studies to address the knowledge gap concerning viable seed production and its effects on recruitment patterns in the areas identified here as most at risk of masting decline (Box 2). While immediate impacts on seedling recruitment may be limited, chronic strain on viable seed supply could ultimately alter forest composition and continuity (55; 56). Integrating early warning signals from seed production records with forest health monitoring - e.g. (57; 58; 59) - offers a proactive approach to mitigating future regeneration failures.

Our projections of masting dynamics under the IPCC (68) climate scenarios — RCP4.5 and SSP2.45 for 2070 (2061–2080), with mean warming of +3.3°C and +3.7°C across the current range, respectively — suggest an uncertain future, with a complete breakdown of masting projected across Europe, particularly at the cold margins. Importantly, this highlights a substantial risk to long-term persistence in beech populations previously deemed climate change-resilient based on tree growth and species distribution modelling (49; 48; 17; 52). While the effects of drought on beech growth and mortality may be buffered in cool sites (49), disruptions to masting are driven by local warming rates, and exacerbated in colder sites. Our findings indicate that the identification of these forests as "winners" under climate change may be premature.

Box 2: Call to action: knowledge gaps.

1. **Evaluating the effects of reduced viable seed supply on recruitment patterns**

   A decline in viable seed supply may increase seed limitation, affecting natural forest regeneration (19; 60; 61; 21). Even if microsite limitation and disturbances such as herbivory are strong filters of regeneration (62), seed limitation is prevalent in forests (19; 60; 21). *Action Needed*: Identify habitats highly vulnerable to seed shortages for natural regeneration, such as those requiring frequent recovery from disturbance. Critical slowing-down indicators can provide a necessary theoretical and analytical framework (63).

2. **Identifying factors that modulate the impact of masting breakdown**

   The decline in viable seed production due to masting breakdown is greatest in the largest trees (41). Other, so far unidentified, factors might also play important roles. Potential modulators include stand density, forest patch size, and (micro)climate conditions (64; 65; 66). *Action Needed*: Identify factors that affect seed supply reductions associated with masting disruptions. Understanding these modulators will guide management strategies that can buffer the decline in viable seed production.

3. **Assessing the potential for acclimation or adaptation in masting cues**

   It is unclear whether trees can adjust their masting cues in response to changing climates or to what extent these cues are locally adapted. *Action Needed*: Evaluate the acclimation potential of trees that will mature and reproduce in future climatic conditions. If masting cues are locally adapted, assisted migration of suitable genotypes may be beneficial. Existing provenance trials may provide useful data to inform these efforts.

4. **Evaluating seed quality and potential assisted regeneration from seeding**

   Beech seeds are intermediate (on the orthodox-recalcitrant spectrum), making them sensitive to desiccation and long-term storage (67). *Action Needed*: Establish how the decline in seed quality during storage can be reduced, to increase assisted regeneration success. Evaluate how seed traits and quality markers, such as germination timing, dormancy depth, and oxidative stress, vary across climate change gradients and over time, to identify where storage may be feasible and supplementation may be required.

5. **Investigating climate change effects on masting in other forest-forming species**

   European beech is vulnerable to climate-induced masting disruptions, potentially classifying it as a "loser" species in a changing climate. However, responses of other species are largely unknown, even if theory exists to guide predictions (31). *Action Needed*: Evaluate how climate change affects masting in other major forest-forming species. Identifying potential "winner" or "loser" species will inform forest management and conservation strategies aimed at maintaining reproductive resilience and ecosystem function in the face of climate change.

However, our temporal CVp projections assume that European beech responses to summer temperature cues and historic mean annual temperatures will remain unchanged, which may not be accurate. Importantly, although local temporal increases in temperature correlate with local declines in CVp, this relationship does not hold spatially; i.e. mean CVp does not vary geographically based on local mean temperatures (46). Possibly, populations may be locally adapted, with the "optimal" summer temperature for triggering masting varying according to local conditions such as the observed interaction with mean annual temperature observed here (also see Box 2). In this case, assisted migration (relocating populations from warmer regions) could help mitigate masting breakdown (11). Alternatively, if the observed differences result from acclimation during an early life stage, trees reaching reproductive maturity after 2060, having grown in significantly warmer conditions, might be partially buffered against reproductive failure. Exploring the adaptation and acclimation potential to varying regimes of environmental cues that regulate masting is required (Box 2).

