Oak masting remains stable despite climate warming

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keywords: climate change | mast seeding | cue sensitivity | climate velocity | seed production | forest regeneration

Abstract

Climate warming alters tree reproduction, but long-term tests of how it affects the large, synchronised interannual fluctuations in seed production known as masting remain rare. Theory predicts that climate-driven declines in masting should be most likely when species combine high reproductive sensitivity to weather cues with rapid climatic change during the corresponding cue windows. We tested this prediction using seed-production records of pedunculate and sessile oaks (*Quercus robur*, *Q. petraea*) from 389 sites in Poland spanning 1988–2022, and compared oak responses with sympatric European beech (*Fagus sylvatica*), where warming-driven masting decline has been documented. Oak seed production responded to spring temperatures, but cue sensitivity was about 60% lower than in beech. In addition, warming during the oak spring cue windows was weaker than warming during the main beech summer cue window, with March temperatures warming 36% more slowly and April–May temperatures 68% more slowly. Consistent with this weaker combination of cue sensitivity and climatic forcing, interannual variability in oak seed production did not decline over time. However, oak variability was lower in decades with warmer March temperatures, indicating that warmer cue regimes can still reduce masting variability when climatic shifts are sufficiently large. In contrast, European beech combined stronger cue sensitivity with faster warming in its main cue window and showed a clear decline in masting variability. These results support the hypothesis that climate-change effects on masting depend on the interaction between cue sensitivity and climate velocity. Because masting governs regeneration pulses and episodic resource supply for seed consumers, species differences in cue sensitivity may determine which forest regeneration processes and food webs are most altered by climate change.

Introduction

Climate warming is putting pressure on forest ecosystems, increasing mortality, often decreasing growth, and disrupting reproduction (McDowell *et al.*, 2020; Klesse *et al.*, 2024; Foest *et al.*, 2026). From these demographic rates, effects of climate change on reproduction remain relatively understudied (Clark *et al.*, 2021; Hacket-Pain & Bogdziewicz, 2021). Yet, reproduction determines whether population losses are replaced and how forests reorganize after disturbance (Seidl & Turner, 2022). Seed output also governs tree dispersal across landscapes, influencing range shifts under changing climates (Nathan *et al.*, 2011; Sharma *et al.*, 2022). Understudied reproduction reflects data constraints: inference on seed production dynamics requires multi-decadal records, and such datasets are rare (Clark *et al.*, 2021). Nonetheless, where long-term data exist, they reveal sensitivity of reproduction to weather variation (Clark *et al.*, 2011; Pearse *et al.*, 2017; Journé *et al.*, 2025), implying significant exposure to ongoing climatic change. Consistent with this expectation, declines in mean seed production have been reported in several systems (Foest *et al.*, 2026), including reductions exceeding 50% in species such as pinyon pine (*Pinus edulis*) (Redmond *et al.*, 2012; Wion *et al.*, 2025), European beech (*Fagus sylvatica*) (Bogdziewicz *et al.*, 2023; Foest *et al.*, 2026), or in community-level fruiting in Gabon (Bush *et al.*, 2020). These observations raise a central question, important from both theoretical and management perspectives: which tree species can maintain reproductive output under rapid warming?

In numerous temperate tree species, viable seed supply is not determined by total seed production alone, but also by the temporal structure of reproduction, i.e., its interannual variation (Pearse *et al.*, 2016; Pesendorfer *et al.*, 2021). Interannual variability in seed production, known as masting, determines how effectively reproductive effort translates into viable seeds and seedling recruitment (Bogdziewicz *et al.*, 2024a). By concentrating reproduction into infrequent years, trees increase pollination success and reduce per-seed predation, thereby increasing the fraction of seeds that successfully disperse (Rapp *et al.*, 2013; Zwolak *et al.*, 2022). Because regeneration depends on viable seed supply, shifts in masting dynamics under climate change may constrain forest regeneration (Bogdziewicz *et al.*, 2023). Evidence that masting is climate-sensitive is accumulating (Hacket-Pain & Bogdziewicz, 2021). Theory predicts that this sensitivity should vary among species depending on the climatic control of reproduction (Bogdziewicz *et al.*, 2024b, 2025), yet these predictions remain largely untested against long-term empirical data.

Masting is driven by the interaction of weather cues and internal resource dynamics (Pearse *et al.*, 2016; Kelly *et al.*, 2025). Weather cues synchronize reproduction by promoting or inhibiting flowering at specific developmental stages (Bogdziewicz *et al.*, 2025). For example, summer temperatures may enhance flowering initiation (Samarth *et al.*, 2021; Journé *et al.*, 2024; Fleurot *et al.*, 2023), while spring weather regulates pollination efficiency (Koenig *et al.*, 2015; Fleurot *et al.*, 2024). Because these cues determine when and to what extent reproductive effort is expressed, changes in cue frequency under warming can alter the temporal distribution of seed production (Bogdziewicz *et al.*, 2024b). Species are predicted to differ in their sensitivity to climate change depending on the structure and strength of their reproductive cues. The few empirical studies illustrate these divergent responses. In Japanese oak (*Quercus crispula*), warmer spring temperatures were associated with increased flowering frequency and reduced inter-annual variability (Shibata *et al.*, 2020). In New Zealand, reduced occurrence of low-temperature conditions required for heavy seeding in tawa (*Beilschmiedia tawa*) led to prolonged reproductive failure (Yukich-Clendon *et al.*, 2023). European beech (*Fagus sylvatica*) showed a decline in variability and synchronisation of seed production, associated with summer warming and increased cue frequency (Bogdziewicz *et al.*, 2020a; Foest *et al.*, 2025). Mechanistically, in beech, more frequent summer temperature cues triggered reproductive allocation before internal resource pools were replenished, leading to repeated depletion (Hacket-Pain *et al.*, 2025). As flowering responsiveness depends on stored resources, depleted trees became less responsive to subsequent cues, resulting in smaller and more regular seed crops (Bogdziewicz *et al.*, 2021; Kelly *et al.*, 2025). In contrast, in North American Pinaceae, interannual variation in seed production has remained largely stable over the last 50 years, coinciding with a relatively slow rate of summer warming (0.09 °C per decade)(LaMontagne *et al.*, 2021).

These masting changes are consequential. In European beech, reduced interannual variation weakens key fitness benefits of masting, including reduced pollination efficiency and increased seed predation, resulting in a decline of over 50% in viable seed supply (Bogdziewicz *et al.*, 2023; Jantzen *et al.*, 2026). Beyond plant reproduction, shifts in seed supply propagate through food webs. In northern red oak (*Quercus rubra*), a long-term increase in seed production associated with warmer springs was accompanied by a long-term increase in rodent abundance and body mass (Dri *et al.*, 2025). Where rodent populations become more abundant, these changes are expected to feed back on plant reproduction through shifts in seed predation and rodent-mediated dispersal (Zwolak *et al.*, 2024), and to propagate through food webs via effects on rodent predators and parasites (Ostfeld & Keesing, 2000). Long-term decline in fruiting in Gabon led to a decline in body condition of frugivores (Bush *et al.*, 2020).

