Climate warming dampens masting-driven pulsed resources

Michał Bogdziewicz*[1], Jessie J. Foest[1], Andrew Hacket-Pain[2], Maciej K. Barczyk[1], Maria Bogdańska[1], Marcin K. Dyderski [3], Szymon Jastrzębowski[4], Rachel Gaulton[5], Jonathan G. A. Lageard [6], Peter A. Thomas [7], Dave Kelly[8], Jakub Szymkowiak[1,2,9]

[1]Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland.
[2]Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom.
[3]Department of Systematic and Environmental Botany, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland.
[4]Department of Silviculture and Forest Tree Genetics, Forest Research Institute, Braci Leśnej 3, Sękocin Stary, 05-090, Raszyn, Poland.
[5]School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, NE1 7RU, United Kingdom.
[6]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK
[7]School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK
[8] School of Biological Sciences, University of Canterbury, Christchurch 8140, New Zealand.
[9]Population Ecology Research Unit, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland.

*corresponding authors: michalbogdziewicz@gmail.com

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Abstract

Pulsed resources arise when environmental forcing synchronizes biological responses. This synchrony generates episodic booms and busts that structure food webs. Mast seeding is a major example, yet climate warming is increasingly disrupting the synchrony that underpins these pulses. Importantly, the ecological consequences of masting depend on which tail is synchronized: spatially coherent seed failures (synchrony in the lower tail) create trophic bottlenecks, whereas coherent mast peaks (upper tail) generate resource pulses that fuel consumer outbreaks. Climate-driven changes in synchrony may be tail-specific, reshaping not only the strength but also the character of resource pulses. Here, we test how warming-driven changes in European beech (*Fagus sylvatica*) masting translate into tail-specific shifts in spatial synchrony and whether these shifts arise from altered coupling between weather cues and reproduction. Using 45 years of individual-tree seed production data from the United Kingdom and 33 years of seed harvest records from Poland, we found that, as predicted, synchrony declined strongly in mast peaks (44% locally; 50% regionally). However, synchrony also declined in failure years, though to a lesser extent (35% locally; 25% regionally) than in mast peaks. This asymmetry was not explained by increasing heterogeneity in responses to the warm-summer cue preceding flowering. Instead, reproductive dynamics shifted toward dominance of the cold-summer cue two years before seedfall, while sensitivity to the warm-summer cue weakened. This flattened previously nonlinear cue–reproduction relationships: reproduction increasingly occurred under conditions that formerly produced synchronized failure, and amplification during favourable years was reduced. Our findings show that warming alters the cue structures that generate masting-driven pulses, weakening and desynchronizing both failures and peaks, and reducing their predictability.

Introduction

Resource pulses, brief and infrequent episodes of strongly elevated resource availability, occur across terrestrial and aquatic ecosystems and arise from climatic forcing, temporal or spatial accumulation and release, and population outbreaks (Ostfeld & Keesing, 2000; Yang *et al.*, 2008, 2010). These pulses alter consumer behaviour, drive population responses, and generate indirect effects that propagate through food webs and across ecosystem boundaries (Yang *et al.*, 2010; Walter *et al.*, 2024). Pulses often emerge from spatially coherent environmental forcing and synchronized responses of primary producers, such as in El Niño–driven productivity boosts, insect outbreaks, or region-wide mast crops (Yang *et al.*, 2010; Anderson *et al.*, 2020; Bogdziewicz *et al.*, 2025). Climate change is expected to alter the spatial synchrony of both weather drivers and ecological phenomena, which can strengthen or weaken pulsed resources (Hansen *et al.*, 2020; Reuman *et al.*, 2025). Therefore, understanding how climate change reshapes synchrony within pulsed-resource systems is important for predicting how resource pulses will propagate through food webs and across landscapes.

Mast seeding is a major example of a pulsed-resource driver (Ostfeld & Keesing, 2000). Masting plants produce interannually variable seed crops that are synchronized within populations and often across large spatial scales (Pearse *et al.*, 2016; Bogdziewicz *et al.*, 2023a). Masting is prevalent especially in temperate and boreal zones, but present across all vegetated continents (Pearse *et al.*, 2020; Journé *et al.*, 2023). A recently described feature of ecological synchrony, including in masting, is its tail-dependence (Szymkowiak *et al.*, 2025), in which spatial synchrony varies between the lower tail (years of seed failure) and the upper tail (years of high seed production) of an ecological variable's distribution (Ghosh *et al.*, 2020; Walter *et al.*, 2022). In masting, synchrony is generally higher in the lower tail, i.e., synchrony of seeding failures among seed-producing individuals or populations is higher and extends over larger spatial scales compared to such synchrony in high-seeding years (Szymkowiak *et al.*, 2024, 2025). This asymmetry matters because famines and abundance generate different ecological dynamics (Holt, 2008). Seed-crop failures impose trophic constraints and trigger threshold responses: once resources fall below tolerable levels, survival and reproduction of consumers decline rapidly, often triggering emigration (Sears *et al.*, 2004; Holt, 2008; Tonelli *et al.*, 2026). Mast peaks, in contrast, create resource surges that trigger graded and saturating increases in consumer numbers (Sears *et al.*, 2004; Holt, 2008; Yang *et al.*, 2010). Because scarcity and abundance involve different mechanisms, the two tails of masting drive distinct ecological cascades.