Disruptions in masting have significant ecological and practical implications at both local and regional scales. At the population level, the reduction in CVp likely reflects a combination of diminished inter-annual variability at the tree level (CVi) and reduced synchronisation among individual trees (Box 1) (34; 33). These localised changes may affect less mobile seed predators, such as insects, by disrupting their food supply dynamics and increasing seed predation rates (Box 1). This aligns with our observation that more seeds are produced during low-seeding years, which could prevent seed consumers from experiencing food shortages. Additionally, since masting triggers cascading effects across the food webs, altering animal community dynamics and behaviour, changes in masting likely have far-reaching ecological consequences (31). Decreased CVp also decreases pollination efficiency (Box 1). At the regional level, decreased masting synchrony has at least three implications. First, large-scale synchrony helps satiating mobile seed consumers, such as wild boar, by overwhelming their capacity to consume seeds during mast years (69; 70; 71). When synchrony between nearby populations declines, these consumers can shift between forest patches with available mast, intensifying seed predation and limiting recruitment (70; 72). Second, regional synchrony decline can disrupt food webs and animal migration patterns shaped by synchronised pulses of seed availability (73; 74; 75).

Finally, reduced regional synchronisation affects the supply and demand of seeds for forest nurseries. Forest nurseries rely on seed harvests for reforestation and restoration projects (76). A decline of viable seed production may lead to shortages, increasing the cost and logistical challenges of seed collection whilst reducing the availability of genetically diverse material for planting (77).

Our projections of masting changes across the species range are based on summer temperature trends and the associated shifts in cue frequency that trigger flowering (Box 1). Long-term studies of snow tussocks (*Chionochloa pallens*) and European beech indicate that resource reserves interact with cue frequency to drive masting (38). Specifically, when resource levels are high, even weak temperature cues trigger substantial reproductive effort, but when resources are depleted, flowering is suppressed despite strong cues (78; 38). Rising global temperatures lead to more frequent cues, which in turn causes repeated resource depletion (39). Consequently, plants tend to flower more regularly but produce smaller seed crops, leading to lower CVp (37; 38). The impact of altered cue frequency can therefore be modulated by local site conditions and resource intake capabilities, though the direction of this effect remains uncertain. For example, limited resource intake may sustain low reproductive outputs despite frequent strong cues, delaying masting breakdown, whereas rapid resource replenishment could lead to more regular seed production and increased vulnerability to breakdown. This interaction may produce more patchy masting responses to increased cue frequency than those shown in Fig. 3, which predicts the mean decline in masting at the regional scale.

While the harvest data provided by the Polish State Forest offered a unique opportunity to link masting trends with temperature across extensive spatio-temporal gradients, it comes with limitations. For example, harvest rates are influenced by demand, which introduces additional noise into the data. However, we were able to mitigate this by incorporating annual demand information into our analysis. Moreover, the ecological importance of declines in the CVp hinges on two assumptions: that reduced CVp translates to lower viable seed supply, and that seed supply is a driver of regeneration. Although our study does not directly address these links, a substantial body of evidence indicates that viable seed production is strongly tied to masting variation (Box 1), and that seed production is closely associated with individual fitness

(79; 12; 30), with persistent supply disruptions leading to recruitment limitation (80; 56; 81; 82). Furthermore, our data do not cover the entire climatic space of the species range; while we sample large parts of the core climatic distribution, populations in very warm and wet sites remain under-represented and should be targeted in future research.

Our study establishes that rising summer temperatures are linked to a strong decline in inter-annual variation of seed production and regional synchrony in European beech, especially at the colder margins. These shifts in reproductive dynamics have consequences for forest regeneration by potentially reducing seedling recruitment, altering seed predator cycles, and disrupting pollination processes. Projections based on current trends suggest that declines will occur across the species range, increasing the risk of seed supply shortages and triggering cascading effects on the ecosystem. Additionally, the stronger masting declines at cold edges challenge the idea of refugia at higher latitudes and elevations. Opportunities remain to enhance European beech forest resilience. Expanding and sustaining long-term seed and recruitment monitoring networks to understand seed supply effects on recruitment, and assessing the potential for local adaptation and acclimation, appear as important next steps (Box 2).

Materials and Methods

Studied species

European beech is a major forest-forming species in temperate Europe, with high economic and ecological importance (83). Its main range extends from southern Italy and northern Spain towards southern Sweden and from Great Britain to Bulgaria, up to 2000 m a.s.l. elevation. Beech is a model masting species, with seed production characterised by large inter-annual variation and synchrony (84; 85). High flower production is positively correlated with temperatures in summer across the whole species range, as the period of sensitivity is anchored to the longest day of the year, the summer solstice (36). High seed production is negatively correlated with growth (86). Masting breakdown, i.e. the decline in inter-annual variation and synchrony of seed production is described in Box 1. The decline in CVp, increased regularity of reproduction, and resulting persistent resource depletion caused by warming has led to a decline in growth rate in European beech (39).