Weather cues are major regulators of masting (Bogdziewicz *et al.*, 2025). While temperature is the major cue across species, plants differ in the sign and season of their weather cue sensitivity, often employing multiple cues along the seed maturation cycle (Journé *et al.*, 2025). Cue sensitivity—the change in reproductive allocation per unit change in a weather cue (e.g., °C)—determines how strongly flowering responds to interannual weather variation (Kelly *et al.*, 2013). Species with high cue sensitivity exhibit steep flowering responses to favorable conditions and therefore large interannual fluctuations in reproductive allocation, generating pronounced masting dynamics (Journé *et al.*, 2025). Cue sensitivity is believed to be an important predictor of how variable reproductive allocation will respond to climate change (i.e., the climate-driven risk to masting).

In highly sensitive species, even modest increases in cue frequency can induce more frequent high reproductive allocation (Bogdziewicz *et al.*, 2025). Because a strong reproductive response to cues depletes resource reserves (Sala *et al.*, 2012; Roncé *et al.*, 2023), warming-driven increases in favorable cue conditions may cause these species to allocate heavily to reproduction before resource pools have been replenished (Hacket-Pain *et al.*, 2025). Because flowering responsiveness depends on resource reserves (Monks *et al.*, 2016; Kelly *et al.*, 2025), repeated depletion reduces subsequent responsiveness to cues, compressing large peaks and resulting in more frequent but smaller events and lowering interannual variation in seed production (Bogdziewicz *et al.*, 2021; Kelly *et al.*, 2025). In contrast, species with low cue sensitivity are expected to exhibit more gradual reproductive allocation responses to weather cues. Their weaker cue sensitivity reduces the risk of recurrent overinvestment and cumulative depletion, thereby buffering temporal variability even as cue frequency increases. The extent to which masting declines under climate change should therefore depend on the interaction between cue sensitivity and climate velocity during the weather cue windows. Rapid warming in a highly sensitive species is expected to accelerate resource depletion cycles and reduce interannual variability (Foest *et al.*, 2024, 2025). Slower climatic change, or low cue sensitivity, should result in limited disruption (Bogdziewicz *et al.*, 2025). Although this interaction emerges from a theory built on recent empirical studies, it has not yet been quantified comparatively across species.

In this study, we test how cue sensitivity and rate of climate change combine to affect masting trends, using long-term seed production records of oaks (*Quercus robur* and *Q. petraea*), and contrast oak trends with those of sympatric European beech (Foest *et al.*, 2025). Three main temperature cues drive oak masting. Low summer temperatures in the year preceding seed fall (t-1) increase flower initiation for the following spring (Hanley *et al.*, 2019; Fleurot *et al.*, 2023; Szymkowiak *et al.*, 2024a). Subsequent spring temperatures (year t) influence pollination dynamics and determine the proportion of female flowers that are fertilized (Schermer *et al.*, 2019; Fleurot *et al.*, 2024). Spring temperatures have two contrasting effects. Early spring temperatures affect flowering synchrony among individuals: warm conditions can reduce synchrony because individuals differ in photoperiod sensitivity (Zohner *et al.*, 2018; Bogdziewicz *et al.*, 2020b). When early spring is warm, less photoperiod-sensitive trees flower earlier than trees requiring a longer day length, which decreases pollen exchange and lowers seed production, even when the prior summer temperature cue has initiated high flowering effort (Bogdziewicz *et al.*, 2020b). Temperatures later in spring, during the pollination period, influence pollen diffusion and fertilization success (Schermer *et al.*, 2020; Fleurot *et al.*, 2024).

In all three cue windows, warming can affect interannual variation in seed production when cue sensitivity or change in climate is rapid, although through different pathways (Table 1). In the summer t-1 window, warming reduces the frequency of favourable cold conditions for flower initiation. This should alter resource-cue dynamics (Kelly *et al.*, 2025): warm summers may allow resources to accumulate without triggering strong flowering, whereas rare cold summers may drive stronger reproductive responses from resource-filled trees. Consequently, warming may lead to prolonged weakening of flowering initiation, thereby increasing interannual variation in seed production. Warmer early springs should reduce interannual variation through reduced flowering synchrony and pollination efficiency, lowering the occurrence of high-seeding years and increasing the frequency of intermediate seed crops. Warmer late springs should act through another resource-mediated pathway: by increasing the frequency of years with efficient pollen diffusion and high fertilization success, warming may increase repeated reproductive investment, prevent the full replenishment of internal resource pools, weaken responses to subsequent cues, and ultimately reduce interannual variability in seed production (Bogdziewicz *et al.*, 2021; Kelly *et al.*, 2025).

Table 1: Expected effects of warming-driven changes in weather cues on crop size and interannual variation in oak masting.

Weather cue	Effect of higher cue values on crop size	Warming effect on cue frequency	Effect on masting interannual variation[*]	Comment
Summer t-1	Decreases crop size via lower flower initiation	Favourable cold summers become less frequent	Increased	Resource-cue interaction: warm summers allow resources to accumulate without triggering strong flowering, resulting in less frequent but stronger high-seeding years when favourable cold summers occur.
Early spring t (March)	Decreases crop size via lower flowering synchrony and pollen limitation	More frequent	Reduced	Poor pollination years become more frequent, producing more intermediate-crop years and lower CV. CV declines mainly through lost high-crop years rather than resource depletion. Higher resources should not strengthen cue responses, because pollen limitation constrains crop size.
Late spring t (April-May)	Increases crop size via higher pollen diffusion	More frequent	Reduced	Resources-cue interaction: more frequent cues cause persistent resource depletion and weaker cue responses. If cues became less frequent, higher resources are unlikely to strengthen responses, because pollination would not improve with resource level.

[*] If sensitivity or climate-change velocity is sufficiently high.

We analysed oak seed production records from 389 sites, spanning 1988–2022, to quantify temporal trends in the coefficient of variation (CV) of seed production. We estimated weather cue sensitivity for each of the three temperature windows (summer t-1, early spring t, and late spring t) and tested for temporal trends in temperature within those windows. Finally, we evaluated whether decades characterized by higher temperatures during cue windows were associated with altered CV, as outlined in Table 1. To place oak responses in context, we compared these patterns with sympatric European beech, where a decline in CV has previously been documented and linked to increasing summer temperatures (Foest *et al.*, 2025). This comparative approach allows us to assess how climatic forcing leads to changes in masting patterns across species that differ in cue sensitivity. We formulated the following predictions. As oak masting is less variable than beech masting (Journé *et al.*, 2023), oak cue sensitivity should be relatively low. In consequence, a temporal decline in seed production CV is expected only if strong temperature trends during cue windows are underway. Regardless of long-term trends, however, decades with warmer temperatures during cue windows should exhibit altered CV associated with changed cue frequency, with the direction of the CV change depending on cue sign (Table 1).

Methods

Study species

We worked on two functionally similar pedunculate and sessile oaks (*Quercus robur* and *Q. petraea*), and European beech (*Fagus sylvatica*). Temperate oaks (*Q. robur* and *Q. petraea*) and European beech together dominate roughly one quarter of temperate European forests (Spiecker, 2021; Kulla *et al.*, 2023). The proximate weather cues governing reproduction differ between these taxa. In oaks, flower initiation occurs during the summer preceding seed fall, whereas temperatures during spring flowering and pollination strongly influence fertilization success and acorn set (Koenig *et al.*, 2015; Schermer *et al.*, 2019; Fleurot *et al.*, 2023).

