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

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Abstract

Reproduction is vital for forest resilience under climate change, enabling tree populations to recover from disturbances and migrate. Yet projections of habitat suitability often overlook seed production. For European beech (*Fagus sylvatica*), viable seed production depends on year-to-year variability and synchrony in reproduction (masting). Using data from 341 sites (mean record: 31.7 years), we show that, especially in colder sites, increased frequency of the main reproductive cue is linked to strong declines in masting (CVp decline up to ~54%). This suggests that high latitudes and elevations offer no refuge, countering common assumptions and trends in other demographic processes. Severe disruptions to masting are projected to become the norm, with the greatest reductions (up to ~83%) at colder margins. Masting disruption may threaten forest regeneration and have far-reaching ecological impacts. Monitoring recruitment and testing adaptive forest management in vulnerable areas will be essential to mitigate reproductive constraints on forest resilience.

Introduction

Under climate change, forests and their carbon sequestering services have become vital in global policies (Steffen *et al.*, 2015; Rockström *et al.*, 2024; Norby *et al.*, 2024). Consequently, the impacts of climate change on forest ecosystems have attracted significant attention, highlighting accelerated disturbance rates, increased mortality, and altered growth patterns (Allen *et al.*, 2010; Bennett *et al.*, 2015; Senf *et al.*, 2018; Forzieri *et al.*, 2022; Hartmann *et al.*, 2022). These efforts have advanced our understanding of how changing climates alter forest dynamics (McDowell *et al.*, 2020; Luyssaert *et al.*, 2018; Chakraborty *et al.*, 2024). However, due to logistical challenges in measuring seed production over sufficient timescales, the reproductive capacity of trees in response to climate change remains comparatively understudied (Clark *et al.*, 2021; Bogdziewicz, 2022). Yet, tree reproduction underpins the persistence and resilience of forest ecosystems (Davis *et al.*, 2019; Sharma *et al.*, 2022).

Current range projections under a changing climate are typically based on climate suitability for adult trees, neglecting whether new climates allow successful reproduction (Bykova *et al.*, 2012; Dyderski *et al.*, 2025; Chakraborty *et al.*, 2021). Seed availability is essential for the resilience and regeneration of existing forests, as well as to support their migration in response to climate change (Caspersen & Saprunoff, 2005; Morin *et al.*, 2008; Kroiss & HilleRisLambers, 2015; Sharma *et al.*, 2022). All these processes depend on successful reproduction and collectively determine the nature of future forests (Seidl *et al.*, 2022). Therefore, integrating reproductive dynamics into climate-based forest management strategies is essential to ensure the sustainability of forest ecosystems (Hanbury-Brown *et al.*, 2022).

Importantly, for most temperate tree species, viable seed supply (here, pollinated and unpredated seeds) is not a simple function of total seed production (Bogdziewicz *et al.*, 2024b). Instead, viable seed production is linked to how variable total seed production is over time. This year-to-year variability, known as masting, is a common reproductive strategy in temperate and boreal forest trees (Pearse *et al.*, 2020; Journé *et al.*, 2023; Qiu *et al.*, 2023). Masting involves the production of large seed crops at irregular, multi-year intervals, synchronised across individuals and populations (Kelly, 1994; Pearse *et al.*, 2016). Masting enhances pollination efficiency and reduces pre-dispersal seed predation, thereby increasing the chances of successful seedling establishment (Rapp *et al.*, 2013; Zwolak *et al.*, 2022; Bogdziewicz *et al.*, 2024a). While regeneration also depends on subsequent factors such as dispersal, establishment, and survival, understanding how masting is changing under climate change is an essential first step in anticipating reproductive constraints on forest resilience (Hacket-Pain & Bogdziewicz, 2021).

