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Widespread breakdown in masting in European beech due to rising summer temperatures

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Abstract

Climate change effects on tree reproduction are poorly understood, even though the resilience of populations relies on sufficient regeneration to balance increasing rates of mortality. Forest-forming tree species often mast, i.e. reproduce through synchronised year-to-year variation in seed production, which improves pollination and reduces seed predation. Recent observations in European beech show, however, that current climate change can dampen interannual variation and synchrony of seed production and that this masting breakdown drastically reduces the viability of seed crops. Importantly, it is unclear under which conditions masting breakdown occurs and how widespread breakdown is in this pan-European species. Here, we analysed 50 long-term datasets of population-level seed production, sampled across the distribution of European beech, and identified increasing summer temperatures as the

general driver of masting breakdown. Specifically, increases in site-specific mean maximum temperatures during June and July were observed across most of the species range, while the interannual variability of population-level seed production (CVp) decreased. The declines in CVp were greatest, where temperatures increased most rapidly. Additionally, the occurrence of crop failures and low seed years has decreased during the last four decades, signalling altered starvation effects of masting on seed predators. Notably, CVp did not vary among sites according to site mean summer temperature. Instead, masting breakdown occurs in response to warming local temperatures (i.e. increasing relative temperatures), such that the risk is not restricted to populations growing in warm average conditions. As lowered CVp can reduce viable seed production despite the overall increase in seed count, our results warn that a covert mechanism is underway that may hinder the regeneration potential of European beech under climate change, with great potential to alter forest functioning and community dynamics.

KEYWORDS
climate change, *Fagus sylvatica*, fecundity, masting, reproduction, seed production

1 | INTRODUCTION

In forests around the globe, increases in disturbance frequency and severity due to anthropogenic climate change have resulted in a twofold increase in tree mortality—a pattern which will likely be exacerbated in the near future (McDowell et al., 2020; Seidl et al., 2017; Westerling et al., 2011). Tree reproduction will therefore play an increasingly important role in forest ecosystem resilience (Bogdziewicz, 2022; Clark et al., 2021), affecting forest persistence, recovery from disturbances, and migration (Falk et al., 2022). In contrast to detailed predictions for tree growth and mortality, little is known about the expected impacts of current climate change on tree reproductive success. The gap is partially associated with the challenges of observing reproductive processes over sufficient spatiotemporal scales to derive generalisable patterns (Bogdziewicz, 2022; Clark et al., 2021). Here, we investigate how seed production patterns in European beech (*Fagus sylvatica*, L., hereafter "beech"), among the continent's most important forest-forming species, respond to recent changes in temperature and precipitation.

Average seed production in trees is changing in response to current climate warming, with both positive and negative trends being documented (Bogdziewicz et al., 2020; Bush et al., 2020; Clark et al., 2021; Pau et al., 2018; Shibata et al., 2019; Yukich Clendon et al., 2023). However, in masting plants, i.e. plants that produce annually variable and synchronised seed crops, trends in mean reproductive effort can be inverse to the trend in viable seeds (Bogdziewicz, 2022). Recent work on beech across the United Kingdom has shown that during four decades of monitoring, seed production has increased while the number of viable seeds has decreased by ~50%–83%, with larger trees showing stronger declines (Bogdziewicz et al., 2020; Bogdziewicz, Kelly, et al., 2023).

Increased temperatures resulted in a "masting breakdown", where declines in interannual variation and among-tree synchrony of seed production led to a decrease in production of viable seeds. Masting occurs throughout the plant kingdom (Dale et al., 2021), and large fluctuations in interannual seed production are common in woody plants (Herrera et al., 1998). Therefore, understanding tree reproductive responses to global change requires understanding mast seeding responses to changes in climate patterns (Hacket-Pain & Bogdziewicz, 2021).

Masting increases fitness through economies of scale, as concentrating reproductive output in intermittent years lowers the cost of reproduction by reducing pollen limitation and seed predation (Pearse et al., 2016). Large and synchronised flower crops increase pollination efficiency (Kelly et al., 2001; Moreira et al., 2014; Rapp et al., 2013). Similarly, masting starves seed predators during synchronous low seed crop years and subsequently satiates predators in high crop years (Bogdziewicz et al., 2018, 2020; Espelta et al., 2008; Fletcher et al., 2010; Kelly et al., 2000; Kelly & Sullivan, 1997; Linhart et al., 2014). Adverse effects on both economies of scale (i.e. predation satiation and pollination efficiency) were found in the UK study: less variable seeding allowed seed-consumer populations to grow, leading to an increase in the pre-dispersal seed predation from ~1% to 40% over four decades (Bogdziewicz et al., 2020). At the same time, less synchronous reproduction decreased pollination efficiency from 50% to 33%. However, it is unclear whether this is a local pattern, or if this trend is widespread throughout the species range. A broad climate change-induced reduction in reproductive potential would severely impact long-term resilience of this major forest-forming masting species (Ohse et al., 2023). Since mast seeding represents a pulsed food resource with numerous cascading effects on wildlife, changes in masting also have the potential

to alter forest community dynamics and their management (Clark et al., 2019; Ostfeld & Keesing, 2000).