Recent evidence shows that masting dynamics are sensitive to climate change (Hacket-Pain & Bogdziewicz, 2021), including in species such as Japanese oak (*Quercus crispula*) (Shibata *et al.*, 2020), tawa (*Beilschmiedia tawa*) (Yukich-Clendon *et al.*, 2023), or blue oak (*Q. douglasii*) (Koenig, 2019). In European beech (*Fagus sylvatica*), a well-studied species in this context, among-tree synchrony of seed production variation has declined, reducing the interannual variability in seed production (Bogdziewicz *et al.*, 2020). This breakdown has been linked to rising summer temperatures, which provide the weather cues for flowering while internal resource dynamics modulate the strength of the flowering response (Bogdziewicz *et al.*, 2021; Kelly *et al.*, 2025). Cold summers two years before seedfall (T2) are believed to prime flowering, possibly by triggering molecular pathways, and warm summers one year before seedfall (T1) then facilitate flower initiation in a manner that depends on the tree's resource state (Piovesan & Adams, 2001; Vacchiano *et al.*, 2017; Kelly *et al.*, 2025). As warm summers become more frequent, reproduction is cued more often, resources remain chronically depleted, and weather cues lose their coordinating function (Bogdziewicz *et al.*, 2021; Hacket-Pain *et al.*, 2025). The desynchronization is now evident across much of the species' range and is strongest at locations where summer warming has been most pronounced (Foest *et al.*, 2024, 2025b). Yet, it remains unclear how these changes in synchrony map onto tail dependence: whether climate change is weakening synchrony in mast peaks, failures, or both, and to what extent.

Tail-dependent synchrony in masting arises from non-linear responses of reproduction to weather cues (Szymkowiak *et al.*, 2024). Variation and synchrony in seed production are driven by weather cues that regulate flowering and seed maturation (Kelly *et al.*, 2013; Koenig *et al.*, 2015; Journé *et al.*, 2024). Spatial synchrony of masting reflects the Moran effect acting through these cues (Koenig & Knops, 2013; Ascoli *et al.*, 2017; LaMontagne *et al.*, 2020; Wion *et al.*, 2020). Masting plants often respond weakly or not at all across a broad range of unfavourable cue values, and show strong reproductive responses once cues cross induction thresholds (Kelly *et al.*, 2013; Fernández-Martínez *et al.*, 2017; Schermer *et al.*, 2020). Such non-linear relationships generate many years of seed failure and create an asymmetric effect of weather variation on reproduction (Szymkowiak *et al.*, 2024). When cues are low, seed production remains suppressed across a wide range of cue values, so spatial variation in weather produces little variation in reproduction, promoting high synchrony of failures (Szymkowiak *et al.*, 2024). When cues are high, small spatial differences in weather translate into large differences in seed production, reducing synchrony in peaks (Szymkowiak *et al.*, 2024).

In this study, we test how the climate-change-induced disruption in European beech masting (Bogdziewicz *et al.*, 2020; Foest *et al.*, 2025b) translates into tail-specific changes in spatial synchrony, and how these changes arise from altered coupling between weather cues and individual reproductive responses. Climate warming increases the frequency of cues, which repeatedly trigger flowering but progressively deplete internal resources (Hacket-Pain *et al.*, 2025; Kelly *et al.*, 2025). The consequences should be asymmetric across the masting distribution: when cues are high, resource depletion should dampen and diversify individual responses, weakening cue–reproduction coupling and reducing synchrony in the upper tail. When cues are low, reproduction is not initiated, and synchrony in the lower tail should show little temporal change.

To test these predictions, we combine two datasets that capture different levels at which masting synchrony emerges. First, we use 45 years of individual-tree seed-production records from 17 sites in UK (Hacket-Pain *et al.*, 2025), which enable us to quantify how the coupling between weather cues and reproduction varies among trees and changes over time. These data provide direct insight into the individual-level processes from which population-level synchrony arises (Koenig *et al.*, 2003; Pesendorfer *et al.*, 2021). Second, we use spatially extensive, population-level seed harvest records from Poland spanning 33 years (Foest *et al.*, 2025b). Although based on annual harvest data rather than direct counts, this dataset offers broad spatial coverage and enables us to test whether tail-specific changes in synchrony detected at the individual level are replicated across landscape scales. These datasets allow us to link mechanistic changes in cue responsiveness to emergent, tail-dependent patterns of synchrony under climate warming.