Weather variation plays a central role in driving masting (Pearse *et al.*, 2016, 2017). This occurs via weather cues that regulate and synchronise year-to-year variation in reproduction (Bogdziewicz *et al.*, 2024b). Changes in temperature and precipitation regimes can alter the frequency of cues, thereby dampening variability and desynchronising reproductive effort (Hacket-Pain & Bogdziewicz, 2021; Bogdziewicz *et al.*, 2024b). This reduces the efficiency benefits derived from masting, leading to substantially decreased reproductive success (detailed in Box 1) (Bogdziewicz *et al.*, 2024b). 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 (Bogdziewicz *et al.*, 2024b). However, these studies are limited due to the logistical challenges of monitoring seed production over decades (Shibata *et al.*, 2020; Clark *et al.*, 2021; LaMontagne *et al.*, 2021; Wion *et al.*, 2025). Long-term research on European beech (*Fagus sylvatica*) in England has revealed that increasing summer temperatures lead to reduced inter-annual variation and synchrony in seed production, and ultimately to $\sim$ 66% reduction in viable seed supply (Box 1). European beech is an important forest-forming species in Europe, providing numerous ecosystem services and serving as the continent's third-largest forest carbon sink (Leuschner, 2020; Chakraborty *et al.*, 2024). The growth of beech is declining under warming and drying conditions (del Castillo *et al.*, 2022; Klesse *et al.*, 2024). 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 (Dyderski *et al.*, 2025; Hanewinkel *et al.*, 2013; Schueler *et al.*, 2014). However, these forecasts overlook the risks associated with the effects on beech reproduction.

Recent work has shown that masting is cued by temperature anomalies whose frequency varies across climate gradients, raising the possibility that populations are locally adapted to the historical frequency of these cues (Journé *et al.*, 2024; Foest *et al.*, 2024). This idea aligns with broader phenological theory, which predicts that organisms should evolve sensitivity to environmental cues that match their local environment (Chevin *et al.*, 2010; Gienapp *et al.*, 2013). In the case of European beech masting, summer temperature anomalies after the summer solstice function as the strongest reproductive cue (Journé *et al.*, 2024; Journé *et al.*, 2023), but cueing can vary spatially due to differences in mean climate conditions. In colder sites, where warm summers are relatively rare, selection may favour stronger responsiveness. Conversely, in warmer regions where such cues are more common,

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 (Bogdziewicz *et al.*, 2020). Combined, this results in a decline in population-level inter-annual variation in masting (CVp) (Koenig *et al.*, 2003; Bogdziewicz *et al.*, 2020), with severe consequences for viable seed production (Fig. IB-D; see Note S1: Methodology)).

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 (Vacchiano *et al.*, 2017; Journé *et al.*, 2024). 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 (Bogdziewicz *et al.*, 2021). Trees are now experiencing shorter intervals between the environmental signals triggering large reproductive efforts. This depletes tree resources (Kelly *et al.*, 2025; Hacket-Pain *et al.*, 2025), leading to a diminished response to cues and greater variability in individual tree responses (Bogdziewicz *et al.*, 2021). The result is less pronounced inter-annual variation and reduced seed production synchrony (Bogdziewicz *et al.*, 2021).

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 (Zwolak *et al.*, 2022). 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)(Bogdziewicz *et al.*, 2020). Secondly, it results in a **decline in pollination efficiency**. Synchronised mass flowering enhances cross-pollination among trees (Kelly *et al.*, 2001; Rapp *et al.*, 2013). 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) (Bogdziewicz *et al.*, 2020).

The combined impact of increased seed predation and decreased pollination efficiency results in a ~66% reduction in viable seed supply (Fig. I) (Bogdziewicz *et al.*, 2020, 2023). Importantly, at the population level, years of peak seed production correspond to pulses of seedling recruitment (Jensen, 1985; Maringer *et al.*, 2020), 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 (Bogdziewicz *et al.*, 2024a).