Masting breakdown in beech is thought to arise due to changes in the frequency of weather cues that trigger reproduction (Bogdziewicz et al., 2021). Weather cues are deviations from baseline conditions (e.g., temperature and precipitation anomalies in summer and spring) that lead to years of high reproductive output (Bogdziewicz, 2022; Espelta et al., 2008; Kelly et al., 2013; Koenig et al., 2016; Vacchiano et al., 2017). In beech, weather affects seed production throughout the reproductive trajectory from flower initiation to seedfall (Journé et al., 2023). Unlike oak, however, where cues vary between populations (Fleurot et al., 2023), seed production in beech is predominantly driven by June–July temperature anomalies throughout its range (Bogdziewicz et al., 2021; Drobyshev et al., 2010; Journé et al., 2023, 2024; Vacchiano et al., 2017). The timing of this dominant temperature cue is exceptionally stable across geographical and climatic space (Bogdziewicz, Journé et al., 2023). This is because the summer solstice, which happens simultaneously across the northern hemisphere, abruptly opens the temperature-sensing window in beech (Journé et al., 2024). Precipitation in the 2 years prior to seed production may also affect seed production (Mund et al., 2020; Piovesan & Adams, 2001; Vacchiano et al., 2017). It is thought that cool and wet summers in year $t-2$ ensure that sufficient resources are available when the

subsequent warmer and dry summer in year $t-1$ triggers flower bud initiation (Mund et al., 2020; Piovesan & Adams, 2001; Vacchiano et al., 2017). While previous research has explored how weather affects the quantity of seeds produced in a given year (i.e. weather cues of masting), we currently do not know how long-term changes in weather patterns affect masting. A warming climate can increase summer temperature anomalies, which trigger high seed crop years in beech and could therefore result in more frequent seed production (Bogdziewicz, 2022; Bogdziewicz et al., 2021). This might reduce the peak seed crop size if insufficient resources have been accumulated (Bogdziewicz, 2022; Rees et al., 2002). Similarly, higher cue frequency is expected to decrease the occurrence of years with no or low seed production (Bogdziewicz, 2022). We would expect such responses to result in dampened variability of seed production.

Given observations consistent with this prediction in UK populations, it is urgent to establish what drives masting breakdown, and if masting breakdown occurs more widely. A widespread breakdown in masting could have far-reaching implications for the resilience of beech forests and the communities they support. We use 50 time series (mean length: 26.7 years, range: 15–43) of annual seed crops, sampled across the distribution of beech (Figure 1), to assess which climate factors drive change in masting at the population level, and how masting has changed over time across Europe. Specifically, we (1) test the hypothesis that increasing summer (June–July) temperatures
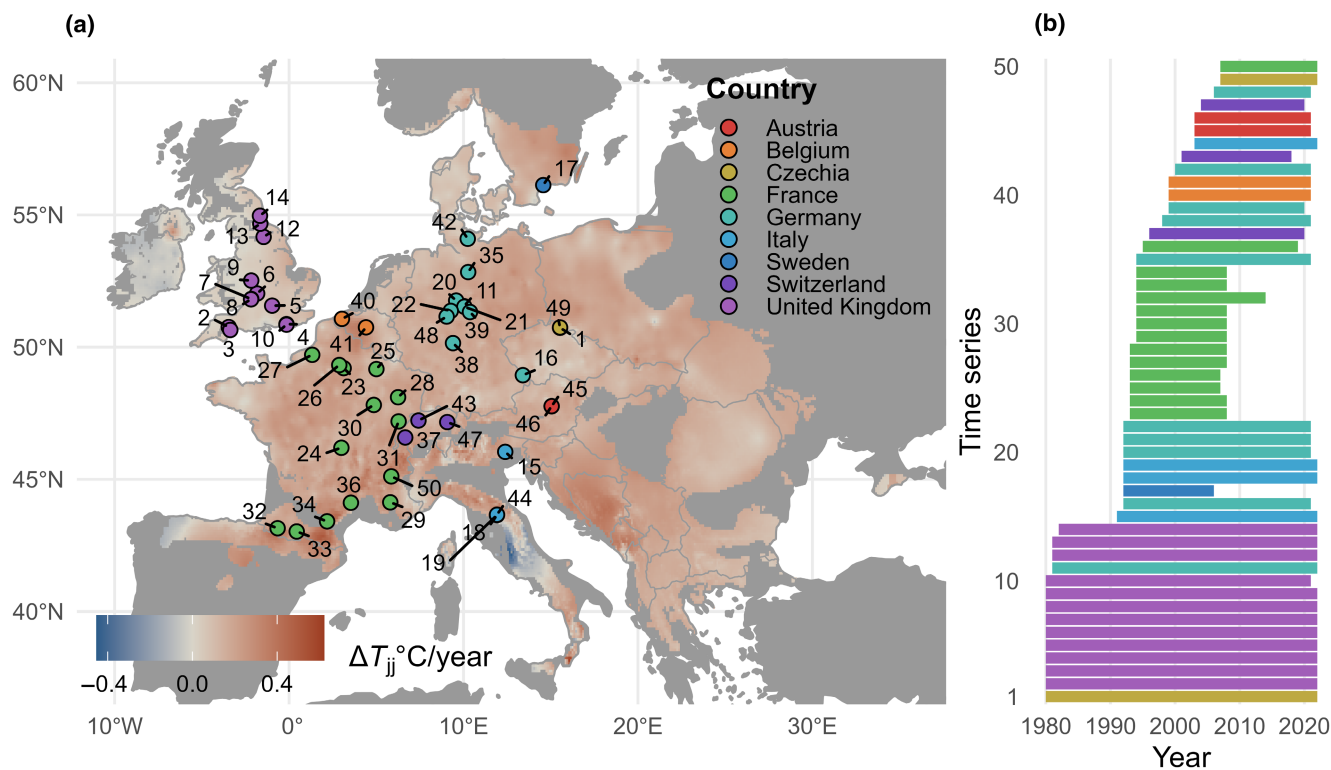
FIGURE 1 Spatial extent of climate change effects on the dominant reproductive cue throughout the range of European beech. The colour of the range in (a) depicts the temporal trends of unscaled mean maximum June–July temperature (ΔT_{jj} °C/year) for each E-OBS grid cell across the European beech range in the last decade of observations (see Section 2 for details). Points show sampled populations, and labels match the time series ID in (b). Panel (b) displays the temporal range of each time series. The matching colour of points in (a) and temporal ranges in (b) specifies the sampling country. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