Data

Reproduction data Information on seed production was obtained from Polish State Forests and is based on annual harvest rates by the local forest inspectorates. This dataset provides information on the amount (kg) of seed collected in each district per year. Seeds are collected from the ground by local companies on behalf of the Polish State Forest, and each inspectorate has assigned seed collection sites. In addition to the information on harvest rates, we obtained information on the annual seed demand (kg) which is derived by Polish State Forests based on the area requiring reforestation (such as after logging or disturbances). We obtained data for 448 districts (referred to as 'sites'; 14,207 observations), but we subset this to sites measured for at least 10 years, with at least some beech seed harvest. Together, this resulted in time series from 341 sites and 10,814 annual observations, with an average length of 31.7 years (range: 13-33). Fig. S1 illustrates the sites distributed across the species' climate range, along with the sampled elevation gradient.

Climate, elevation, and species range data Historical monthly climate data (maximum and minimum temperature, precipitation sum, 2.5 minute resolution) were obtained from WorldClim v. 2.1 (87). These were used to calculate summer (June-July) temperature anomalies, and average climate (mean annual temperature [MAT], mean annual precipitation [MAP]). The summer temperature anomalies were calculated by subtracting the site-level mean of maximum June-July temperatures during the baseline period (1960-1979) from the mean maximum June-July temperature in a focal year. Baseline MAT estimates were obtained by taking the average of the monthly maximum and minimum temperatures for each year between 1960-1979, and then taking an average. Similarly, baseline MAP was obtained by summing the monthly precipitation, and taking the average of these during 1960-1979. Elevation data, derived from SRTM, were obtained via WorldClim v. 2.1 (87).

To predict masting under future climate conditions in the intermediate future (i.e. 2070, range: 2060-2080), we obtained climate change projections for the IPCC RCP 4.5 and SSP2.45

scenarios from WorldClim (v. 1.4 and 2.1 respectively (87); 30 second resolution, bilinearly resampled to match historical data resolution). Following (53), we averaged three global climate change projections of maximum June-July temperatures for each scenario, since these reflect low, moderate, and high levels of occurrence changes. The projections used for RCP 4.5 were HadGEM2-ES, IPSL-CM5A-LR, MPI-ESM-LR, and for SSP2.45 we used HadGEM3-GC31-LL, IPSL-CM6A-LR, and MPI-ESM1-2-HR. Current and predicted species ranges under the two scenarios were obtained from (53; 17).

Data analysis

All models were build in R (v. 4.4.1) using glmmTMB (v. 1.1.10) and validated with DHARMa (v.0.4.7) unless indicated differently (88; 89; 90)).

Moving windows For each time series, we calculated long-term values of reproductive metrics, including the coefficient of variation (CVp) of seed production, the long-term mean seed crop size, as well as the 25th percentile of seed crop size (representing seed production during low seeding years) with 10-year moving windows. In this approach, the first window of 10 observations is used to estimate metrics such as the CVp, and the window then skips a set number of years (the step size; here, we used 5 years as step size) along the time series, after which the estimation of the metric is repeated in each new window. Since time windows can overlap, we checked for temporal autocorrelation in model residuals.

To calculate temporal changes in regional masting synchrony, we used moving time windows with 10 years length and 5 years step, with the first window always starting in 1987 i.e., the first year of seed production records in our dataset. Within each window, we calculated between-site synchrony of seed production based on pairwise Spearman correlation coefficients for data series that overlapped for at least 5 years. Pairwise correlation coefficients were then averaged at the site level to obtain the average seed production synchrony of a given site in a given time window. Synchrony was subsequently normalised to fall between $[0, 1]$ following the formula $y_i = (y_i + 1)/2$ and back-transformed to a correlation coefficient scale for visualisation according to the equation $y_i = y_i * 2 - 1$.

A 10-year moving window approach was also used to calculate long-term estimates of predictor values. Firstly, a long-term estimate of demand of European beech seed was calculated, as this variable was used to correct for variation in sampling effort. We also calculated the long-term mean of the summer temperature anomalies.

Temporal trends in reproduction To model temporal changes in annual seed production, we constructed a Tweedie model with a log-link. Year was included as a predictor of seed harvest size, and the previous year's seed harvest was added to account for negative temporal autocorrelation. We used ln + 1 transformed seed demand as an offset, and added site ID as a random intercept.