Methods

Study species

European beech (*Fagus sylvatica L.*) is a dominant forest-forming species in temperate Europe (Leuschner & Ellenberg, 2017). It is a masting species with large interannual variation and spatial synchrony in seed production (Nilsson & Wastljung, 1987; Ascoli *et al.*, 2017). Specifically, a combination of cold summer two years before seedfall (T2) and then warm summer one year before seedfall (T1) leads to a large flowering commitment and high seed production (Vacchiano *et al.*, 2017; Journé *et al.*, 2024). Masting in beech improves pollination efficiency and decreases pre- and post-dispersal seed predation rates (Zwolak *et al.*, 2016; Pesendorfer *et al.*, 2024). Recent warming-related disruption of masting has increased pre-dispersal seed predation from 2–3% of seeds to over 40%, reduced pollination efficiency by about 20%, and, consequently, halved viable seed production (Bogdziewicz *et al.*, 2023b; Foest *et al.*, 2025b). In England, the decline in variability, increased regularity of reproduction, and resulting resource depletion under warming have been linked to a 28% reduction in annual tree ring increments (Hacket-Pain *et al.*, 2025).

Seed production data

Individual-level seed production was quantified for 229 trees and 17 sites spaced across England annually between 1980 and 2024 (45 years) (Bogdziewicz *et al.*, 2023b). The ground below each tree was searched for seeds for 7 minutes, and all seeds found were counted (Foest *et al.*, 2025a). The other dataset included spatially extensive, population-level records of European beech seed production obtained from the Polish State Forests and is based on annual harvest rates by the state forests inspectorates (Foest *et al.*, 2025b). This dataset provides information on the amount (kg) of seeds collected in each district per year and the focal sampling effort. The data have been collected from 1987 to 2022 across 238 sites. Seeds are collected from the ground by local companies on behalf of the Polish State Forest, and each inspectorate has assigned seed collection sites. In both datasets, a decline in synchrony and interannual variation of seed production linked to summer temperature increases has been detected (Bogdziewicz *et al.*, 2020, 2021; Foest *et al.*, 2025b). The seeding time series are provided in Figure 1.