and precipitation drive a decrease in the temporal variability of seed production (i.e. masting), as estimated by the coefficient of variation of population-level seed production (CVp: the most commonly used metric to describe the strength of masting; Kelly & Sork, 2002). Moreover, we test (2) if larger increases in summer temperatures are associated with larger decreases in CVp. Since we are also interested in the general direction of change over time, we test how (3) masting drivers and (4) reproductive patterns (CVp, mean seed production, low and high seed crops) in beech have varied over recent decades across Europe. These additional reproductive patterns allow us to further understand what drives changes in the temporal variability of seed crops (Bogdziewicz et al., 2020; Bogdziewicz, Kelly, et al., 2023) and illustrate potential consequences; namely, temporal changes in the 25th percentile (i.e. how many seeds are produced during low seeding years, which may starve predators) and 90th percentile of seed crop size (i.e. how many seeds are produced in high seed production years, which may satiate predators) relate to masting fitness benefits. Combined, these analyses provide unprecedented insights into continent-wide effects of climate change on the reproduction of stand-forming tree species.

2 | MATERIALS AND METHODS

2.1 | Study species

Since the last glacial retreat, beech has rapidly colonised large parts of Europe and would cover the majority of central Europe if humankind left land undisturbed (Magri, 2008). It is an increasingly economically important forest-forming species and one of the most diversely used trees in Europe (Houston Durrant et al., 2016). Reproduction in beech populations is driven by a series of weather effects on the sequential processes of bud initiation (floral transition) in the year before reproduction, flowering and pollination in spring, and fructification throughout the summer until seed drop in autumn (Journé et al., 2023). The dominant cue for seed production, that is, summer temperature, is spatially conserved, suggesting that flower initiation occurs at the same time throughout the range (Journé et al., 2024).

2.2 | Data

We obtained annual observations of population-level beech reproductive effort from MASTREE+ (Hacket-Pain et al., 2022), and supplemented these with 405 new observations (year × site). All time series are based on total seed crop size and meet the following criteria: a minimum of 15 local annual observations of beech fruit or seed production of continuous data (excluding time series representing regional scales, indices and ordinal time series). We included 50 time series (mean length: 26.7 years, range: 15–43) with 1336 annual observations in this analysis. We used E-OBS climate data (spatial resolution: 0.1°; temperature: °C; precipitation: mm; v. 27.0; Cornes

et al., 2018) to analyse the relationship between reproduction and local climate. This data was also used to visualise spatial trends in summer temperatures across the distributional range of beech. This range is a combination of the EUFORGEN (v. 16; Caudullo et al., 2023) and the potential range (Bohn et al., 2004).

2.3 | Moving windows and site-level scaling

For each time series, we estimated the CVp, the 25th, and the 90th percentile of seed crop size, and the long-term mean seed crop with 10-year moving windows (i.e. for each time series, the first window of 10 observations are used to calculate a value such as the CVp. Then, the 10-year window is moved along the time series according to the step size, and the calculation is repeated). These variables, together with annual seed crop size, are referred to as the reproductive variables. Using the same moving window approach as for the reproductive variables, we obtained long-term averages of site-level weather conditions. These include conditions related to productivity, namely mean annual temperature (MAT) and annual precipitation (AP), as well as seed production cues mean maximum June–July temperature (T_{jj}) and June–July precipitation (P_{jj}). To exclude site effects in the analyses, we site-scaled all variables via subtraction of the site mean conditions from each observation and subsequent division by the standard deviation of the site's conditions. Thus, no random effect was needed in the analyses.