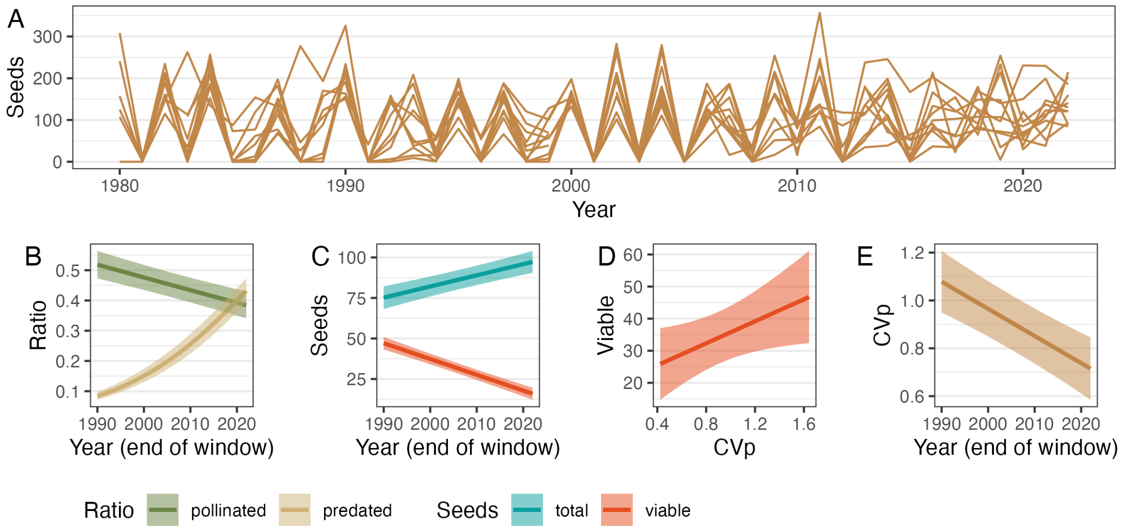

Figure I: A) population-level seed production in European beech measured across 15 sites and 130 trees in England. Temporal changes in B) pollination and pre-dispersal seed predation rates, and C) seed production: total (all seeds), and viable (pollinated and not predated). D) Relationship between population-level 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.

selection may favour higher cue thresholds or reduced sensitivity to avoid excessive reproductive effort and resource depletion (Hacket-Pain *et al.*, 2025; Kelly *et al.*, 2025). Congruently, some recent studies suggest a potential local adjustment of cue responsiveness. For instance, the timing of cue sensitivity is anchored to photoperiod, yet populations are triggered by different summer temperatures (Journé *et al.*, 2024). Moreover, while masting is responsive to temporal changes in summer temperatures, population-level masting is similar across regions with contrasting climates (Foest *et al.*, 2024). Spatial variation in masting–climate relationships, observed in species such as *Fagus crenata* and *Pinus edulis*, aligns with this interpretation (Kon *et al.*, 2005; Wion *et al.*, 2020). If local adaptation occurs, rapid summer warming could increase cue frequency most dramatically in cold-adapted populations, pushing them outside their evolved response range. This could lead to overstimulation and a subsequent breakdown of synchronised mast seeding (Bogdziewicz *et al.*, 2021; Hacket-Pain *et al.*, 2025; Kelly *et al.*, 2025). In warmer populations, adapted to more frequent cueing, such disruption may be weaker or absent. This framework predicts an interaction between local climate and warming rate, where masting would decline most severely in colder regions under rapid summer warming.

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. Harvests track planting demand and inventory: they are lower in low-planting years or when stocks are full. Since beech seeds store poorly, stock carryover is short, prompting frequent collection and higher demand. The annual demand (kg of seeds) was recorded, and we can therefore separate effort from production. This makes harvest records one of the few long-term indicators of reproduction across European forests. Building on previous research suggesting that warming summer temperatures disrupt masting behaviour (Bogdziewicz *et al.*, 2021; Foest *et al.*, 2024), we expected that increasing temperatures would be associated with a decline in inter-annual variation in masting (measured as 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 historic 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.

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 nearly 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 (β = 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 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 –