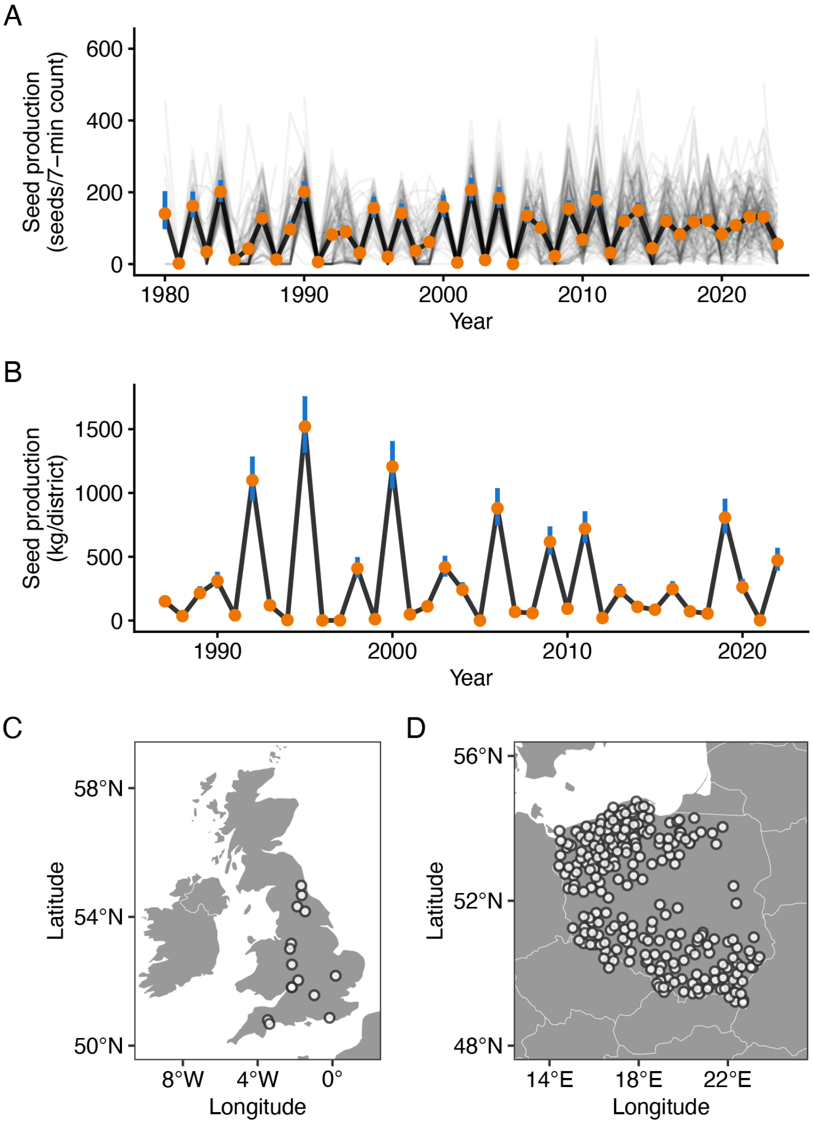

Figure 1: **Seed production patterns of European beech in UK and Poland**. A) For the UK each line shows individual tree seed production (229 trees, 17 sites), while a black thick line shows the country-level mean (orange points) and associated 95% confidence intervals (blue whiskers). Note that the number of trees and sites varies across analyses due to data filtering (see Methods). B) Country-level, annual mean (±95% CI, blue whiskers) seed output in Poland, based on harvest records from 238 sites. Means and confidence intervals were estimated using a Tweedie GLM with intercept set at zero, with year fitted as a factor variable. Panels C) and D) show the locations of study sites in the UK and Poland, respectively.

Analysis

Masting–weather cue coupling To quantify temporal changes in the coupling between weather cues and reproduction, we used the UK seed-production dataset, which is based on long-term ecological monitoring at the individual-tree level. Because population-level synchrony emerges from the aggregation of individual reproductive responses (Koenig *et al.*, 2003), we estimated cue–reproduction relationships separately for each tree. We fitted tree-specific zero-inflated Tweedie models with a log link function, using annual seed production as the response variable, while mean June-July maximum temperatures two years (T2) and one year (T1) before seedfall, and seed production in the previous year (log-transformed), were used as predictors. The zero-inflated formula included log-transformed previous year seed production. We fitted separate models for each tree rather than mixed-effects models with random slopes, to avoid shrinkage of individual responses toward the population-level mean. To assess temporal changes in cue coupling, models were fitted separately for two periods: 1980-2006 and 2007-2024. This division reflects the documented abrupt decline in masting synchrony in the UK, with a clear transition around 2006 (Bogdziewicz *et al.*, 2020; Hacket-Pain *et al.*, 2025). In each period, we included only trees with at least $n = 10$ years of seed-production records to ensure reliable estimation of individual cue responses. As a result, we used 84 trees (11 sites) in the 1980-2006 subset, and 96 trees (11 sites) in the 2007-2024 subset.

In addition to the tree-specific models, we fitted generalized linear mixed models (GLMMs) to characterise the aggregate relationship between seed production and weather cues at the dataset level (UK). These models used a Tweedie error distribution with a log link, included mean June-July maximum temperatures at T1 and T2, and previous year seed production (log-transformed) as fixed effects, and incorporated tree ID and site ID as random intercepts. As above, models were fitted separately for the periods 1980-2006 and 2007-2024. Moreover, in addition to models with separate T1 and T2 predictors, we also fitted models using the temperature difference between summers one and two years before seedfall ($\Delta T = T1 - T2$) as a single predictor. This formulation captures the established cueing system of European beech reproduction, in which cold summers two years before seedfall, followed by warm summers one year before seedfall, promote flowering (Vacchiano *et al.*, 2017). ΔT provides a parsimonious representation of the combined effect of T1 and T2 and facilitates visualisation and interpretation of changes in cue dependence (Kelly *et al.*, 2013; Szymkowiak *et al.*, 2024). This analysis was based on 106 trees (11 sites) in the 1980-2006 data subset, and 169 trees (15 sites) in the 2007-2024 subset.

Tail-dependent synchrony and its temporal change

Categorization of masting data into tails Our framework follows that of Walter *et al.* (2022), modified by Szymkowiak *et al.* (2024). For seed production scaled at individual tree (UK data) or site (Polish data) to values between 0 and 1, masting lower tail includes annual values of seed production ≤ 0.5, while upper those > 0.5. The thresholds are arbitrary in the sense that masting is not a categorical variable, but they enable analysis of tail-dependence (Ghosh *et al.*, 2021; Walter *et al.*, 2022; Szymkowiak *et al.*, 2024). We also tested other thresholds (0.2/0.8, 0.4/0.6, 0.6/0.4, 0.8/0.2), and these provided qualitatively similar results.