2.4 | Statistical analysis

All data wrangling and statistical modelling was performed in R v. 4.3.1 (R Core Team, 2023). Regression analyses, except where specified differently, were performed in glmmTMB (v. 1.1.7), and model validation was performed using DHARMa (Brooks et al., 2017; Hartig & Lohse, 2022). To test how long-term variation in June–July weather conditions affect CVp, we fitted a linear model with moving window estimates (Brooks et al., 2017). We included CVp as the dependent variable, and long-term summer temperature and precipitation (i.e. T_{jj} and P_{jj}) as well as their interaction as independent variables. To test for the effect of climate and productivity on CVp, we also included long-term MAT, AP and their interaction. The step size of the moving window estimates was set to 5 years in this regression model to account for temporal autocorrelation, and we found no significant autocorrelation in the model residuals (Durbin-Watson, DW = 2.11, p = .77). In addition, we applied several other modelling approaches to verify the robustness of results. Firstly, we repeated the linear regression model with a 10-year step size (i.e. non-overlapping windows), and fitted another model with a 1 year step size with the CVp of the previous year included as a predictor. Moreover, we constructed Siegel repeated median models, which are non-parametric and robust estimators of trends, for each climate variable (mblm, v. 0.12.1; Komsta, 2019). All alternative approaches yielded qualitatively similar results.

Another linear model was constructed to test how temporal changes in long-term T_{jj} relate to changes in CVp (in other words, do populations experiencing larger increases in T_{jj} experience stronger decreases in CVp?). The degree of change (Δ) in CVp and T_{jj} was obtained for each time series by calculating the difference between subsequent values of the moving window estimates. The dependent variable (ΔCVp) was then regressed against ΔT_{jj}. Since residuals showed a longitudinal trend, Longitude was also added as a predictor in the model.

Additionally, we investigated if trends in CVp across spatial temperature gradients match temporal patterns. We fitted a linear model with site-mean CVp as the dependent variable and site-mean unscaled June–July temperature, time series length and seed collection method (i.e. seed count or seed trap) as the independent variables.

To test our hypotheses about long-term changes in beech masting, we examined temporal trends in reproductive variables (i.e. annual seed crop, long-term mean seed crop, CVp, 25th and 90th percentile seed crop) on our sites with a linear model for each site-scaled dependent reproductive variable (apart from the annual seed crop variable for which no moving window approach was used, these were obtained with moving windows with a step size of 1 year), including 'year' as the independent variable. We formulated a similar temporal model for the long-term climatic driver (i.e. T_{jj}), increasing the step size to five to account for temporal autocorrelation in the model residuals.

We tested for recent changes in June–July temperatures across the species range by fitting linear models using stats (v. 4.3.1; R Core Team, 2023). In these, we fitted unscaled June–July temperature of the 10 most recent years of observation (i.e. 2013–2022) as the dependent, and 'year' as the independent variable for each spatial grid cell.

To test for trends in the frequency of June–July temperature cues, we fitted two binomial mixed models. These models tested for changes in the occurrence of unscaled June–July temperature one SD above and below the long-term site-specific summertime mean temperature, following Bogdziewicz et al. (2021). Here, we included 'site' as a random intercept. In addition, we fitted a linear model, regressing unscaled June–July temperature over time, with 'site' as a random intercept. When required for model convergence, we scaled the 'year' variable and subsequently back-transformed coefficients.

3 | RESULTS

3.1 | Mechanism of change: Masting and climate

The analysis of 10-year moving windows revealed that interannual variability of reproduction (CVp) is negatively correlated with increases in June–July temperatures (−0.43 SD±0.09 SE, $p<.001$; Figure 2a; Table 1). No significant effect on CVp was found for long-term MAT and precipitation, or June–July precipitation. Perhaps most importantly, CVp has fluctuated jointly with June–July temperatures (Figure S1), and the directionality of change in CVp depends on temporal changes in summer temperature. The largest decreases in CVp were observed when populations experienced the largest increases in June–July temperature (−0.25 SD±0.09 SE, $z=−2.70$, $p<.01$; Figure 2b). In
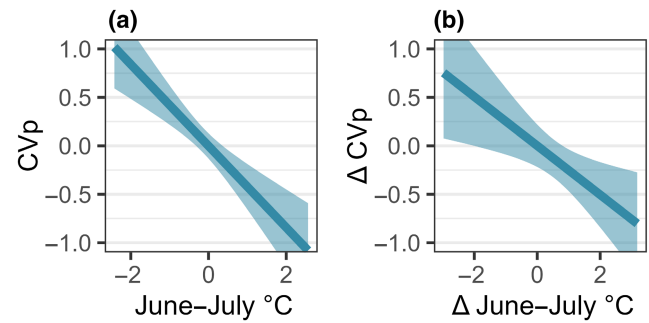

FIGURE 2 Summer warming drives the masting breakdown in beech. (a) Site-scaled 10-year mean maximum June–July temperature is linked to lower site-scaled CVp. (b) Larger degree of site-scaled summer warming between subsequent 10-year moving windows (i.e. more positive Δ June–July °C) is associated with a stronger decrease in site-scaled CVp (i.e. more negative Δ CVp). The prediction lines and associated 95% confidence interval are derived from linear models. See Section 2 for details. Figure S3f,g show versions of these plots with partial residuals.

contrast to the effects of temporal change in summer temperature on CVp, spatial gradients in site-mean CVp are not explained by average summer temperatures (0.03±0.03 SE, $z=0.97$, $p=.34$; Figure S2).