In European beech, flowering initiation is promoted by low temperatures two years preceding seed fall (t-2), and high summer temperatures in the year preceding seed fall (t-1) (Vacchiano *et al.*, 2017; Szymkowiak *et al.*, 2024b; Hirsch *et al.*, 2025). Increasing frequency of the t-1 cue under climate warming has led to more frequent reproductive investment and depletion of internal resource pools, ultimately reducing both interannual variability and synchrony of seed production (Bogdziewicz *et al.*, 2021; Foest *et al.*, 2025). As a result, beech masting dynamics have shifted from rare large events to more frequent but smaller seed crops, with substantial reductions in viable seed production (Bogdziewicz *et al.*, 2023).

Seed production data

Annual seed harvests were reported by local forest districts (*Nadleśnictwa*, hereafter “sites”) to the Polish State Forests based on collections made between 1988 and 2022 within designated seed stands (Fig. 1) (Foest *et al.*, 2025; Szymkowiak *et al.*, 2025; Foest *et al.*, 2026). Seeds were collected by contracted crews from the ground or canopy as needed to meet local seed demand. The dataset includes annual observations of harvested seed mass (kg) for *Quercus petraea* and *Q. robur*. Prior to 2007–2008, oak harvests were not reported separately for the two species and were therefore pooled (389 sites, n = 13,335). We have also used data for European beech

(*Fagus sylvatica*; 241 sites, n = 8,335). The dataset also includes annual seed demand (kg) at the site level. Demand is calculated by the State Forests as the planned regeneration area multiplied by fixed species-specific sowing coefficients that reflect planting density and nursery practices. These coefficients are constant across Poland and over time, but annual demand in each forest district varies with regeneration plans and available seed stocks. Seed harvesting is restricted to the State Forests system, and seeds are not exported, so demand provides a composite index of sampling effort. We excluded time series consisting of >80% seed production values of zero to avoid model convergence issues. Lowering this threshold to 70% or 50%, does not change the results qualitatively.

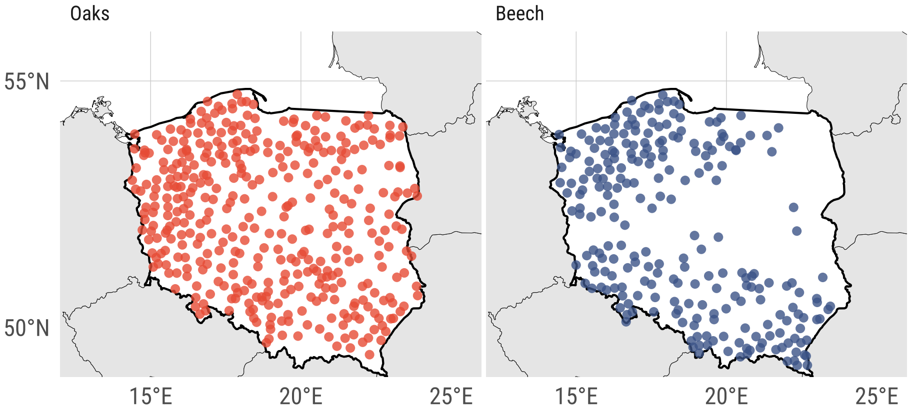

Figure 1: Oaks (389 sites, n = 13,335) and beech (241 sites, n = 8,335) study sites across Poland. Annual seed harvests were reported by local forest districts to the Polish State Forests based on collections made between 1988 and 2022 within designated seed stands.

Climate data

We obtained daily maximum temperature for each site from the corresponding 0.1° grid cells of the E-OBS dataset (v.31.0e) (Cornes *et al.*, 2018).

Analysis

Trends in masting We quantified temporal change in masting as a change in the interannual variability of seed production. For each site (forest district) we calculated the coefficient of variation (CV) of annual seed harvest within moving time windows. Our main analysis used

10-year windows advanced in 5-year steps; each window was indexed by its mid-year. Because CV is positive and right-skewed, we analysed log(CV).

To test whether CV changed over time, we fitted Gaussian generalized linear mixed-effects models (GLMM) with log(CV) as the response, mid-year as the fixed effect capturing long-term trend, and log(x+1)-transformed mean seed demand within the same window as a covariate controlling for sampling effort. Site identity was included as a random intercept to account for repeated windows from the same site. Given the large area covered by our analysis (Fig. 1), we also allowed the year effect to vary among sites (random slopes for year). We repeated the analysis across alternative step sizes (including 1-year and 10-year steps) to verify that inference was not sensitive to the rolling-window configuration (Table S1).

Weather cues We focused on three temperature windows expected to influence oak reproduction: (i) summer (June to August) temperature in the year preceding seedfall (t-1), linked to flower initiation; (ii) early spring temperature (March of year t), expected to influence flowering phenology (and thus pollination efficiency); and (iii) late spring temperature (April-May of year t), expected to influence pollen diffusion (and thus pollination success). For each site and year, we calculated mean temperatures within each cue window. Cue temperatures were centred and scaled to facilitate comparison of effect sizes.

We estimated cue sensitivity as the strength of the association between annual seed production and interannual temperature variation within each cue window. Seed production data include many zeros and are right-skewed. Therefore, we modelled annual seed production (kg) at the site-by-year level using generalized linear mixed models with a Tweedie error distribution and a log link. In these models, the response was annual seed production, and predictors included: the focal cue temperature (June-August t-1, March, and April-May), previous-year seed harvest to account for temporal dependence consistent with resource dynamics, and log(x+1)-transformed seed demand to control for sampling effort. The site was included as a random intercept.

Trends in cue temperatures To quantify climate change during the cue windows, we tested for long-term trends in temperature within each window using a Gaussian error GLMM with cue temperature as the response and year as the predictor. The site was included as a random intercept. We additionally allowed for site-specific warming rates (random slopes for year).

Do warmer cue regimes reduce masting variability? To test whether warmer conditions in cue windows are associated with reduced variability (i.e., lower CV), we linked rolling-window log(CV) to rolling-window mean cue temperature. Using the same rolling windows as for CV estimation, we fitted a Gaussian GLMM with log(CV) as the response and mean cue temperature within the windows as predictors, controlling for log(x+1) transformed mean demand within the window. The site was included as a random intercept. These models quantify whether decades (windows) characterised by higher temperatures during cue windows exhibit lower interannual variability in seed production.

Comparative benchmark with European beech To place oak responses in context, we repeated the workflow for European beech using its primary summer cue window (June-July temperature in t-1). Specifically, we estimated beech cue sensitivity using the same Tweedie mixed-model framework (annual seed production as response; cue temperature, previous-year seed production, and demand as predictors; site random intercept), quantified warming trends in the cue window, and related rolling-window log(CV) to rolling-window mean cue temperature.

Results

Temporal trends in masting variability Interannual variability in oak seed production did not show a significant long-term trend over the study period (Fig. 2). The coefficient of variation (CV) of seed production remained stable (mean = ~1.21) across the observation period (Year effect: $\beta = -0.001$, SE = 0.001, $p = 0.32$). This result was robust across alternative rolling-window configurations (Table S1).