We tested temporal trends in long-term reproductive patterns using the moving window approach described in the previous section. Linear mixed models using a Gaussian distribution were used to assess for temporal patterns in ln-transformed CVp. Predictors were year (i.e. the end-year of the moving window), and a standard-deviation scaled estimate of centred seed demand. Site ID was included as a random intercept. Tweedie distribution models were constructed to test for temporal changes in mean seed production and the 25th quantile of seed production (estimates: step size of 5). These models included year as a predictor, site ID as a random intercept, and the model was offset with ln + 1 transformed estimates of seed demand.

We also fitted a GLMM to test for temporal trend in seed production synchrony. The model included mean site-level synchrony in a given time window as a response, scaled and centred seed demand and year as predictors, and site ID as a random intercept. The model was fitted with Tweedie distribution and logit link function. To report slopes on the back-transformed scale, we calculated the average of year-to-year differences (slopes) over time.

Linking environmental variation to reproduction patterns CVp and synchrony estimates were regressed against summer temperature anomalies in two models with random slopes for site ID. Summer temperature effects were allowed to vary with baseline period (1960-1979) MAT and MAP (i.e. summer temperature × MAT + summer temperature × MAP). Non-significant terms (MAP, MAP × summer temperature) were removed from the final models. Scaled and centred seed demand was added as a covariate in the Gamma-family log-link model of CVp, and in the Tweedie distribution with logit-link synchrony model. To report on CVp and synchrony slopes on the back-transformed scale, we calculated the average of year-to-year differences (slopes) over temperature anomalies. To further examine the effect of mean annual climate on masting, we firstly constructed versions of the temporal models of CVp described above using random slopes for site . We then extracted these slopes, and regressed them against baseline MAT and MAP in a Gaussian model. We ran another Gaussian model regressing these slopes against elevation.

Projections across the species range **Warming rates and baseline climate** To analyse spatial diversity in summer warming rates under climate change scenarios, we gathered climate data for grid cells within the species' current and future ranges. We calculated summer temperature anomalies by subtracting the historic baseline (1960–79 average) from each projection. For the recent past, we used the 2002–2021 summer temperature average, while future scenarios followed RCP4.5 and SSP2.4. Since the historic baseline was based on WorldClim 2.1 and RCP4.5 on version 1.4, we adjusted for dataset differences to minimise downscaling noise. We also calculated baseline MAT (1960–79 average) for all grid cells.

Using summer temperature anomalies and baseline MAT, we predicted CVp across the species' range, restricting predictions to areas where MAT fell within the sampled range. We then estimated baseline CVp (anomaly = 0) and calculated the percentage change in CVp for each scenario relative to this baseline.

Acknowledgements

This study was funded by the European Union (ERC, ForestFuture, 101039066). Views and opinions expressed are however those of the authors only and do not necessarily reflect those of the European Union or the European Research Council. Neither the European Union nor the granting authority can be held responsible for them. Additional financial support was provided by the Institute of Dendrology, Polish Academy of Sciences. We would like to express our gratitude to the Directorate-General of State Forests for providing data on the abundance and quality of seeds of major forest-forming species. These data, collected by the Forest Research

Institute (IBL) as part of projects commissioned by the State Forests Directorate (DGLP), were made available for scientific and research purposes in accordance with letter ZG.7021.3.2024, dated March 22, 2024. The data were shared at the request of the Institute of Dendrology, Polish Academy of Sciences.

Author Contributions Statement

All authors conceived the study. JJF, MB, JSz, MKD designed the study. JJF, JSz, MB, and MKD designed and conducted the analysis. JJF and MB co-wrote the first draft of the manuscript. 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 supporting the results will be archived in a permanent repository upon acceptance.

References

[1] Steffen W, et al. (2015) Planetary boundaries: Guiding human development on a changing planet. *Science* 347(6223).

[2] Rockström J, et al. (2024) Planetary boundaries guide humanity's future on earth. *Nature Reviews Earth & Environment* 5(11):773–788.

[3] Norby RJ, et al. (2024) Enhanced woody biomass production in a mature temperate forest under elevated co2. *Nature Climate Change* 14(9):983–988.

[4] Allen CD, et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259(4):660–684.

[5] Bennett AC, Mcdowell NG, Allen CD, Anderson-Teixeira KJ (2015) Larger trees suffer most during drought in forests worldwide. *Nature Plants* 1:15139.

[6] Senf C, et al. (2018) Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications* 9(1):1–8.

[7] Forzieri G, Dakos V, McDowell NG, Ramdane A, Cescatti A (2022) Emerging signals of declining forest resilience under climate change. *Nature* 608(7923):534–539.

[8] Hartmann H, et al. (2022) Climate change risks to global forest health: Emergence of unexpected events of elevated tree mortality worldwide. *Annual Review of Plant Biology* 73:673–702.