3.2 | Temporal trends in climate

June–July warming occurred across large parts of the range of beech in the last decade (Figure 1). Across our sites, long-term June–July temperatures rose 0.045 SD (±0.007 SE, $z=6.352$, $p<.001$) per year (Figure 3). This warming translated into strong changes in the frequency of the June–July cue for seed production, with particularly striking changes from the mid-2000s onwards (Figure 4). The occurrence probability of cool summers (one SD below local long-term site-specific mean conditions) significantly decreased over time from ~44.41% in 1980 to ~4.30% in 2022, whereas the probability of warm summers (one SD above the mean) significantly increased from ~6.93% to ~27.03%. The annual trend in unscaled mean maximum June–July temperatures was overall positive (0.041°C±0.004 SE, $p<.001$; Figure 4).

3.3 | Temporal changes in reproduction

We observed temporal trends in masting metrics across the species range (Figure 5; Table 2). Mean annual crop size, interannual variability (CVp), the size of low seed production years (estimated 25th percentile) and size of peak years (estimated 90th percentile) all changed over the 43-year study period (Figure 5; Table 2). The CVp significantly decreased by 0.025 SD per year (±0.004 SE, $p<.001$; Figure 5c). On average, annual seed crops were 0.26 SD larger in 2022 than in 1980 (Figure 5a). This trend is even more pronounced when looking at long-term seed crops (i.e. 10-year moving window average); during the period 2013–2022, seed crops were 1.12 SD

Term	Estimate	SE	z	p
(Intercept)	0.026	0.066	0.396	.692
Long-term mean annual temperature (MAT)	0.111	0.082	1.358	.175
Long-term annual precipitation (AP)	−0.085	0.083	−1.031	.303
Long-term June–July temperature (T_{jj})	**−0.429**	**0.090**	**−4.767**	**<.001**
Long-term June–July precipitation (P_{jj})	−0.067	0.082	−0.820	.412
Long-term MAT × Long-term AP	0.052	0.060	0.876	.381
Long-term T_{jj} × Long-term P_{jj}	0.070	0.074	0.948	.343

TABLE 1 The effect of long-term variation in weather on interannual variation (CVp) in seed production.

Note: Variables were calculated using 10-year moving windows and scaled at the site level (see Section 2 for details). Predictor variables of the linear regression are mean annual temperature, annual precipitation, mean maximum June–July temperatures and June–July precipitation. Bold font was used to emphasise the statistically significant predictor.
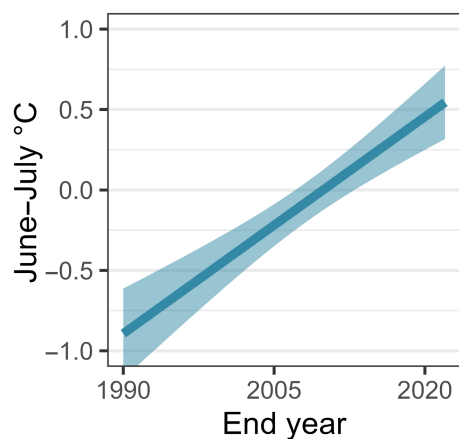

FIGURE 3 Summer warming over time. The prediction line shows the temporal trend in the 10-year moving mean of site-scaled mean maximum June–July temperature. End year: the moving mean is attributed to the last year of each window. The prediction lines and associated 95% confidence intervals are derived from linear models. See Section 2 for details. Figure S3e shows a version of this plot with time series.

larger than between 1980 and 1989 (Figure 5b). The estimated 90th percentile of seed production increased slightly over time (0.008 SD ± 0.004 SE per year, $p < .05$; Figure 5e), indicating that seed crops were larger during peak reproductive events. Increases in seed production were not solely concentrated in peak years: the 25th percentile of seed production also significantly increased over time (0.022 SD ± 0.004 SE per year, $p < .001$; Figure 5d). This indicates that there were fewer years of low or absent reproduction as time progressed.

4 | DISCUSSION

4.1 | Widespread masting breakdown linked to climate warming

We show that climate warming is dampening the variability of seed production of European beech across its geographical range. Decades with warmer summer temperatures are associated with a

lower CVp, and larger increases in summer temperatures are linked to greater decreases in CVp. Notably, this contrasts with variation in average CVp across climate space, where no significant effect of summer temperature was found. Thus, masting is not weaker at warmer sites, but masting breaks down when sites are warming. The impact of climate warming on reproduction has been largely overlooked, which could result in an overestimation of forest resilience and adaptability (Bogdziewicz, 2022; Clark et al., 2021). The observed decrease in variability of seed production due to summer warming is important, as this likely impacts viable seed production via economies of scale (Bogdziewicz et al., 2020; Linhart et al., 2014; Moreira et al., 2014). We find that reproductive peaks are becoming larger and low seed crop years are simultaneously becoming less likely, with a net effect of reduced interannual variability. Therefore, economies of scale may now be diminished in beech, increasing costs of reproduction. While previous research efforts have made strides into assessing the impact of climate change on reproduction in masting trees (Bogdziewicz et al., 2020; Shibata et al., 2019), their spatial scope has been limited. Our findings unveil a concerning reality: masting breakdown is occurring in populations across the distribution of beech, indicating that the reproductive potential of this dominant forest tree species could be hampered by climate warming, and forest food webs may be transformed.