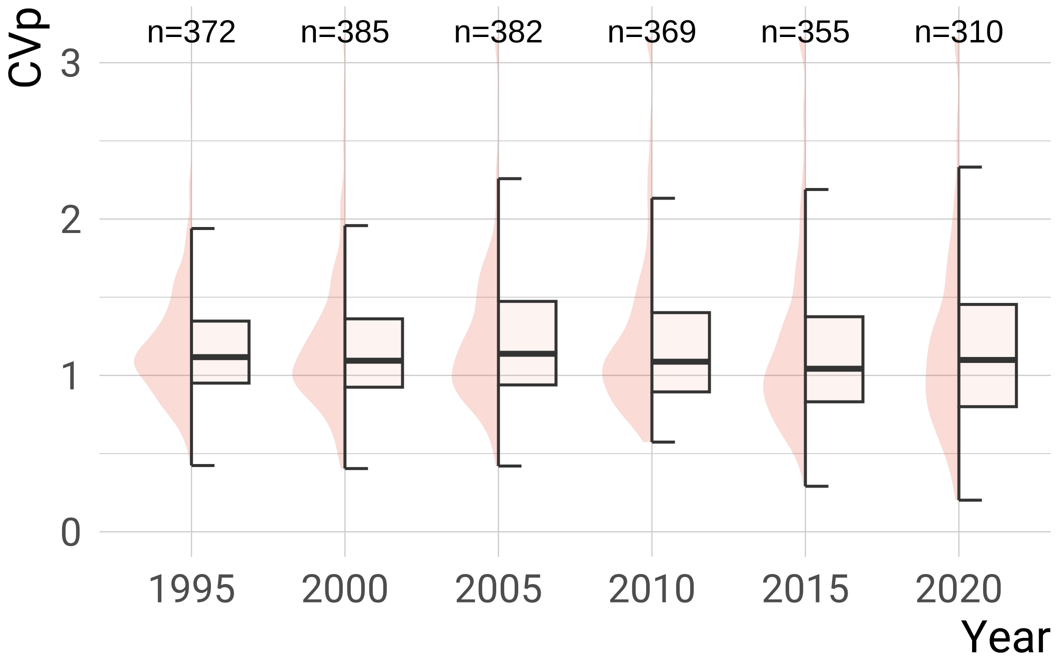

Figure 2: **Oak masting remains stable over time.** Temporal changes in the coefficient of variation (CV) of oak seed production in oaks. Boxplots summarize the distribution of CV within 5-year bins across all sites, with each bin indexed by its mid-year. The n values represent the number of observations within each bin.

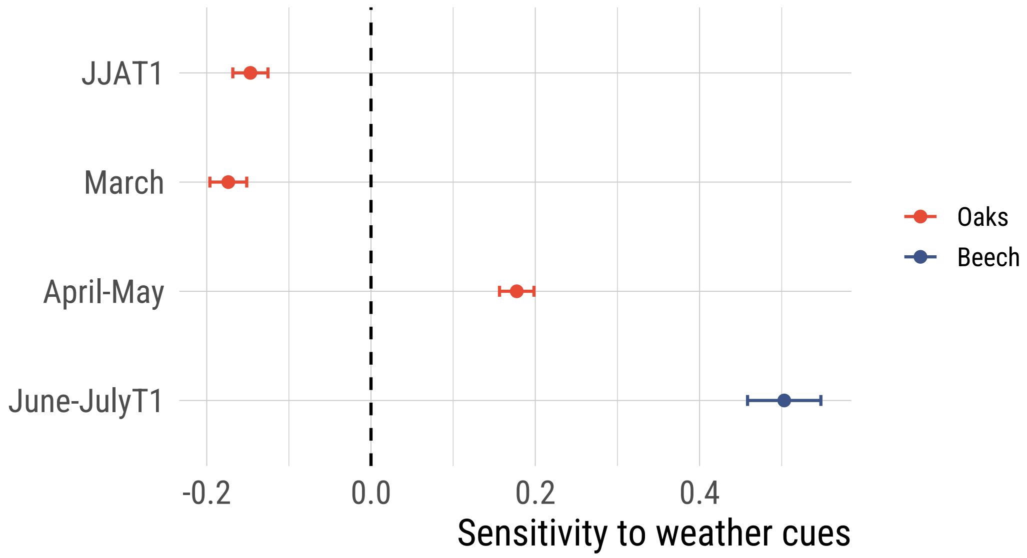

Figure 3: Seed production sensitivity to weather cues is higher in beech than in oaks. Relationships between seed production and weather cues across three seasonal windows in oaks: previous summer (June-August of year $t-1$, JJA1), early spring (March), and late spring (April-May); and in beech: previous summer (June-July of year $t-1$). Coefficients were estimated using Tweedie GLMMs. Points show estimated coefficients (red for oaks, blue for beech), and whiskers indicate 95% CI. Models are based on 389 sites and 13,335 observations in oaks, and 241 sites, 8,335 observations in beech.

Cue sensitivity of oak reproduction Annual oak seed production was associated with temperature variation during spring and summer cue windows (Fig. 3). As predicted, warmer temperatures during March were associated with lower seed production ($\beta = -0.18$, SE = 0.01, $p < 0.001$). For example, a warm March (10 °C) was associated with seed harvest of ~1630kg (95% CI: 1503-1750), and was 1.4-fold lower when March was cold (5 °C, seed harvest of ~2256kg, 95% CI: 2087-2424). Warmer temperatures during April–May were associated with higher seed production, with roughly the same effect size ($\beta = 0.18$, SE = 0.01, $p < 0.001$).

The summer (June-July-August) temperature cue in the year preceding seedfall showed a negative relationship with seed production (standardized, $\beta = -0.15$, SE = 0.01, $p < 0.001$). When summer was warm (26 °C), seed harvest in the following year was ~1516kg (95% CI: 1393-1639), which increased 1.76-fold when summer was relatively colder (20 °C, seed harvest of ~2673kg, 95% CI: 2441-2905). Seed production also exhibited negative temporal dependence, with higher seed production in the previous year associated with reduced production in the following year (β = -7.8e-06, SE = 2.5e-06, p = 0.002; Table S2).

Trends in cue temperatures Temperatures increased significantly during all cue windows over the study period. March temperatures increased at a rate of $\beta = 0.046$ °C (SE = 0.002, $p < 0.001$) per year. Thus, the mean estimated March temperature increased by 1.67 °C during the study period, from 6.65 °C (95% CI: 6.52-6.77) in 1988 to 8.32 °C (95% CI: 8.20-8.44) in 2021. April–May temperatures increased at a rate of $\beta = 0.023$ °C (SE = 0.001, $p < 0.001$) per year; resulting in an increase by 0.85 °C, from 16.16 (95% CI: 16.07-16.26) in 1988 to 17.01 (95% CI: 16.91-17.11) in 2021. Finally, summer temperature increased at the rate of $\beta = 0.073$ (SE = 0.0009, $p < 0.001$), which resulted in 2.63 °C increase, from 22.27 (95% CI: 22.19-22.36) in 1988 to 24.90 (95% CI: 24.80-25.00) in 2021.

Temperature regimes and masting variability Decadal variability in oak seed production was weakly negatively associated with mean temperatures in early spring (March), but not in late spring (April-May) or summer (June-July-August) (Fig. 4). Decades characterized by warmer March temperatures exhibited lower CV in seed production ($\beta = -0.018$, SE = 0.008, $p = 0.03$). For example, decades with cold springs (mean 4 °C) had an estimated CV of 1.2, while springs over twice as warm (mean 10 °C) had an estimated CV of 1.0. No relationship was observed between April–May temperatures and CV ($\beta = 0.016$, SE = 0.01, $p = 0.12$), and between summer temperatures and CV ($\beta = -0.008$, SE = 0.008, $p = 0.36$) (Table S3).