[9] McDowell NG, et al. (2020) Pervasive shifts in forest dynamics in a changing world. *Science* 368(6494).

[10] Luyssaert S, et al. (2018) Trade-offs in using European forests to meet climate objectives. *Nature* 562(7726):259–262.

[11] Chakraborty D, et al. (2024) Assisted tree migration can preserve the european forest carbon sink under climate change. *Nature Climate Change* 14(8):845–852.

[12] Clark JS, et al. (2021) Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications 2021 12:1* 12(1):1–11.

[13] Bogdziewicz M (2022) How will global change affect plant reproduction? a framework for mast seeding trends. *New Phytologist* 234(1):14–20.

[14] Davis KT, et al. (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences* 116(13):6193–6198.

[15] Sharma S, et al. (2022) North american tree migration paced by climate in the west, lagging in the east. *Proceedings of the National Academy of Sciences* 119(3):e2116691118.

[16] Bykova O, Chuine I, Morin X, Higgins SI (2012) Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography* 39(12):2191–2200.

[17] Dyderski MK, Paź-Dyderska S, Jagodziński AM, Puchałka R (2025) Shifts in native tree species distributions in Europe under climate change. *Journal of Environmental Management* 373:123504.

[18] Chakraborty D, et al. (2021) Provisioning forest and conservation science with high-resolution maps of potential distribution of major european tree species under climate change. *Annals of Forest Science* 2021(2):26.

[19] Caspersen JP, Saprunoff M (2005) Seedling recruitment in a northern temperate forest: The relative importance of supply and establishment limitation. *Canadian Journal of Forest Research* 35(4):978–989.

[20] Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: New predictive insights from a process-based model. *Journal of Ecology* 96(4):784–794.

[21] Kroiss SJ, HilleRisLambers J (2015) Recruitment limitation of long-lived conifers: implications for climate change responses. *Ecology* 96(5):1286–1297.

[22] Hanbury-Brown AR, Ward RE, Kueppers LM (2022) Forest regeneration within earth system models: current process representations and ways forward. *New Phytologist* 235(1):20–40.

[23] Pearse IS, LaMontagne JM, Lordon M, Hipp AL, Koenig WD (2020) Biogeography and phylogeny of masting: do global patterns fit functional hypotheses? *New Phytologist* 227(5):1557–1567.

[24] 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.

[25] Qiu 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.

[26] Kelly D (1994) The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* 9(12):465–470.

[27] Pearse IS, Koenig WD, Kelly D (2016) Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist* 212(3):546–562.

[28] Rapp JM, Mcintire EJ, Crone EE (2013) Sex allocation, pollen limitation and masting in whitebark pine. *Journal of Ecology* 101(5):1345–1352.

[29] 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(11):e2105655119.

[30] Bogdziewicz M, et al. (2024) Masting and efficient production of seedlings: Balancing costs of variation through synchronised fruiting. *Ecology letters* 27(9):e14514.

[31] Bogdziewicz M, et al. (2024) Evolutionary ecology of masting: mechanisms, models, and climate change. *Trends in Ecology & Evolution* 39:851–862.

[32] Hacket-Pain A, Bogdziewicz M (2021) Climate change and plant reproduction: trends and drivers of mast seeding change. *Philosophical Transactions of the Royal Society B* 376(1839):20200379.

[33] Bogdziewicz M, Kelly D, Thomas PA, Lageard JGA, Hacket-Pain A (2020) Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants* 6:88–94.

[34] Koenig WD, et al. (2003) Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* 102:581–591.

[35] Vacchiano G, et al. (2017) Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytologist* 215(2):595–608.

[36] Journé V, et al. (2024) Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants* 10:367–373.

[37] Bogdziewicz M, et al. (2021) Climate warming causes mast seeding to break down by reducing sensitivity to weather cues. *Global Change Biology* 27(9):1952–1961.

[38] Kelly D, Szymkowiak J, Hacket-Pain A, Bogdziewicz M (2024) The interaction of resources and weather cues enables optimization of reproductive delay in masting plants. *EcoEvoRxiv*.

[39] Hacket-Pain A, et al. (2025) Growth decline in european beech associated with temperature-driven increase in reproductive allocation. *PNAS*.

[40] Kelly D, Hart DE, Allen RB (2001) Evaluating the wind pollination benefits of mast seeding. *Ecology* 82(1):117–126.

[41] Bogdziewicz M, et al. (2023) Reproductive collapse in European beech results from declining pollination efficiency in large trees. *Global Change Biology* 29:4595–4604.

[42] Jensen TS (1985) Seed-Seed Predator Interactions of European Beech, Fagus silvatica and Forest Rodents, Clethrionomys glareolus and Apodemus flavicollis. *Oikos* 44(1):149–156.