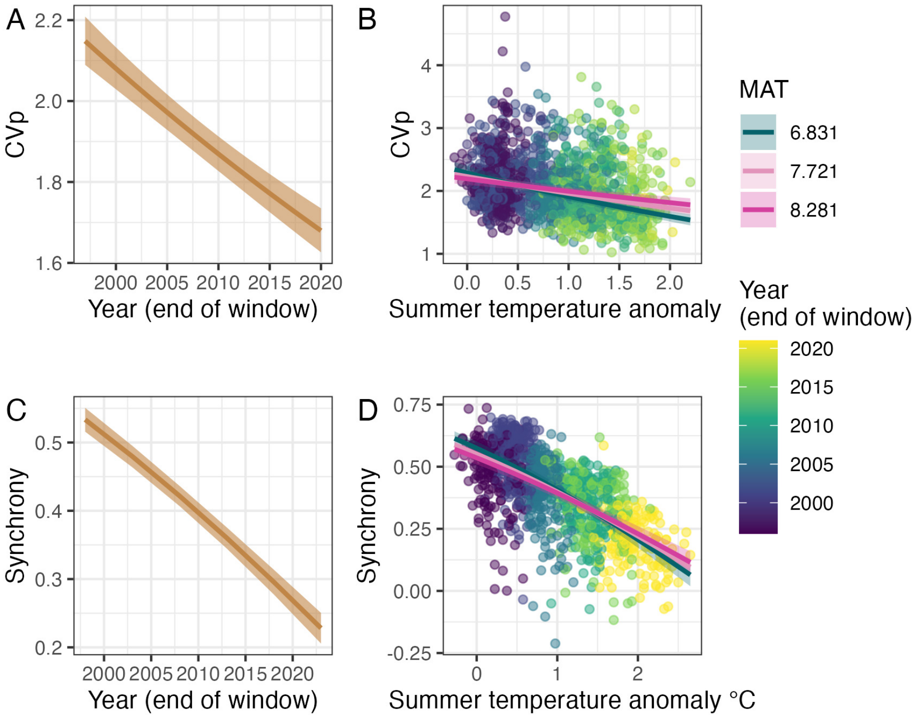

Figure 1: Temporal declines in masting (CVp) and seed production synchrony in European beech, measured across 341 sites, are associated with increasing summer temperatures. Temporal trend in A) masting (CVp) and C) masting regional synchrony. The relationship between B) CVp and D) synchrony and summer 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.

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 $-0.01 \pm 2.02 \times 10^{-4}$ 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%.