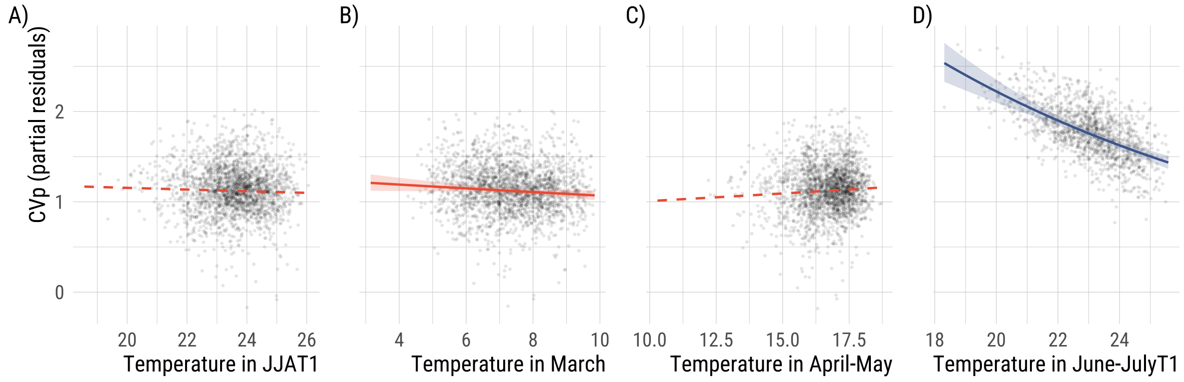

Figure 4: Oak masting is sensitive to early spring warming, but shows milder responses than European beech masting under altered cues. Relationships between rolling CV of seed production and mean weather cues across seasonal windows in oaks: A) previous summer (June-August of year $t-1$), B) early spring (March), and C) late spring (April-May); and in beech: D) previous summer (June-July of year $t-1$). Lines show predicted responses from LMMs (red for oaks, blue for beech), holding mean rolling demand constant at their median values; ribbons indicate 95% confidence intervals. Separate models were fitted for each cue. Points show partial residuals. Analysis is based on 389 sites and 13,335 observations in oaks, and 241 sites, 8,335 observations in beech.

Comparison with European beech European beech exhibited about twice as strong cue sensitivity compared to oaks, with the effect size of summer temperatures in the year preceding seedfall of $\beta = 0.44$ (SE = 0.02, $p < 000.1$). When summer was cold (20 °C), seed harvest in the following year was ~119kg (95% CI: 103-135.), which increased 4.17-fold when summer was relatively warmer (25 °C, seed harvest of ~497kg, 95% CI: 442-553). At the same time, warming in summer ($\beta = 0.072$, SE = 0.01, $p =< 2e - 16$) was about twice as strong as the spring temperatures trend - temperatures in June-July increased by 2.58 °C, from 21.73 (95% CI: 21.60-21.86) in 1988 to 24.31 (95% CI: 24.16-24.46) in 2021. Finally, decades with higher June-July mean temperatures were associated with a substantial decline in interannual variability of seed production ($\beta = -0.078$, SE = 0.009, $p < 000.1$). For example, in cold decades (20 °C), the estimated CV was 2.21 (95% CI: 2.09-2.34), which declined to 1.50 (95% CI: 1.44-1.56) when the mean June-July decadal temperature was 25 °C.

Discussion

Despite substantial warming over the past three decades, we found no evidence that the temporal structure of oak reproduction has changed. This stability can be explained by two features of oak masting. First, oak seed production showed relatively weak sensitivity to weather cues: although temperatures during spring correlated with seed production, the magnitude of these responses was about 60% weaker compared with European beech. Second, warming rates during the key spring reproductive windows were moderate (roughly 50% lower than summer, crucial for beech masting), limiting the increase in cue frequency that could otherwise drive repeated reproductive allocation and long-term depletion of internal resource pools (Hacket-Pain *et al.*, 2025). These results suggest that the interaction between cue sensitivity and rate of climate change has so far buffered the temporal structure of oak masting. At the same time, at the decadal level, we found that higher early spring temperatures were associated with lower interannual variability in seed production, indicating that regions experiencing faster warming during this cue window may face declines in masting variability. These findings are important because oaks are increasingly promoted in forest management as species expected to perform well under warmer and drier climates (Saha *et al.*, 2017; Nicolescu *et al.*, 2025). At the same time, we must note that seed supply may decline for other reasons than masting disruptions (Clark *et al.*, 2021; Foest *et al.*, 2026), and seedling recruitment is a climate-sensitive process (Davis *et al.*, 2019).

The relationship between decadal mean early-spring (March) temperature and seed-production variability supports the theoretical framework linking weather-cue frequency and masting variability (Bogdziewicz *et al.*, 2024b). Warmer March decades were associated with lower CV in oak seed production, showing that increases in cue frequency can shift the temporal dynamics of reproduction even though long-term masting variability remained stable. This effect was modest: across about 5 °C of variation in March temperature among decades, CV varied by 20%. This relatively weak response indicates that, when cue sensitivity is relatively low, substantial climatic change is required to produce a detectable shift in masting variability. The same reasoning may explain why April-May temperature was not related to CV: although reproduction responded to late spring temperature at the annual scale, decadal variation in April-May temperature was much smaller than in March (roughly 12-18 °C versus 4-10 °C), limiting its ability to shift decadal masting variability. By contrast, European beech showed a much steeper decline in masting variability per degree of warming, 5 °C change resulted in CV decline by 37%, consistent with its stronger cue sensitivity.

The decadal association between warmer cue regimes and lower CV suggests that climate-driven shifts in masting dynamics may be reversible. If frequent cues maintain resource pools at persistently low levels, trees may become less responsive to subsequent cues, producing more regular but smaller seed crops (Kelly *et al.*, 2025). Under this mechanism, a reduction in cue frequency would allow resource reserves to recover, restoring stronger reproductive responses and higher interannual variability. This interpretation implies that the breakdown of masting observed in species such as European beech does not represent a permanent shift in reproductive dynamics. Such reversibility could arise through two, non-exclusive processes: changes in cue regimes themselves, or adaptation of populations to the cue regimes they experience. Consistent with the first process, century-long records show that European beech alternates between periods of frequent and rare large-scale masting events, with these shifts partly associated with decadal variation in NAO-driven weather regimes (Ascoli *et al.*, 2017). Consistent with the second process, the absence of systematically lower CV in warmer regions (Foest *et al.*, 2024) suggests that populations may already be locally adapted to their prevailing cue environments, an idea that warrants testing in future work.