[43] 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(3):1088–1100.

[44] LaMontagne JM, Redmond MD, Wion AP, Greene DF (2021) An assessment of temporal variability in mast seeding of north american Pinaceae. *Philosophical Transactions of the Royal Society B: Biological Sciences* 376(1839):20200373.

[45] Wion AP, Pearse IS, Broxson M, Redmond MD (2025) Mast hindcasts reveal pervasive effects of extreme drought on a foundational conifer species. *New Phytologist* 246(2).

[46] Foest J, et al. (2024) Widespread breakdown in masting in European beech due to rising summer temperatures. *Global Change Biology* 30:e17307.

[47] Leuschner C (2020) Drought response of European beech (*Fagus sylvatica* L.)—a review. *Perspectives in Plant Ecology, Evolution and Systematics* 47:125576.

[48] del Castillo EM, et al. (2022) Climate-change-driven growth decline of European beech forests. *Communications Biology* 5(1):163.

[49] Klesse S, et al. (2024) No future growth enhancement expected at the northern edge for european beech due to continued water limitation. *Global Change Biology* 30(10).

[50] Hanewinkel M, Cullmann DA, Schelhaas MJ, Nabuurs GJ, Zimmermann NE (2013) Climate change may cause severe loss in the economic value of european forest land. *Nature Climate Change* 3(3):203–207.

[51] Schueler S, et al. (2014) Vulnerability of dynamic genetic conservation units of forest trees in Europe to climate change. *Global Change Biology* 20(5):1498–1511.

[52] Wessely J, et al. (2024) A climate-induced tree species bottleneck for forest management in Europe. *Nature Ecology & Evolution* 8(6):1109–1117.

[53] Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten european forest tree species distributions? *Global Change Biology* 24(3):1150–1163.

[54] Tebaldi C, et al. (2021) Climate model projections from the Scenario Model Intercomparison Project (ScenarioMIP) of CMIP6. *Earth System Dynamics* 12(1):253–293.

[55] Crone EE (2001) Is survivorship a better fitness surrogate than fecundity? *Evolution* 55(12):2611–2614.

[56] Ashman TL, et al. (2004) Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology* 85(9):2408–2421.

[57] Lambers JHR, Clark JS, Beckage B (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417(6890):732–735.

[58] Rhoades J, et al. (2024) Historic land use modifies impacts of climate and isolation in rear edge european beech (fagus sylvatica l.) populations. *Global change biology* 30(11):e17563.

[59] Astigarraga J, et al. (2024) Relative decline in density of northern hemisphere tree species in warm and arid regions of their climate niches. *Proceedings of the National Academy of Sciences of the United States of America* 121(28).

[60] Clark CJ, Poulsen JR, Levey DJ, Osenberg CW (2007) Are plant populations seed limited? a critique and meta-analysis of seed addition experiments. *American Naturalist* 170(1):128–142.

[61] Norghauer JM, Newbery DM (2010) Recruitment limitation after mast-seeding in two african rain forest trees. *Ecology* 91(8):2303–2312.

[62] Kuijper DP, et al. (2010) Fluctuating ungulate density shapes tree recruitment in natural stands of the białowieza primeval forest, poland. *Journal of Vegetation Science* 21(6):1082–1098.

[63] Scheffer M, et al. (2009) Early-warning signals for critical transitions. *Nature* 461(7260):53–59.

[64] Wion AP, Pearse IS, Rodman KC, Veblen TT, Redmond MD (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.

[65] Szymkowiak J, et al. (2024) Masting ontogeny: the largest masting benefits accrue to the largest trees. *Annals of Botany*.

[66] Pesendorfer MB, et al. (2024) Positive spatial and temporal density-dependence drive early reproductive economy-of-scale effects of masting in a european old-growth forest community. *Journal of Ecology*.

[67] Pukacka S, Hoffmann SK, Goslar J, Pukacki PM, Wójkiewicz E (2003) Water and lipid relations in beech (Fagus sylvatica L.) seeds and its effect on storage behaviour. *Biochimica et Biophysica Acta (BBA) - General Subjects* 1621(1):48–56.

[68] EmissionsGapReport (2023) *Emissions Gap Report 2023: Broken Record – Temperatures*

hit new highs, yet world fails to cut emissions (again). (United Nations Environmental Programme).

[69] Curran LM, Webb CO (2000) Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting dipterocarpaceae. *Ecological Monographs* 70(1):129–148.

[70] Curran LM, Leighton M (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting dipterocarpaceae. *Ecological Monographs* 70(1):101–128.