4.2 | Frequency of cues and seed production patterns

The decline of interannual variability of beech seed production is primarily attributed to rising June–July temperatures. This variable has often been correlated with the occurrence of high-seeding years in beech (Bogdziewicz et al., 2021; Bogdziewicz, Kelly, et al., 2023; Drobyshev et al., 2010; Piovesan & Adams, 2001; Vacchiano et al., 2017). The long-term and spatially extensive nature of our data offered a unique opportunity to assess how site-specific fluctuations in June–July temperatures relate to CVp. This provided outstanding evidence for a major role of the summer temperature cue: when June–July temperatures increase, CVp
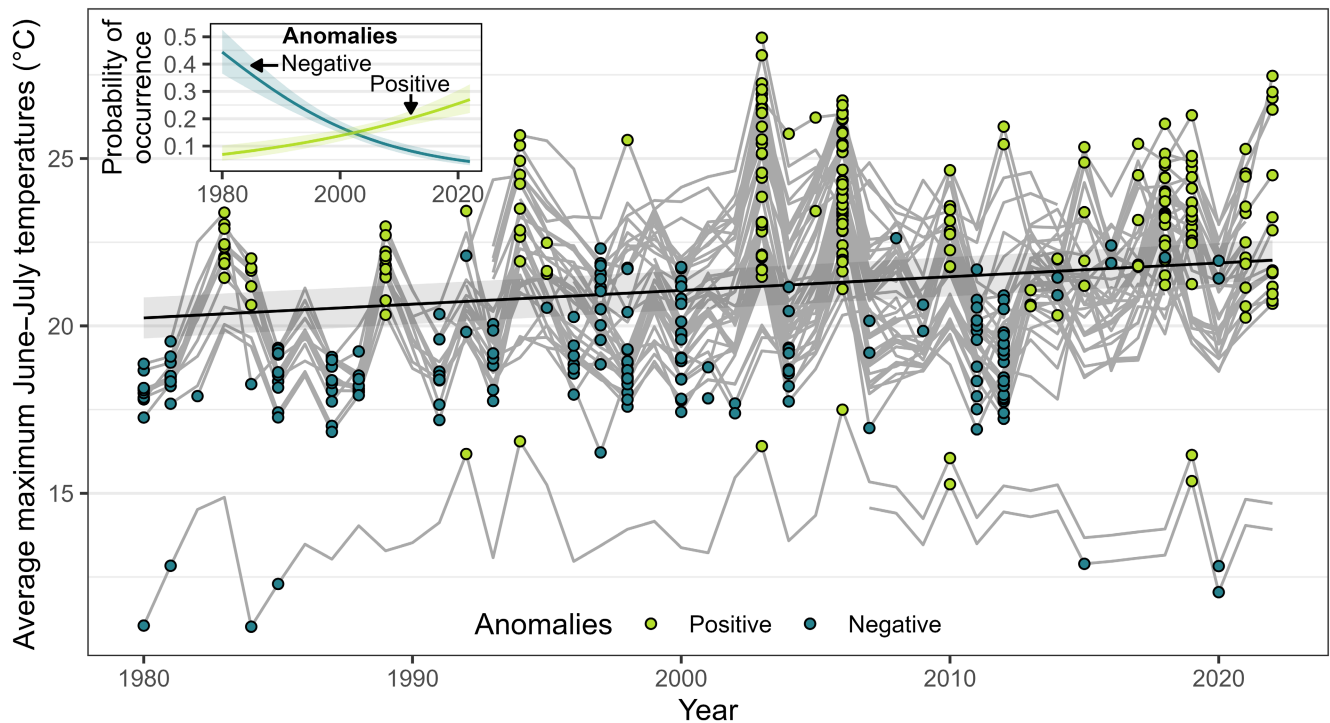
FIGURE 4 Climate change effects on probability of weather cues for beech reproduction. Anomalies visualised as years with mean maximum June–July temperatures one SD above or below site-specific mean conditions. Grey lines show unscaled site-level annual mean maximum June–July temperatures. The black line shows the significant temporal trend (+95% confidence intervals), obtained from a linear mixed model. Two high elevation Czech sites have relatively low temperatures. The inset plot shows the probability of occurrence of positive and negative anomalies over time. See Section 2 for details.

declines, while in reverse, a decline in summer temperatures coincides with a higher CVp (Figure 2; Figure S1). Common gardens, which help distinguish between processes of adaptation and acclimation, would improve our understanding of why spatial and temporal trends differ.

Several reasons may explain the observed increases in mean seed crop sizes, including ageing populations and improved resource availability (Pesendorfer et al., 2020). Nevertheless, our findings indicate it is likely that increased seed production has, at least in part, occurred because of more frequent cueing of masting. The observed increase in seed crop size during low seeding years conforms with the prediction that increased cue frequency reduces the occurrence of years in which there is either no or limited seed production (Bogdziewicz, 2022). We did not find support for the hypothesis that insufficient resource acquisition between large seed crop events leads to reductions in seed crop size in peak reproduction years (Bogdziewicz, 2022), because the magnitude of peak crops increased over time. This could be explained by increased resource availability or acquisition, or by shifts in resource allocation. Regardless, we expect the observed masting breakdown to intensify as the rate of CVp decline increases with the rate of summer warming, and climate warming is predicted to continue over the coming decades throughout the entire range of European beech (Gutiérrez et al., 2023; IPCC, 2023).