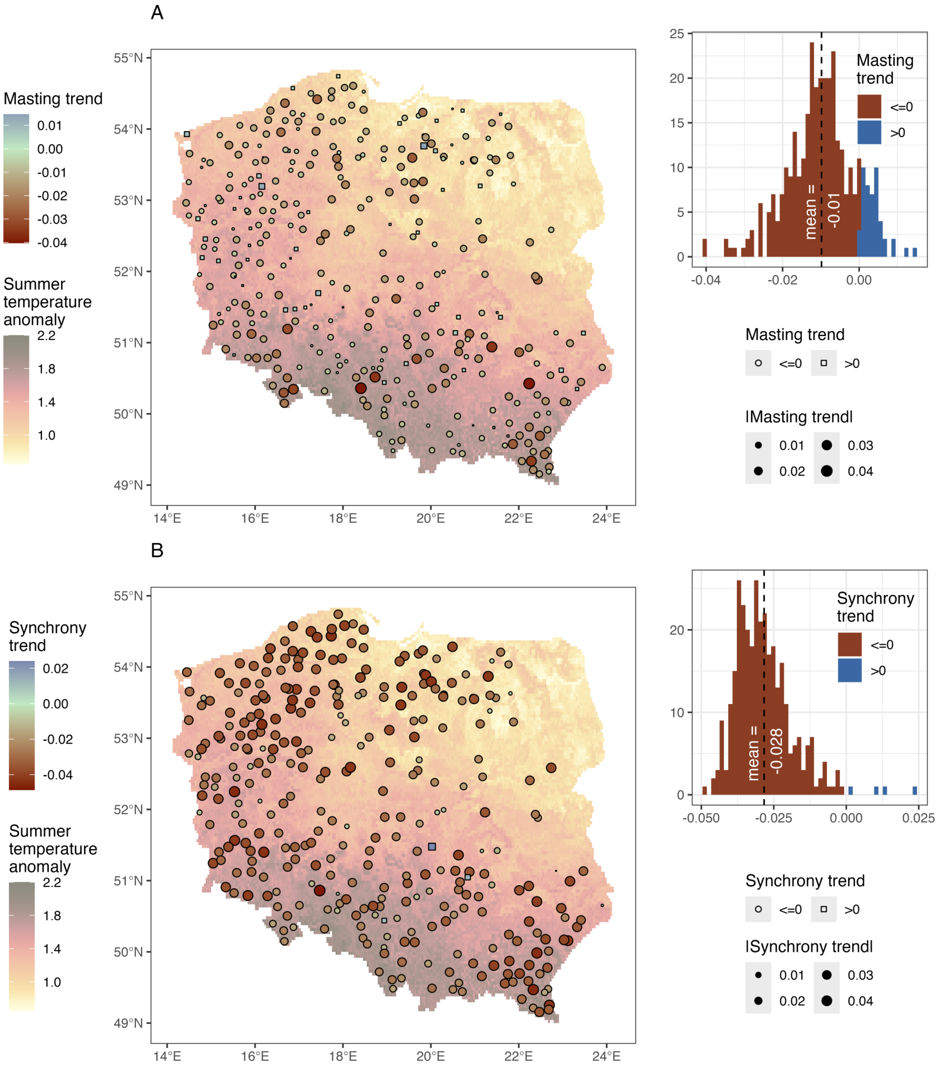

Figure 2: Pervasive decreases in masting (CVp) and seed production synchrony in the context of summer warming. Temporal trends in A) masting (natural logarithm of CVp, where CVp is the coefficient of variation (SD/mean)), and B) masting regional synchrony (mean Spearman cross-correlation) across our 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.

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 (i.e., CVp change) under both contemporary and future climate scenarios (Fig. 3).

The risk of masting disruption is extensive, reflecting widespread recent summer warming. 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 °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 $\geq$ 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 — the 'intermediate' climate change scenarios by the IPCC (Tebaldi *et al.*, 2021) — 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.

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) (Bogdziewicz *et al.*, 2020, 2023). Similarly, a recent analysis detected a general decline in masting in Europe using data from 50 sites, though without assessing spatial variation (Foest *et al.*, 2024). These findings underscore the urgent need for studies to address the knowledge gap concerning viable seed production and its effects on recruitment patterns, which may also depend on subsequent processes (e.g. seed dispersal, seedling emergence, establishment, survival) in the areas identified here as most at risk of masting decline

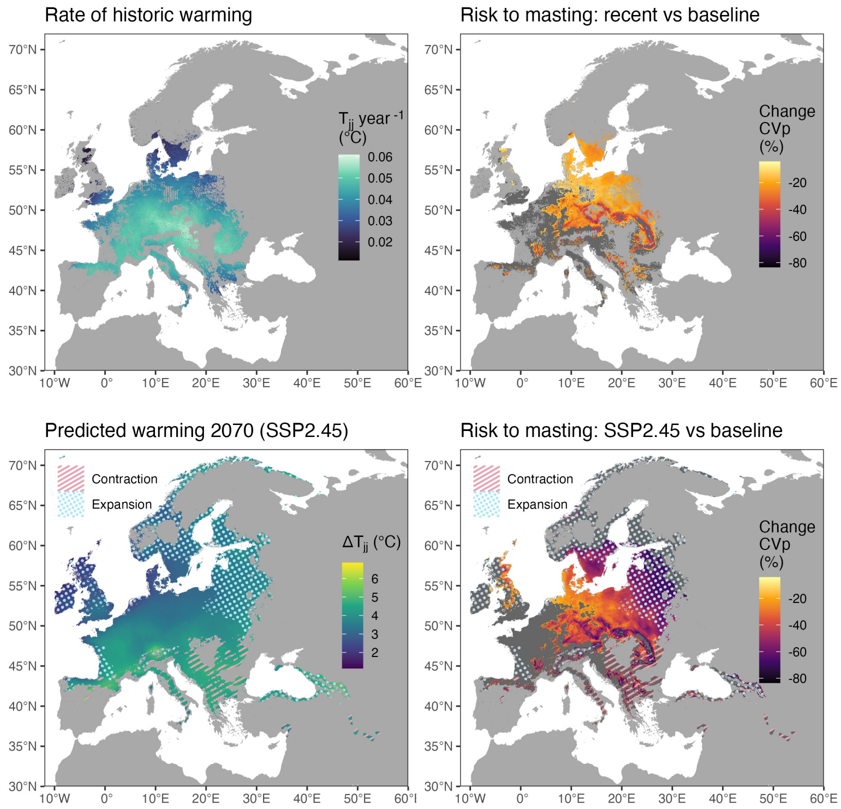

Figure 3: Maps projecting the warming-related change in European beech masting (CVp) across the species range. Left-side panels show summer temperature changes; top: historic warming (the temporal trend in temperature from the baseline (1960-1979) until the most recent time window (end-year 2021). Bottom: 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 (Dyderski *et al.*, 2018). Overlay symbols in the bottom panels show European beech range changes derived from (Dyderski *et al.*, 2025), 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.