Importantly, regeneration risk cannot be inferred from masting dynamics alone. Climate change can also reduce the mean supply of viable seeds, shifting populations away from the climatic optima for reproduction and imposing stage-specific bottlenecks during flower initiation, pollination, and seed maturation. In Polish forests, viable seed production declined across dominant tree species over the past three decades, including in oaks, with summer warming emerging as the dominant driver (Foest *et al.*, 2026). These declines matter because even resilient masting dynamics may generate too few recruits if the absolute seed crop is low. Conversely, abundant seed crops do not guarantee regeneration: seedling establishment is also climate sensitive, responding nonlinearly and species-specifically to temperature and soil moisture (Ibáñez *et al.*, 2007; Davis *et al.*, 2019), while oak germination, survival, and early performance depend on interactions between regional climate, microclimate, and forest structure (Meeussen *et al.*, 2022). At the stand scale, light availability, browsing, competition, and ground vegetation further filter seedlings through successive bottlenecks (Annighöfer *et al.*, 2015; Woziwoda *et al.*, 2019; Kuehne *et al.*, 2020). Thus, successful regeneration requires the alignment of several processes: masting must provide temporally concentrated seed crops, mean fecundity must remain high enough to create dense seedling cohorts, and climatic and microsite conditions must allow those cohorts to pass through establishment and recruitment filters. This sequence is supported by long-term regeneration data showing that the presence of established sessile oak saplings after ten years was driven primarily by initial seedling density, with later outcomes further shaped by light and competition (Kuehne *et al.*, 2020).

A limitation of our study is that it relies on seed-harvest records rather than standardized ecological monitoring. These data were collected to support regeneration programs rather than to quantify reproduction, and therefore reflect not only biological variation in seed availability but also fluctuations in seed demand and collection effort. We reduced this problem by accounting for seed demand in our models and by using records collected under a nationwide protocol, but some non-biological variation inevitably remains. This limitation should be weighed against the scarcity of ecological monitoring datasets with comparable spatial and temporal coverage.

A second limitation is that pedunculate and sessile oaks were not reported separately before 2007–2008, which required pooling *Quercus robur* and *Q. petraea* for most of the time series. This prevents a species-specific assessment of long-term trends and may obscure differences in climatic sensitivity between the two oaks. However, the two species show significant temporal synchrony of seed production where separate records are available after 2008 (Fig. S1), suggesting that the pooled series likely captures the dominant regional signal in oak reproduction.

Although research on forest responses to climate change has focused on important and often dramatic increases in mortality and disturbance (Senf *et al.*, 2018; Hartmann *et al.*, 2022; Grünig *et al.*, 2026), many of the longest-lasting consequences will unfold through reproduction, because seed production governs regeneration potential and the assembly of future forest communities (Clark *et al.*, 2021; Seidl & Turner, 2022). By combining theory on cue-driven mast seeding with long-term seed records, we show that these impacts are not uniform across species: unlike European beech, oaks have so far maintained stable interannual variability in seed production, likely because their reproductive responses to weather cues are weaker and warming within key cue windows has been moderate. At the same time, lower variability in warmer decades indicates that oak masting is not insensitive to climate, and that continued warming could disrupt masting where cue temperatures increase rapidly. Our results support the idea that climate-change effects on masting depend on the interaction between cue sensitivity and climate velocity, providing a general framework for predicting which species are most vulnerable to reproductive disruption under warming.

Acknowledgements

The study was supported by grant no. 2024/54/E/NZ8/00007 from the Polish National Science Centre. We would like to express our gratitude to the Directorate-General of State Forests for providing data on the abundance of seeds. JF was supported by the MSCA Postdoctoral Fellowship FECUND (ID: 101244227) and by the Foundation for Polish Science (FNP). VJ was supported by the JSPS KAKENHI JP26K18386.

Author Contributions Statement

Declaration of interests

No competing interests to declare.

Data availability statement

The data supporting the results are archived in the Open Science Framework and analysis will be available at: `https://github.com/ValentinJourne/MastingTrends`.

References

Annighöfer, P., Beckschäfer, P., Vor, T. & Ammer, C. (2015). Regeneration patterns of european oak species (Quercus petraea (matt.) liebl., Quercus robur l.) in dependence of environment and neighborhood. *PLOS ONE*, 10, e0134935.

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

Bogdziewicz, M., Chybicki, I., Szymkowiak, J., Ulaszewski, B., Burczyk, J., Szarek-Łukaszewska, G. *et al.* (2024a). Masting and efficient production of seedlings: Balancing costs of variation through synchronised fruiting. *Ecology letters*, 27, e14514.

Bogdziewicz, M., Hacket-Pain, A., Kelly, D., Thomas, P.A., Lageard, J. & Tanentzap, A.J. (2021). Climate warming causes mast seeding to break down by reducing sensitivity to weather cues. *Global Change Biology*, 27, 1952–1961.

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

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

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

Bogdziewicz, M., Kelly, D., Zwolak, R., Szymkowiak, J. & Hacket-Pain, A. (2025). Dynamics, mechanisms, and consequences of mast seeding. *Annual Reviews in Ecology, Evolution, and Systematics*, 56, 119–144.

Bogdziewicz, M., Szymkowiak, J., Bonal, R., Hacket-Pain, A., Espelta, J.M., Pesendorfer, M. *et al.* (2020b). What drives phenological synchrony? warm springs advance and desynchronize flowering in oaks. *Agricultural and Forest Meteorology*, 294, 108140.

Bush, E.R., Whytock, R.C., el din, L.B., Bourgeois, S., Bunnefeld, N., Cardoso, A.W. *et al.* (2020). Long-term collapse in fruit availability threatens central african forest megafauna. *Science*, 370, eabc7791.

Clark, J.S., Andrus, R., Aubry-Kientz, M., Bergeron, Y., Bogdziewicz, M., Bragg, D.C. *et al.* (2021). Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications 2021 12:1*, 12, 1–11.

Clark, J.S., Bell, D.M., Hersh, M.H. & Nichols, L. (2011). Climate change vulnerability of forest biodiversity: Climate and competition tracking of demographic rates. *Global Change Biology*, 17, 1834–1849.

Cornes, R.C., van der Schrier, G., van den Besselaar, E.J. & Jones, P.D. (2018). An ensemble version of the e-obs temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123, 9391–9409.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T. *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, 6193–6198.

Dri, G.F., Bogdziewicz, M., Hunter, M., Witham, J. & Mortelliti, A. (2025). Coupled effects of forest growth and climate change on small mammal abundance and body weight: Results of a 39-year field study. *Journal of Animal Ecology*, 94, 2118–2129.

Fleurot, E., Keurinck, L., Boulanger, V., Debias, F., Delpierre, N., Delzon, S. *et al.* (2024). Reconciling pollen limitation theories: Insights from temperate oak masting. *Ecology Letters*, 27, e70009.

Fleurot, E., Lobry, J.R., Boulanger, V., Debias, F., Mermet-Bouvier, C., Caignard, T. *et al.* (2023). Oak masting drivers vary between populations depending on their climatic environments. *Current Biology*, 33, 1117–1124.E4.

Foest, J., Bogdziewicz, M., Ascoli, D., Pesendorfer, M., Cutini, A., Nussbaumer, A. *et al.* (2024). Widespread breakdown in masting in European beech due to rising summer temperatures. *Global Change Biology*, 30, e17307.

Foest, J.J., Szymkowiak, J., Dyderski, M.K., Jastrzębowski, S., Fuchs, H., Ratajczak, E. *et al.* (2025). No refuge at the edge for european beech as climate warming disproportionately reduces masting at colder margins. *Ecology Letters*, 28, e70284.

Foest, J.J., Szymkowiak, J., Dyderski, M.K., Kelly, D., Kunstler, G., Jastrzębowski, S. *et al.* (2026). Forest fecundity declines as climate shifts. *Ecology Letters*. In press.