4.3 | Potential consequences

Despite positive trends in mean seed production, regeneration concerns arise because CVp is tightly linked to two economies of scale: predation satiation and pollination efficiency. The masting breakdown in beech, particularly the increased reproduction during low seed years, likely results in decreased predator satiation. Less effective starvation in low seed years results in larger populations of seed-consumers in high seed years, increasing predation (Bogdziewicz et al., 2020; Zwolak et al., 2022). Added predation pressure could exacerbate recruitment limitations, reducing the resilience of beech within its current range and limiting its ability to track its climate niche.

Changes in pollination efficiency are challenging to assess without additional information. Individual-level data show that successful pollination in masting plants depends on within-population synchrony (Bogdziewicz et al., 2020; Moreira et al., 2014). The dampening of variability we observed implies reduced synchrony, which would negatively impact pollination efficiency. However, we also noted an increase in the magnitude of peak seed production, potentially signalling higher flowering effort or increased synchrony in years of peak reproductive effort.

Synthesising existing seed viability data and expanding individual-level data collection across the species range is necessary
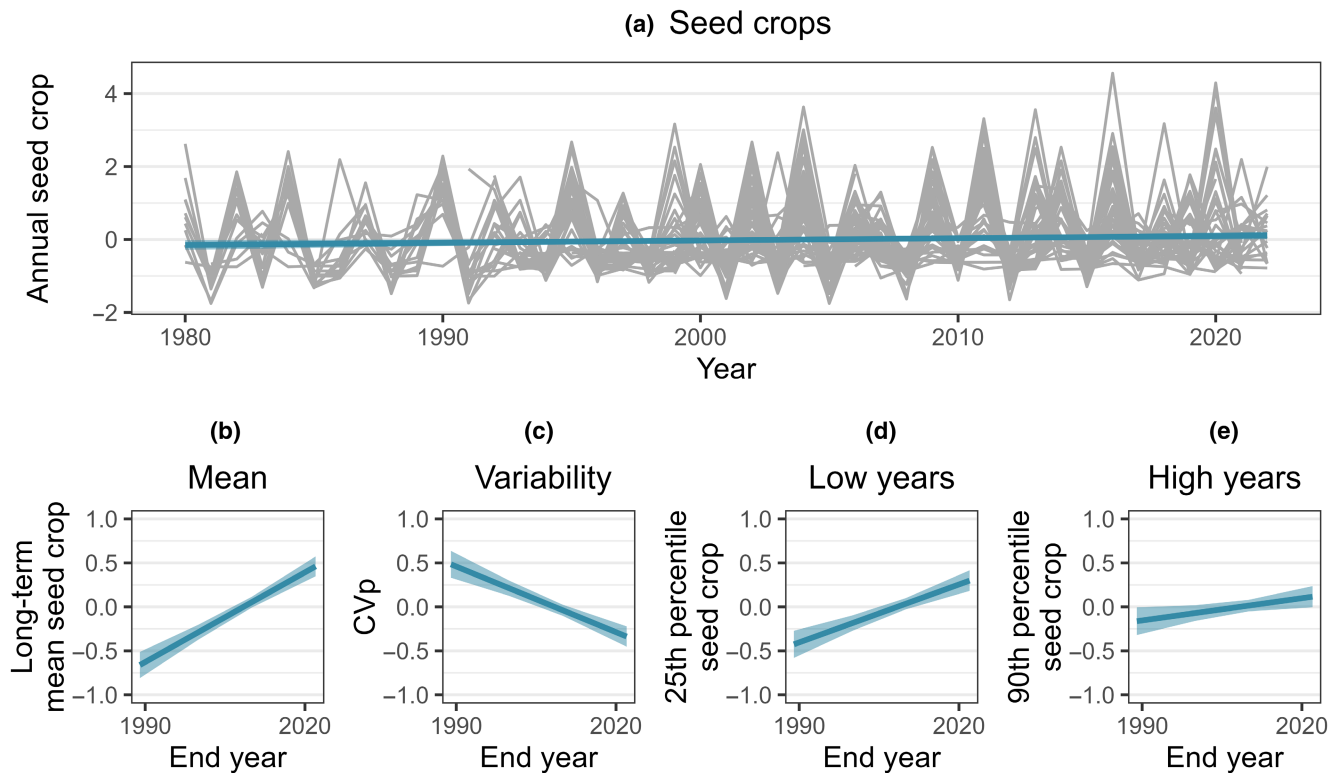
FIGURE 5 Changes in reproductive variables across the range of European beech ($N = 50$ populations). While (a) annual and (b) long-term mean seed crops have increased, (c) interannual variability has declined as fewer years of (d) extremely low or (e) high reproduction has been observed. End year: the moving mean is attributed to the last year of each window. Trends are derived from site-scaled linear models and are shown with associated 95% confidence intervals. See Section 2 for details. Figure S3a–d show versions of plot (b–e) with time series.

TABLE 2 Temporal trends in long-term reproductive patterns from 50 beech populations.