(Ibanez *et al.*, 2007; Conlisk *et al.*, 2017; Davis *et al.*, 2023). While immediate impacts of masting disruption on seedling recruitment may be limited, chronic strain on viable seed supply could ultimately alter forest composition and continuity (Crone, 2001; Ashman *et al.*, 2004). Integrating early warning signals from seed production records with forest health monitoring - e.g., (Lambers *et al.*, 2002; Rhoades *et al.*, 2024; Astigarraga *et al.*, 2024) - offers a proactive approach to mitigating future regeneration risks.

Our projections of masting dynamics under the IPCC (EmissionsGapReport, 2023) 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 strong reductions in 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 (Klesse *et al.*, 2024; del Castillo *et al.*, 2022; Vacek *et al.*, 2023; Dyderski *et al.*, 2025; Wessely *et al.*, 2024). While the effects of drought on beech growth and mortality may be buffered in cool sites (Klesse *et al.*, 2024), 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.

However, our temporal CVp projections assume that European beech responses to summer temperature cues and historic mean annual temperatures will remain fixed over time; an assumption that may not hold. This is particularly relevant given our findings, together with recent empirical work (Journé *et al.*, 2024; Foest *et al.*, 2024), support the hypothesis of local adjustment of cue sensitivities. That is, the "optimal" summer temperature for triggering masting varies according to local conditions, such as the observed interaction with mean annual temperature. If local adaptation underlies the observed spatial variation in sensitivity, assisted migration (relocating populations from warmer regions) could help mitigate masting breakdown under climate change (Chakraborty *et al.*, 2024). Alternatively, if these differences reflect acclimation during early life stages, trees reaching reproductive maturity after 2060, having developed under warmer conditions, might be partially buffered against reproductive failure. Further research is needed to evaluate the potential for both adaptation and acclimation to shifting regimes of environmental cues regulating masting. Moreover, forecasting under climate change inevitably requires extrapolation, and therefore additional uncertainty. Given the spatially consistent mechanism of beech reproduction cueing summer temperatures anchored to the solstice (Journé *et al.*, 2024), we consider these projections biologically grounded. Nonetheless, it remains an open question if current masting–climate relationships hold under continued warming.

The interaction we observe between local climate and summer temperature anomalies, where masting declines are steepest in colder sites, appear to align with a broader principle: that populations are often locally adapted to the historical frequency or predictability of key environmental cues (Chevin *et al.*, 2010; Stemkovski *et al.*, 2025). Accordingly, populations' climate-change sensitivity often depends on local climatic history (Chevin *et al.*, 2010), a pattern increasingly documented across systems. For example, in the tundra cushion plant (*Silene acaulis*), populations from colder sites begin to experience growth declines under warming at lower temperature thresholds than those from warmer sites (Peterson *et al.*, 2018). Similarly, common poppy (*Papaver rhoeas*) populations from historically unpredictable rainfall regimes evolved greater drought resilience than those from more stable climates (Springer *et al.*, 2023). Reef-building corals from historically heat-stressed regions bleached less under subsequent warming than those from thermally stable areas (Thompson & van Woesik, 2009). Our finding of stronger masting declines in colder regions thus illustrates a vulnerability: cold-adapted populations may be especially sensitive to rapid shifts in cue frequency, especially when those shifts outpace the potential for adaptive or plastic responses.

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) (Koenig *et al.*, 2003; Bogdziewicz *et al.*, 2020). These localised changes may affect less mobile seed predators, such as insects, by disrupting their food supply dynamics and increasing seed predation rates (Bogdziewicz *et al.*, 2020). 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 (Bogdziewicz *et al.*, 2024b). Decreased CVp also decreases pollination efficiency (Bogdziewicz *et al.*, 2020). 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 (Curran & Webb, 2000; Curran & Leighton, 2000; Ascoli *et al.*, 2021). When synchrony between nearby populations declines, these consumers can shift between forest patches with available mast, intensifying seed predation and limiting recruitment (Curran & Leighton, 2000; Bogdziewicz *et al.*, 2022). Second, regional synchrony decline can disrupt food webs and animal migration patterns shaped by synchronised pulses of seed availability (Widick *et al.*, 2025; Szymkowiak & Thomson, 2019; Woodman *et al.*, 2025). 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 (Fargione *et al.*, 2021). 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 (Pearse *et al.*, 2021).