Grünig, M., Rammer, W., Senf, C., Albrich, K., André, F., Augustynczik, A.L.D. *et al.* (2026). Climate change will increase forest disturbances in europe throughout the 21st century. *Science*, 391, eadx6329.

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, 20200379.

Hacket-Pain, A., Szymkowiak, J., Journé, V., Barczyk, M.K., Thomas, P.A.., Lageard, J.G.A. *et al.* (2025). Growth decline in european beech associated with temperature-driven increase in reproductive allocation. *PNAS*, 122, e2423181122.

Hanley, M.E., Cook, B.I. & Fenner, M. (2019). Climate variation, reproductive frequency and acorn yield in English Oaks. *Journal of Plant Ecology*, 12, 542–549.

Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J. *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.

Hirsch, M., Puhlmann, H., Klemmt, H.J. & Seifert, T. (2025). Modelling fructification intensity at the tree level reveals species-specific effects of tree age, social status and crown defoliation across major european tree species. *European Journal of Forest Research*, pp. https://doi.org/10.1007/s10342–025–01822–0.

Ibáñez, I., Clark, J.S., LaDeau, S. & Lambers, J.H.R. (2007). Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, 77, 163–177.

Jantzen, C., Burant, J., Gamelon, M., Bakker, E.L. & Visser, M.E. (2026). Masting breakdown in european beech reduces fitness benefits of masting, partly explained by climate change. Preprint.

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.

Journé, V., Kelly, D., Hacket-Pain, A., Pearse, I.S., Szymkowiak, J., Foest, J.J. *et al.* (2025). Weather drivers of reproductive variability in perennial plants and their implications for climate change risks. *Nature Communications*, 16, 9226.

Journé, V., Szymkowiak, J., Foest, J., Hacket-Pain, A., Kelly, D. & Bogdziewicz, M. (2024). Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants*, 10, 367–373.

Kelly, D., Geldenhuis, A., James, A., Holland, E.P., Plank, M.J., Brockie, R.E. *et al.* (2013). Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters*, 16, 90–98.

Kelly, D., Szymkowiak, J., Hacket-Pain, A. & Bogdziewicz, M. (2025). Fine-tuning mast seeding: as resources accumulate, plants become more sensitive to weather cues. *New Phytologist*, 246, 1975–1985.

Klesse, S., Peters, R., Alfaro-Sánchez, R., Badeau, V., Baittinger, C., Battipaglia, G. *et al.* (2024). No future growth enhancement expected at the northern edge for european beech due to continued water limitation. *Global Change Biology*, 30.

Koenig, W.D., Knops, J.M., Carmen, W.J. & Pearse, I.S. (2015). What drives masting? the phenological synchrony hypothesis. *Ecology*, 96, 184–192.

Kuehne, C., Pyttel, P., Modrow, T., Kohnle, U. & Bauhus, J. (2020). Seedling development and regeneration success after 10 years following group selection harvesting in a sessile oak (Quercus petraea [mattuschka] liebl.) stand. *Annals of Forest Science*, 77, 71.

Kulla, L., Roessiger, J., Bošeła, M., Kucbel, S., Murgaš, V., Vencurik, J. *et al.* (2023). Changing patterns of natural dynamics in old-growth european beech (fagus sylvatica l.) forests can inspire forest management in central europe. *Forest Ecology and Management*, 529, 120633.

LaMontagne, J.M., Redmond, M.D., Wion, A.P. & Greene, D.F. (2021). An assessment of temporal variability in mast seeding of north american Pinaceae. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200373.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L. *et al.* (2020). Pervasive shifts in forest dynamics in a changing world. *Science*, 368.

Meeussen, C., De Pauw, K., Sanczuk, P., Brunet, J., Cousins, S.A.O., Gasperini, C. *et al.* (2022). Initial oak regeneration responses to experimental warming along microclimatic and macroclimatic gradients. *Plant Biology*, 24, 745–757.

Monks, A., Monks, J.M. & Tanentzap, A.J. (2016). Resource limitation underlying multiple masting models makes mast seeding sensitive to future climate change. *New Phytologist*, 210, 419–430.

Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F.M. & Katul, G.G. (2011). Spread of north american wind-dispersed trees in future environments. *Ecology Letters*, 14, 211–219.

Nicolescu, V.N., Vor, T., Brus, R. *et al.* (2025). Management of sessile oak (Quercus petraea (matt.) liebl.), a major forest species in europe. *Journal of Forestry Research*, 36, 78.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15, 232–237.

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

Pearse, I.S., LaMontagne, J.M. & Koenig, W.D. (2017). Inter-annual variation in seed production has increased over time (1900–2014). *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171666.

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

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

Redmond, M.D., Forcella, F. & Barger, N.N. (2012). Declines in pinyon pine cone production associated with regional warming. *Ecosphere*, 3, 1–14.

Roncé, I.L., Dardevet, E., Venner, S., Schönbeck, L., Gessler, A., Chuine, I. *et al.* (2023). Reproduction alternation in trees: testing the resource depletion hypothesis using experimental fruit removal in quercus ilex. *Tree Physiology*, 43, 952–964.

Saha, S., Kühne, C. & Bauhus, J. (2017). Lessons learned from oak cluster planting trials in central europe. *Canadian Journal of Forest Research*, 47, 139–148.

Sala, A., Hopping, K., McIntire, E.J., Delzon, S. & Crone, E.E. (2012). Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist*, 196, 189–199.

Samarth, Lee, R., Kelly, D., Turnbull, M.H., Macknight, R.C., Poole, A.M. *et al.* (2021). Molecular control of the floral transition in the mast seeding plant celmisia lyallii (asteraceae). *Molecular Ecology*, 30, 1846–1863.

Schermer, E., Bel-Venner, M.C., Fouchet, D., Siberchicot, A., Boulanger, V., Caignard, T. *et al.* (2019). Pollen limitation as a main driver of fruiting dynamics in oak populations. *Ecology Letters*, 22, 98–107.

Schermer, E., Bel-Venner, M.C., Gaillard, J.M., Dray, S., Boulanger, V., Roncé, I.L. *et al.* (2020). Flower phenology as a disruptor of the fruiting dynamics in temperate oak species. *New Phytologist*, 225, 1181–1192.

Seidl, R. & Turner, M.G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world. *Proceedings of the National Academy of Sciences*, 119, e2202190119. Publisher: Proceedings of the National Academy of Sciences.

Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M. *et al.* (2018). Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications*, 9, 1–8.

Sharma, S., Andrus, R., Bergeron, Y., Bogdziewicz, M., Bragg, D.C., Brockway, D. *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, e2116691118.

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

Spiecker, H. (2021). Production of valuable oak wood in europe. *Annals of Forest Research*, 64, 5–12.

Szymkowiak, J., Bogdziewicz, M., Marino, S. & Steele, M.A. (2024a). Community-wide masting improves predator satiation in north american oaks. *Forest Ecology and Management*, 569, 122172.

Szymkowiak, J., Foest, J., Dyderski, M.K., Jastrzebowski, S., Barczyk, M., Hacket-Pain, A. *et al.* (2025). Geography of masting creates greater synchrony in seed scarcity than in seed abundance. *Proceedings of the National Academy of Sciences*, 122, e2518918122.