[71] Ascoli D, et al. (2021) Modes of climate variability bridge proximate and evolutionary mechanisms of masting. *Philosophical Transactions of the Royal Society B: Biological Sciences* 376(1839):20200380.

[72] Bogdziewicz M, 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(1970):20212636.

[73] Widick IV, Strong C, LaMontagne JM, Young MA, Zuckerberg B (2025) Continent-Wide Patterns of Climate and Mast Seeding Entrain Boreal Bird Irruptions. *Global Change Biology* 31(2):e70076.

[74] Szymkowiak J, Thomson RL (2019) Nest predator avoidance during habitat selection of a songbird varies with mast peaks and troughs. *Behavioral Ecology and Sociobiology* 73(7):91.

[75] Woodman JP, et al. (2025) Continent-Wide Drivers of Spatial Synchrony in Breeding Demographic Structure Across Wild Great Tit Populations. *Ecology Letters* 28(2):e70079.

[76] Fargione J, et al. (2021) Challenges to the reforestation pipeline in the united states. *Frontiers in Forests and Global Change* 4.

[77] Pearse IS, Wion AP, Gonzalez AD, Pesendorfer MB (2021) Understanding mast seeding for conservation and land management. *Philosophical Transactions of the Royal Society B: Biological Sciences* 376(1839):34657466.

[78] Miyazaki Y, et al. (2014) Nitrogen as a key regulator of flowering in fagus crenata: understanding the physiological mechanism of masting by gene expression analysis. *Ecology Letters* 17(10):1299–1309.

[79] Moran EV, Clark JS (2012) Causes and consequences of unequal seedling production in forest trees: a case study in red oaks. *Ecology* 93(5):1082–1094.

[80] Clark JS, et al. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany* 86(1):1–16.

[81] Clark JS, LaDeau S, Ibanez I (2004) Fecundity of trees and the colonization–competition hypothesis. *Ecological Monographs* 74(3):415–442.

[82] Ohse B, et al. (2023) Demographic synthesis for global tree species conservation. *Trends in Ecology & Evolution* 38:579–590.

[83] Leuschner C, Ellenberg H (2017) Beech and mixed beech forests. *Ecology ofCentral European Forests: Vegetation Ecology of Central Europe* 1:351–441.

[84] Nilsson SG, Wastljung U (1987) Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* 68(2):260–265.

[85] Mund M, 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(1):111–125.

[86] Hacket-Pain AJ, et al. (2018) Climatically controlled reproduction drives interannual growth variability in a temperate tree species. *Ecology Letters* 21(12):1833–1844.

[87] Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12):4302–4315.

[88] R Core Team (2024) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria).

[89] Brooks ME, et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9(2):378–400.

[90] Hartig F (2024) *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. R package version 0.4.7.

Supporting Information

No refuge at the edge for European beech as climate warming disproportionately reduces masting at colder margins

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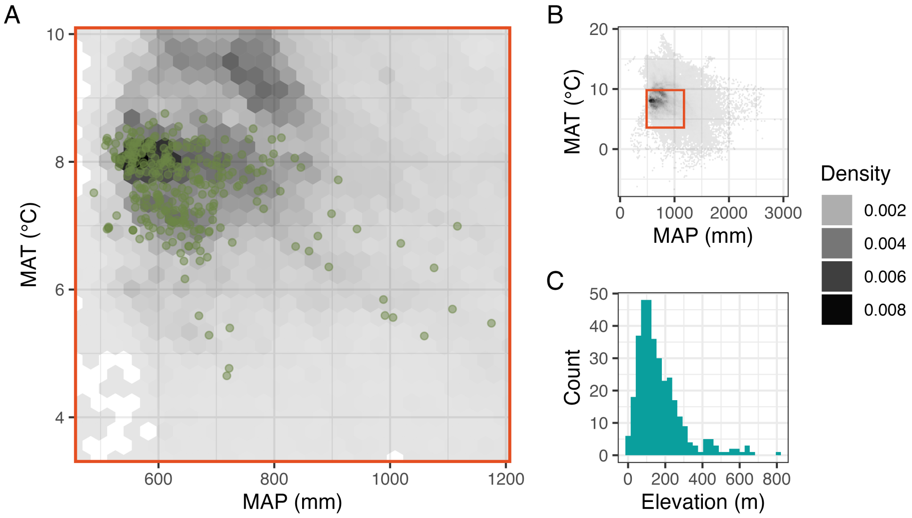

Figure S1: **Sites cover large climate and elevation gradients** Sampled sites (green points; A), in the context of the climate envelope of the European beech range (B). The extent of (A) matches the orange box in (B). Grey shading at A) and B) shows the density of WorldClim grid cells across the species range in each part of the envelope, i.e. darker shading represents the most common climate conditions within the species' range, while lighter areas are less frequent. The elevation gradient sampled is shown in (C). MAT = Mean annual temperature, MAP = Mean annual precipitation.