Tail-dependent masting synchrony We estimated the synchrony in masting tails using a partial Spearman correlation, defined as the portion of the standard Spearman rank correlation arising due to the range of values in the two variables being bounded by tails thresholds (Walter *et al.*, 2022). Pairwise correlations were calculated separately for the lower (≤ 0.5) and upper (> 0.5) tails of the seed production time series. In cases when the annual value of seed production for the two time series falls into opposite tails, the value was included in both tails when calculating the partial Spearman correlation (Szymkowiak *et al.*, 2024, 2025). Thus, if one individual or site experienced a mast peak and the other a year of seed scarcity in the same year, synchrony was reduced in both tails. This approach ensures that mismatches across individuals or sites reduce synchrony in both tails, reflecting the ecological interpretation that opposite outcomes indicate asynchrony. Note that scaling of the mast data does not affect the correlations calculated via Spearman correlation, as these are calculated on ranked data.

The tail-dependent synchrony was estimated at two levels: among trees, within populations (UK data), and among-sites, regional (Polish data). The within-site synchrony has been summarized as mean (±SD) lower/upper synchrony across all trees within a given population. In the case of regional synchrony, we calculated the distance-decay of within-tail seed production synchrony using non-parametric spatial covariance functions (Bjørnstad & Falck, 2021). We used the matrices of partial Spearman correlations within the lower and upper tails as the response (synchrony variables), explained by the matrices of pairwise geographical distances between sites (Szymkowiak *et al.*, 2024). To calculate 95% confidence bands for each function, we used the standard bootstrapping procedure (Bjørnstad & Falck, 2021).

Temporal changes in tail-dependent synchrony To quantify temporal shifts in tail-dependent masting synchrony, we divided the datasets into time periods reflecting documented or expected changes in masting dynamics. In the UK, the decline in synchrony occurred abruptly, with a clear transition around 2006 (Bogdziewicz *et al.*, 2020; Hacket-Pain *et al.*, 2025); we therefore analysed two periods, 1980-2006 (84 trees, 11 sites) and 2007-2024 (96 trees, 11 sites). In Poland, the spatially extensive dataset and the heterogeneous pattern of summer warming did not permit identification of a single transition period (Foest *et al.*, 2025b). Instead, we partitioned the time series into three equal 12-year periods (1987-1998, 1999-2010, and 2011-2022). Tail-specific synchrony was estimated separately within each period following the procedures described above.

Results

Spatial synchrony in European beech seed production declined in both tails of the masting distribution, but the decline was consistently stronger in the upper tail. Local (UK) upper-tail synchrony decreased by approximately 50%, i.e., from 0.38 (± 0.07; mean partial Spearman cross-correlation among trees within site ± SD) in the first period (1980–2006) to 0.21 (± 0.14) in the second period (2007-2024; Fig. 2). Lower-tail synchrony also declined, but to a lesser extent, i.e., by 36%, i.e., from 0.56 (± 0.09) to 0.37 (± 0.16) (Fig. 2).

In the case of regional synchrony (Poland), the decline in synchrony was similarly asymmetric as in the case of local synchrony. The upper tail synchrony decline was also stronger compared to the lower tail, i.e., the upper tail decreased by over 50% from 0.26 (±0.005; mean partial Spearman cross-correlation among sites ±SD) to 0.12 (±0.007) (Fig. 3). In contrast, the lower tail synchrony declined by about 25%, from 0.37 (±0.01) to 0.30 (±0.02) (Fig. 3). Thus, although the asymmetry in decline matched our prediction of a stronger decrease of synchrony in mast peaks than in failures, the magnitude of change was substantial in both tails.