Szymkowiak, J., Foest, J., Hacket-Pain, A., Journé, V., Ascoli, D. & Bogdziewicz, M. (2024b). Tail-dependence of masting synchrony results in continent-wide seed scarcity. *Ecology Letters*, 27, e14474.

Vacchiano, G., Hacket-Pain, A., Turco, M., Motta, R., Maringer, J., Conedera, M. *et al.* (2017). Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytologist*, 215, 595–608.

Wion, A.P., Pearse, I.S., Broxson, M. & Redmond, M.D. (2025). Mast hindcasts reveal pervasive effects of extreme drought on a foundational conifer species. *New Phytologist*, 246, 450–460.

Woziwoda, B., Dyderski, M.K., Kobus, S., Parzych, A. & Jagodziński, A.M. (2019). Natural regeneration and recruitment of native Quercus robur and introduced Q. rubra in european oak-pine mixed forests. *Forest Ecology and Management*, 449, 117473.

Yukich-Clendon, O.M.M., Carpenter, J.K., Kelly, D., Timoti, P., Burns, B.R., Boswijk, G. *et al.* (2023). Global change explains reduced seeding in a widespread new zealand tree: indigenous tūhoe knowledge informs mechanistic analysis. *Frontiers in Forests and Global Change*, 6, 1172326.

Zohner, C.M., Mo, L. & Renner, S.S. (2018). Global warming reduces leaf-out and flowering synchrony among individuals. *eLife*, 7, e40214.

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

Zwolak, R., Clement, D., Sih, A. & Schreiber, S.J. (2024). Granivore abundance shapes mutualism quality in plant–scatterhoarder interactions. *New Phytologist*, 241, 1840–1850.

Supporting Information

title

Table S1: Mixed-effects model estimates across 10 years rolling-window and step-size combinations. Demand was included as control variable and was log-transformed.

Step	Term	Estimate	SE	*p*	AIC	nobs
1	Intercept	1.041	0.057	0.00000	-1532.6	9512
1	Year	-0.001	0.001	0.46800		
1	Demand	-0.114	0.007	0.00000		
2	Intercept	1.072	0.074	0.00000	406.9	4778
2	Year	0.000	0.001	0.81000		
2	Demand	-0.118	0.010	0.00000		
3	Intercept	1.102	0.084	0.00000	872.7	3310
3	Year	-0.002	0.001	0.13900		
3	Demand	-0.125	0.011	0.00000		
4	Intercept	1.101	0.089	0.00000	975.8	2567
4	Year	0.000	0.001	0.91300		
4	Demand	-0.124	0.011	0.00000		
5	Intercept	1.175	0.091	0.00000	1017.4	2173
5	Year	-0.001	0.001	0.32000		
5	Demand	-0.134	0.012	0.00000		
10	Intercept	1.068	0.109	0.00000	698.6	1115
10	Year	-0.002	0.001	0.21900		
10	Demand	-0.121	0.014	0.00000		

Table S2: Coefficient estimates from Generalised Linear Mixed Models (GLMMs) with June-July-August of previous year cue (JJA1), current March (Mar) or April-May (AprMAy) cue. Model coefficients are reported with average estimate, standard error, and p-value. The cue variable was standardised. Demand was log transformed.

Predictor	*Estimate*	*SE*	*p-value*
Intercept	5.952e+00	6.967e-02	< 2e-16
JunJulAug$_1$	1.479e-01	1.092e-02	< 2e-16
Seeds$_1$	-7.800e-06	2.509e-06	0.00188
Demand	2.134e-01	7.943e-03	< 2e-16
Intercept	5.942e+00	6.927e-02	< 2e-16
Mar	-1.758e-01	1.138e-02	< 2e-16
Seeds$_1$	-6.450e-06	2.509e-06	0.00999
Demand	2.142e-01	7.915e-03	< 2e-16
Intercept	5.915e+00	6.917e-02	< 2e-16
AprMay	1.799e-01	1.070e-02	< 2e-16
Seeds$_1$	-8.454e-06	2.513e-06	0.000769
Demand	2.186e-01	7.920e-03	< 2e-16

Table S3: Model with rolling CV (log transformed) and mean cues based on 10 years window with 5 years steps. We included mean demand as predictor of the rolling window (log-transformed) and site as random intercept.

Predictor	*Estimate*	*SE*	*p-value*
Intercept	1.407224	0.231232	1.16e-09
JunJulAug_1	-0.008208	0.008946	0.359
Demand	-0.140272	0.010646	< 2e-16
Intercept	1.351429	0.106926	< 2e-16
Mar	-0.018094	0.008593	0.0352
Demand	-0.140922	0.010638	< 2e-16
Intercept	0.94739	0.18790	4.6e-07
AprMay	0.01588	0.01024	0.121
Demand	-0.14003	0.01060	< 2e-16

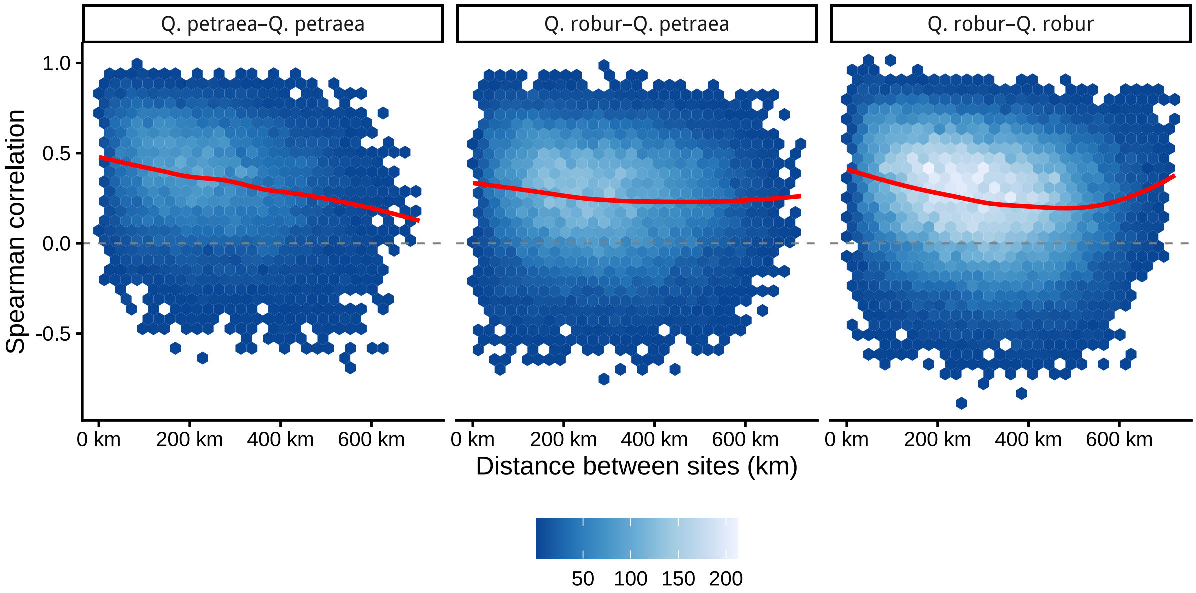

Figure S1: **Within and among-oak masting synchrony.** Hexes are pairwise Spearman correlations between sites calculated for the period when separate records for the two species are available (2008-2022). The hex color is scaled to the number of observations within each hex. Pairwise correlations were calculated for series with at least 5 years of overlap. Lines show the mean loess smoothers.