.1 Note S1

.1.1 Methodology Box 1: Evidence from the UK

The reproductive patterns of UK beech trees were re-analysed using models more closely related to the models used on the Polish reproductive data. We subset the individual-level EBMS data to trees with at least 10 annual observations, and for site level estimates of CVp we used only those sites with ≥ 5 trees.

Firstly, we used a moving window approach (window length: 10 years, step size: 5 years) to obtain long-term estimates of the mean of each pattern - i.e. pollination rates (ratio of pollinated to total seed count), pre-dispersal seed predation rates (ratio of predated to pollinated seeds), the number of total and viable (pollinated and not predated) seeds, and the CVp.

We then constructed (generalised) linear mixed models (i.e (G)LMM) for each pattern. Specifically, for the models examining the fertilisation and predation ratios over time, we constructed two beta family model with logit links, using year as the predictor, and adding a random intercepts for tree ID. The predation ratio was linearly rescaled to a range of 0.0001, 0.9999) to satisfy the beta distribution requirements. The temporal changes in total and viable seeds, as well as CVp were tested with LLMs, using year as the predictor, and a random intercept for tree ID. Lastly, the relationship between viable seed number and CVp was tested with a LLM, with viable seeds as the response, and CVp as the predictor, correcting for tree ID with a random intercept.

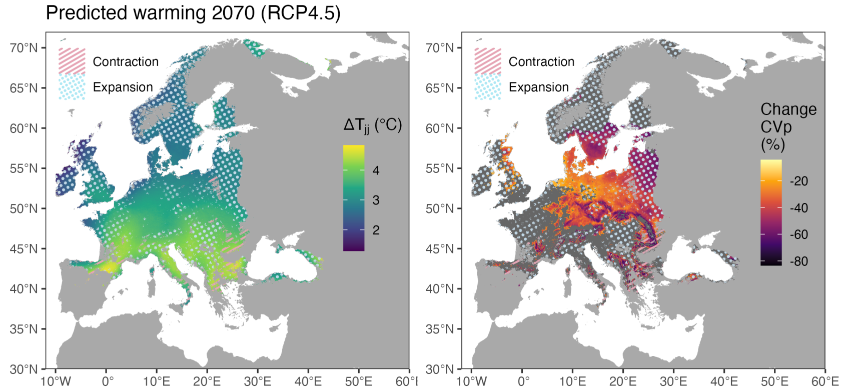

Figure S2: Maps projecting the warming-related change in European beech masting (CVp) across the species range, for the RCP4.5 scenario. The left-side panel shows warming as predicted for 2070 in the SSP2.45 scenario, compared to the baseline. The right-side panels shows predicted decreases in CVp derived from the temperature anomalies, and the decline in CVp associated with increasing summer temperatures and local mean temperatures (Fig. 1B). Overlay symbols in the panels show European beech range changes derived from (53), with hashed lines highlighting predicted range contractions, dots marking range expansions, and a transparent symbol overlay indicating stability. See Fig. 3 for the results of the SSP2.45 scenario.

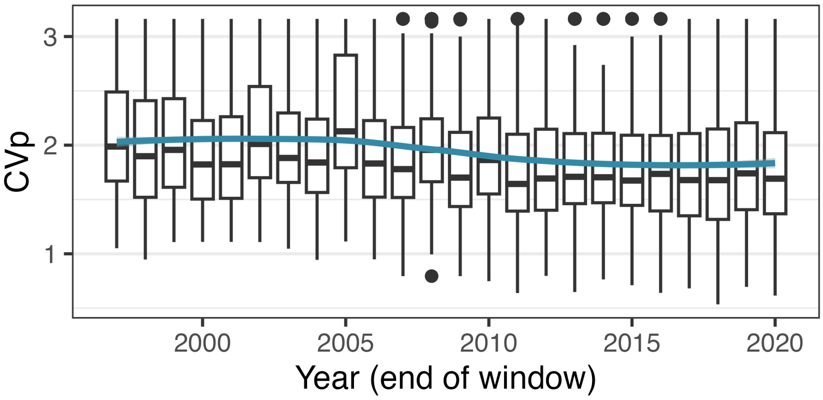

Figure S3: Changes in masting (CVp) over time in the Polish European beech sites. Estimates for each site were derived from 10 year moving windows, using a step size of 1 year. Time is shown as the end-year of this window. A loess regression line is given in blue.