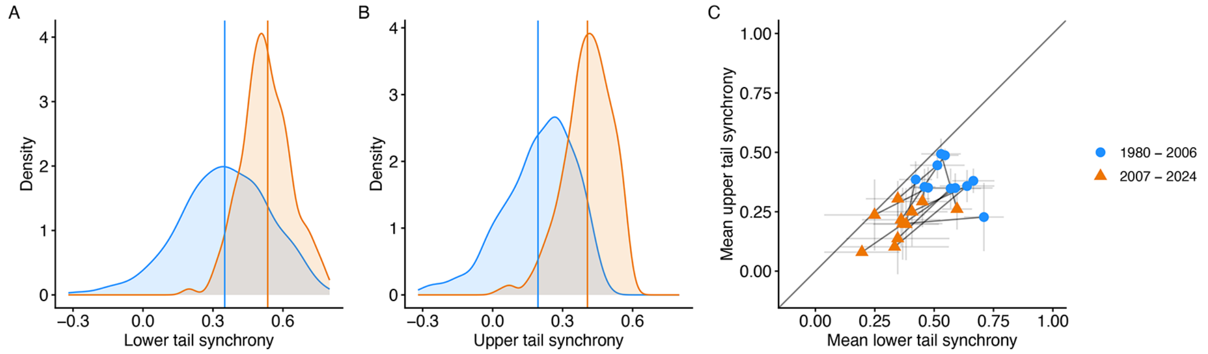

Figure 2: The temporal decline in local (within-site) masting synchrony is stronger in upper-tail (high-seeding years) years, than in lower-tail (poor-seeding years). Density plots show local (among trees, within-site) synchrony in A) lower, and B) upper tail of masting, estimated separately for two periods, before the masting breakdown (i.e., the abrupt decline in interannual variation and synchrony of seed production; 1980-2006; n = 84 trees at 11 sites), and after breakdown (2007-2024; n = 96 trees at 11 sites). The vertical line shows tail- and period-level means. C) Site-level tail-dependence. Points show site-level mean tail-dependent synchrony, while whiskers show SDs. Synchrony for each site was calculated for the two time periods (1980-2006, and 2007-2024); these points are joined by a line. The estimates are based on partial Spearman correlations, with the lower tail being seed production below 0.5, while the upper being above, for annual seed production values scaled within each site to between 0 and 1 (see Methods).

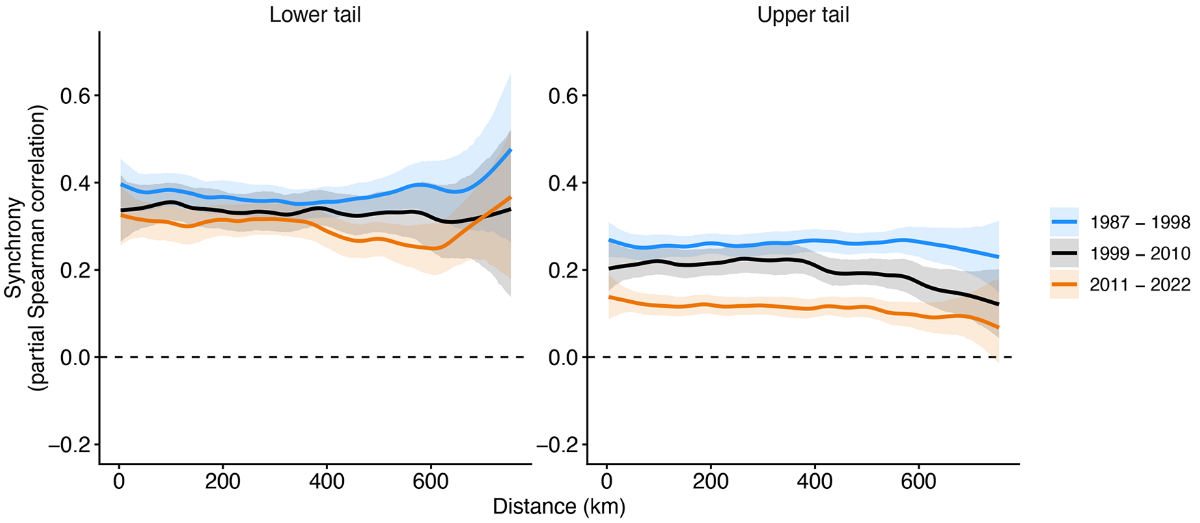

Figure 3: The temporal decline in regional (among-sites) masting synchrony is stronger in upper-tail (high-seeding) years than in lower-tail (poor-seeding years). Distance decay of beech masting synchrony in the upper and lower tail, estimated separately for the three periods (1987-1998, 1999-2010, and 2011-2022). The estimates are based on partial Spearman correlations and seed production records from 238 sites in Poland. The lower tail is seed production below 0.5, while the upper is above, for annual values scaled within each site to between 0 and 1 (see Methods).

The decline in synchrony reflected changes in the coupling between seed production and weather cues that differed from our expectations. The association between seed production and the T1 temperature cue weakened markedly and, in many cases, nearly disappeared. The mean slope of the tree-level responses to the T1 cue was 0.53 ±0.42 (SD) in the first studied period (1980-2006), and declined 3-fold to 0.19 ±0.25 (SD) in the second period (2007-2024; Fig. 4). In contrast, the decline in responses to the T2 cue was smaller; the mean slope in the first period was -0.31 ±0.28 (SD), which declined to -0.21 ±0.21 (SD). Visual inspection of these relationships further reveals that the decline in the response to the T1 cues was not due to weakening and diversification of responses specifically under high cue values (Fig. S1). Instead, seed production responses to the T1 cue generally flattened across the whole gradient of cues. While cold T1 summers largely prevented seed production in the first period of the study, that was no longer the case in the second period.