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 (Kelly *et al.*, 2025). 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 (Miyazaki *et al.*, 2014; Kelly *et al.*, 2025). Rising global temperatures lead to more frequent cues, which in turn causes repeated resource depletion (Hacket-Pain *et al.*, 2025). Consequently, plants tend to flower more regularly but produce smaller seed crops, leading to lower CVp (Bogdziewicz *et al.*, 2021; Kelly *et al.*, 2025). The impact of altered cue frequency can therefore be modulated by 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 disruption, whereas rapid resource replenishment could lead to more regular seed production and increased vulnerability to disruption. 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.

The ecological importance of declines in the CVp hinges on two assumptions: that reduced CVp translates to a lower viable seed supply, and that seed supply is a driver of regeneration. Although this study does not directly address these links, a substantial body of evidence indicates that viable seed production is strongly tied to masting variation, and that seed production is closely associated with individual fitness (Moran & Clark, 2012; Clark *et al.*, 2021; Bogdziewicz *et al.*, 2024a), with persistent supply disruptions leading to recruitment limitation (Clark *et al.*, 1999; Ashman *et al.*, 2004; Clark *et al.*, 2004; Ohse *et al.*, 2023). Moreover, harvest data from the Polish State Forest provided rare spatio-temporal coverage to assess climate–masting links, but its dependence on harvest demand introduces non-biological signals. We incorporated annual demand in our models, to correct for fluctuating sampling effort. The congruence between the climate-masting links observed here and in other studies of disrupted masting (Bogdziewicz *et al.*, 2021; Foest *et al.*, 2024) further suggests robustness of the results. 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 to the extent that CVp declines lead to higher predation and lower pollination, and triggering cascading effects on the ecosystem (Touzot *et al.*, 2020; Bisi *et al.*, 2018; Tattoni *et al.*, 2021). Additionally, the stronger masting declines at cold edges challenge the idea of refugia at higher latitudes and elevations. At the same time, considerable variation around our model predictions suggests that some sites may be less affected than others, offering scope for targeted management. More broadly, our findings highlight the need to enhance monitoring of regeneration factors influencing 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.

Materials and Methods

Studied species

European beech is a major forest-forming species in temperate Europe, with high economic and ecological importance (Leuschner & Ellenberg, 2017). 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 (Nilsson & Wastljung, 1987; Mund *et al.*, 2020). 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 (Journé *et al.*, 2024). High seed production is negatively correlated with growth (Hacket-Pain *et al.*, 2018). Masting disruption, 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 (Hacket-Pain *et al.*, 2025).

Data

Reproduction data and seed demand 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 harvest demand (kg) which is derived by Polish State Forests based on the area requiring regeneration (such as after logging or disturbances) and reforestation. 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 (Fick & Hijmans, 2017). These were used to calculate summer (June-July) temperature anomalies, and average climate (mean annual temperature [MAT], mean annual precipitation [MAP]). We define the baseline climate as the 1960–1979 period, which we use both as the reference for calculating anomalies and to estimate long-term mean site conditions. The summer temperature anomalies were calculated by subtracting the site-level mean of maximum June-July temperatures during the baseline period from the mean maximum June-July temperature in a focal year. 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, 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 (Fick & Hijmans, 2017).

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 (Fick & Hijmans, 2017); 30 second resolution, bilinearly resampled to match historical data resolution). Following (Dyderski *et al.*, 2018), 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 (Dyderski *et al.*, 2018, 2025).

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 (R Core Team, 2024; Brooks *et al.*, 2017; Hartig, 2024)).

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 1988 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 mean of European beech seed demand 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 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, applying the previously described model relating CVp to summer temperature anomalies and climate, whilst restricting predictions to areas with MAT within the sampled range. We then estimated baseline CVp (summer temperature anomaly = 0) and calculated the percentage change in CVp for each scenario relative to this baseline.

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Declaration of interests

No competing interests to declare.