Term	Estimate	SE	z	p
Annual seed crop	0.006	0.003	2.424	**.015**
CVp	−0.025	0.004	−6.809	**<.001**
Long-term mean seed crop	0.034	0.004	9.516	**<.001**
25th Percentile seed crop	0.022	0.004	5.925	**<.001**
90th Percentile seed crop	0.008	0.004	2.226	**.026**

Note: Long-term variation in response variables was obtained prior to regression using 10-year moving windows, and variables were scaled at the site level (see Section 2 for details). A linear model was fitted for each reproductive pattern, with time (Year) as the predictor. CVp stands for the coefficient of variation of seed production, and describes the temporal variability of seed production at the species level. Bold font was used to emphasise statistically significant p-values.

to confirm changes in seed predation and pollination efficiency in situ. Additionally, further research is warranted to understand how changes in economies of scale affect later life stages; while masting breakdown might limit recruitment (Maringer et al., 2020), increased reproductive effort may, in certain contexts, compensate for reduced reproductive efficiency. Research on reproductive outcomes

is especially pertinent in the northern parts of the range. Beech expansion is anticipated in the north (Kramer et al., 2010), but northern populations experience increasing masting cue frequencies.

The now-dampened feast-famine cycles that have historically characterised beech forests may carry far-reaching consequences on ecosystem dynamics across Europe, beyond their impact on tree regeneration. Peak seed crops represent a resource pulse to a wide variety of seed consumers and their predators. For instance, beech mast has been associated with migration of seed consuming birds like bramblings that depend on mast as a winter food (Jenni, 1987; Lithner & Jönsson, 2002), increased rodent densities (Bregnard et al., 2021; Reil et al., 2016), as well as higher densities of secondary consumers such as owls and pine martens (Lithner & Jönsson, 2002; Maag et al., 2024). Birds may also suffer from increased densities of rodents, for instance through higher nest predation rates (Elliott & Kemp, 2016; Szymkowiak & Thomson, 2019). Furthermore, as a consequence of higher rodent populations and their parasites such as ticks, anthropogenic health risks of e.g. Lyme disease or haemorrhagic fever caused by Hantaviruses will likely increase (Bregnard et al., 2021; Reil et al., 2016). Based on our findings, disease risk may show reduced year-to-year fluctuation. Similarly, changes in the variability of seed availability may impact human-wildlife conflicts, including with large mast-consuming mammals (Baruch-Mordo et al., 2014; Bautista et al., 2022; Bisi, 2018). Seed-consumer responses to masting breakdown are poorly understood, and mechanistic models

linking climate and mast availability to population dynamics will be of high value (Touzot et al., 2020). Observed changes in the reproductive patterns of plants have the potential to severely modify the dynamics of forest ecosystems as we know them.

4.4 | Concluding remarks

We demonstrate that the breakdown of masting is related to increasing summer temperatures and that breakdown is not restricted to local populations (Bogdziewicz et al., 2020; Bogdziewicz, Journé et al., 2023). Breakdown occurs in response to warming local temperatures, such that the risk is not restricted to populations growing in warm conditions (i.e. beech responds to relative rather than absolute temperatures). The breakdown raises concerns for the long-term population dynamics of masting plants, which are found throughout the plant kingdom and occur in boreal, temperate and tropical regions (Bogdziewicz, 2022; Dale et al., 2021; Pearse et al., 2016). While the links between weather and masting appear to be species-specific (Hacket-Pain & Bogdziewicz, 2021) and, in some cases, population-specific (Fleurot et al., 2023), climate warming is likely to affect many of these species directly through altered weather patterns, or indirectly via altered resource availability (Bogdziewicz, 2022). Intensification of seed and seedling monitoring is required to address the impacts of climate change on reproduction across systems.

AUTHOR CONTRIBUTIONS

Jessie J. Foest: Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Michał Bogdziewicz:** Conceptualization; supervision; writing – review and editing. **Mario B. Pesendorfer:** Conceptualization; resources; writing – review and editing. **Davide Ascoli:** Conceptualization; writing – review and editing. **Andrea Cutini:** Resources; writing – review and editing. **Anita Nussbaumer:** Resources; writing – review and editing. **Arne Verstraeten:** Resources; writing – review and editing. **Burkhard Beudert:** Resources; writing – review and editing. **Francesco Chianucci:** Resources; writing – review and editing. **Francesco Mezzavilla:** Resources; writing – review and editing. **Georg Gratzer:** Resources; writing – review and editing. **Georges Kunstler:** Resources; writing – review and editing. **Henning Meesenburg:** Resources; writing – review and editing. **Markus Wagner:** Resources; writing – review and editing. **Martina Mund:** Resources; writing – review and editing. **Nathalie Cools:** Resources; writing – review and editing. **Stanislav Vacek:** Resources; writing – review and editing. **Wolfgang Schmidt:** Resources; writing – review and editing. **Zdeněk Vacek:** Resources; writing – review and editing. **Andrew Hacket-Pain:** Conceptualization; data curation; resources; supervision; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

All authors declare they have no competing interests.

DATA AVAILABILITY STATEMENT

The reproductive data that support the findings of this study are openly available in DRYAD at https://doi.org/10.5061/dryad.qz612 jmps. They will also become available as a MASTREE+ update on GITHUB at https://github.com/JJFoest/MASTREEplus. E-OBS data that support the findings of this study are openly available at https://doi.org/10.24381/cds.151d3ec6 and https://surfobs.climate.coper nicus.eu/dataaccess/access_eobs.php#datafiles.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.