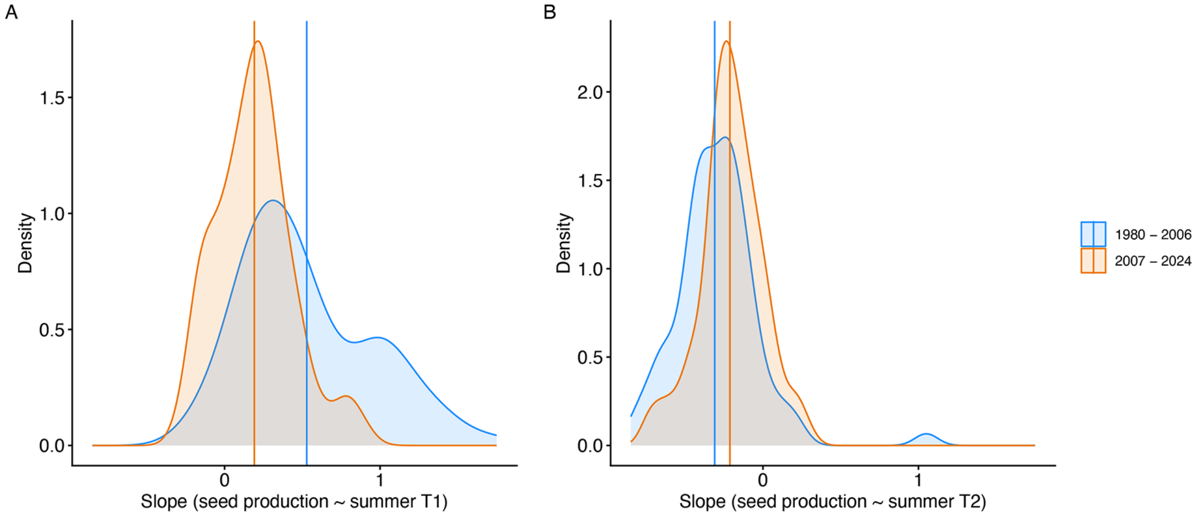

Figure 4: **Masting dynamics are increasingly dominated by a summer T2 cue**. Density plots of slopes of the tree-level relationships between seed production and summer T1 (A), and summer T2 (B) cues. Summer is June-July mean maximum temperature in one (T1) and two (T2) years before seedfall. Models were fitted for each tree individually, and included this and this. Models were fitted for two time periods, i.e., 1980-2006 (yellow; n = 84 trees at 11 sites), and 2007-2024 (purple; n = 96 trees at 11 sites). Estimated relationships are visualized in Fig. S1.

Consequently, before the breakdown of masting synchrony (1980-2006), large seed crops followed the canonical sequence of weather cues, with cold summers two years before seedfall (T2) followed by warm summers one year before seedfall (T1). When expressed as the temperature contrast between these two summers ($\Delta T = T1 - T2$), seed production was generally suppressed for negative ΔT values and increased sharply once ΔT became positive, that is, when the summer preceding flowering (T1) was warmer than the priming summer (T2) (Fig. 5).

After 2006, this relationship changed markedly. Seed production was no longer strongly suppressed at negative ΔT values, and high seed crops occurred even when T1 summers were relatively cool. In other words, cold summers in T2 increasingly appeared sufficient to trigger reproduction, largely independent of conditions in T1 (Fig. 5). As a result, the steep, non-linear increase in seed production with increasing ΔT observed before the breakdown was replaced by a flatter relationship (Fig. 5). Together, these changes indicate a shift toward reproductive dynamics dominated by the T2 cue, with diminished modulation by T1.