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Supporting Information

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

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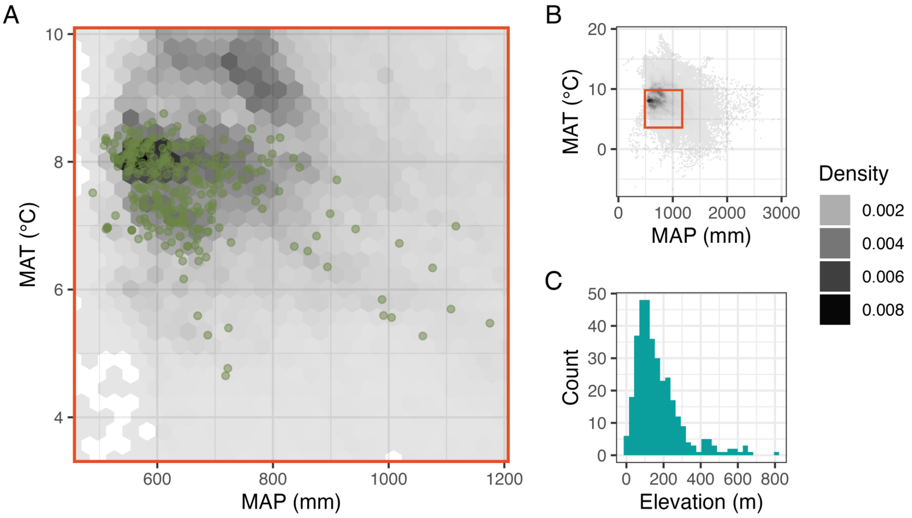

Figure S1: Sites cover large climate and elevation gradients Sampled sites (green points; A), in the context of the climate envelope of the European beech range (B). The extent of (A) matches the orange box in (B). Grey shading at A) and B) shows the density of WorldClim grid cells across the species 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.

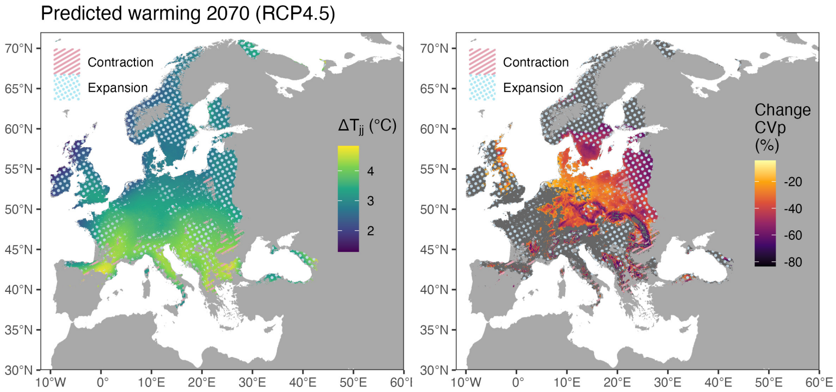

Figure S2: Maps projecting the warming-related change in European beech masting (CVp) across the species range, for the RCP4.5 scenario. The left-side panel shows warming as predicted for 2070 in the SSP2.45 scenario, compared to the baseline. The right-side panels shows predicted decreases in CVp derived 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 (Dyderski *et al.*, 2018), 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.

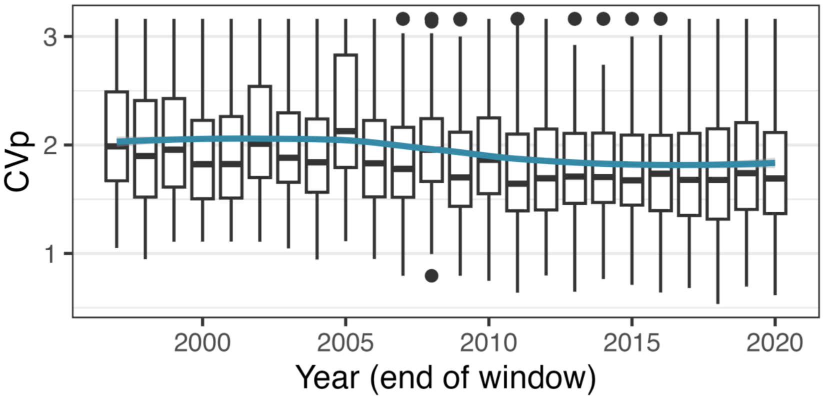

Figure S3: Changes in masting (CVp) over time in the Polish European beech sites. Estimates for each site were derived from 10 year moving windows, using a step size of 1 year. Time is shown as the end-year of this window. A loess regression line is given in blue.

.1 Note S1

.1.1 Methodology

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.