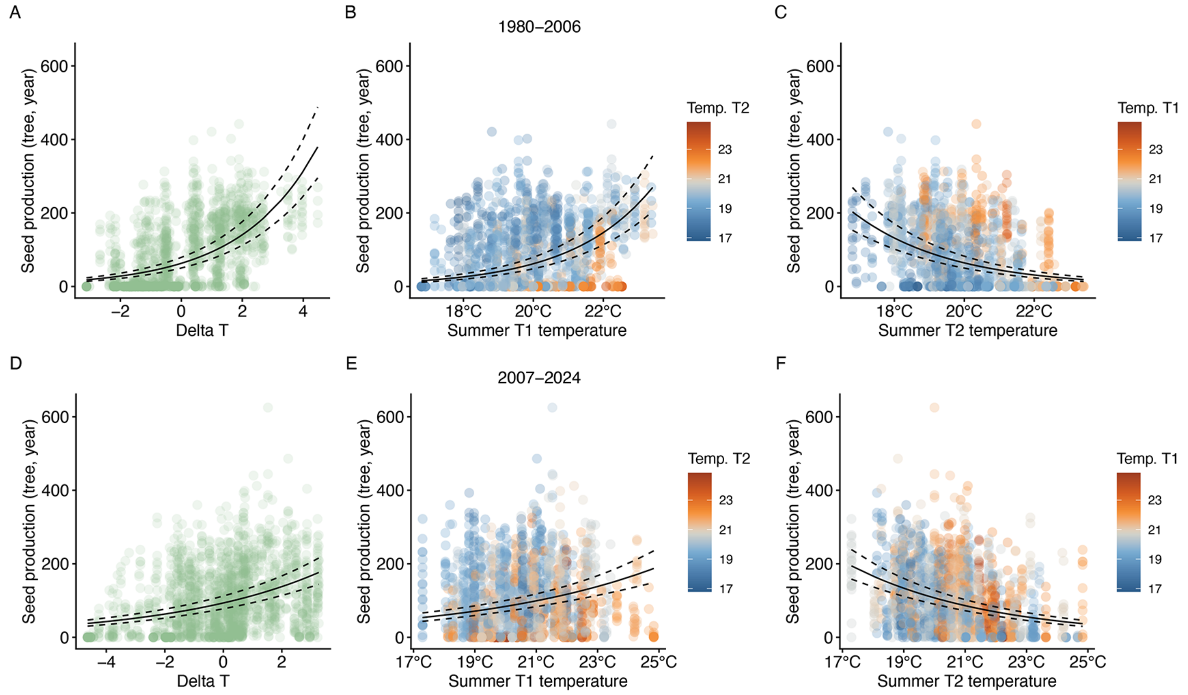

Figure 5: Population-level relationship between weather cues and masting indicates flattening of responses in recent times. Plots show relationships between seed production and ΔT (A and D), summer T1 (B and E), and summer T2 (C and F) cues. Summer is June-July mean maximum temperature in one (T1) and two (T2) years before seedfall. Prediction lines and associated 95% confidence intervals were estimated with GLMM models with Tweedie error distributions and log links that included tree identity and site as random intercepts. Points show annual, tree-level seed production records. Models were fitted for two time periods, i.e., 1980-2006 (top row; n = 106 trees at 11 sites) and 2007-2024 (bottom row; n = 169 trees at 15 sites). Model summaries are provided in Table S1 and Table S2.

Discussion

Our analyses show a tail-dependent decline in masting synchrony in European beech, consistent across spatial scales and datasets. Synchrony weakened more in the upper tail compared to the lower tail. This concordance indicates that the tail-dependent decline of synchrony is a general feature of beech reproduction under warming. However, contrary to expectations, lower-tail synchrony also declined substantially. Thus, climate-driven disruption extends to both extremes of the seed-production distribution. This pattern can be linked to a restructuring of cue–reproduction relationships. Rather than increased heterogeneity in responses to the warm-summer cue (T1), we found that reproductive dynamics became increasingly dominated by the cold-summer cue two years before seedfall (T2), with the influence of T1 markedly weakened. Consequently, the steep, non-linear response to combined cues that previously induced years of widespread failure and synchronized peaks was replaced by a flatter response across a broad range of cue conditions. This flattening of cue dependence translates directly into a flattening of masting-driven resource pulses: failures are no longer uniformly severe across space, and peaks are less synchronous both locally and regionally.

The erosion of tail-dependent masting synchrony has direct consequences for ecosystems structured by pulsed seed resources. Desynchronization of failures weakens the trophic bottlenecks that underpin many cascade effects. For example, in boreal North America, synchronous conifer cone production failures drive large-scale southward irruptions of granivorous birds (Strong *et al.*, 2015; Widick *et al.*, 2025), triggering downstream ecological and epidemiological consequences, including elevated transmission of avian salmonellosis (Tonelli *et al.*, 2026). To the extent that climate warming disrupts lower-tail synchrony, such irruptive dynamics may cease to operate, because seed failure no longer occurs coherently across space. At the opposite end of the distribution, mast peaks generate short-lived resource surges that fuel outbreaks of seed consumers, with consequences for rodent populations, tick abundance, and human exposure to Lyme disease (Jones *et al.*, 1998; Bregnard *et al.*, 2021). The observed weakening of upper-tail synchrony implies that these outbreaks may become less spatially extensive and less episodic. However, reduced pulsing does not necessarily imply reduced disease risk: more regular but moderate seed production may sustain consistently higher consumer populations, potentially increasing long-term disease exposure even as extreme outbreaks become rarer. Higher consumer populations may also translate into a decrease in tree recruitment (Zwolak *et al.*, 2024). Similar dependencies on pulsed reproduction occur in other systems, such as specialist frugivores whose breeding is tightly coupled to mast events (Fidler *et al.*, 2008), raising the possibility that flattened resource pulses could disrupt animal reproductive cycles. Two important research directions emerge: first, quantifying how flattened pulsed resources alter interaction strength across trophic levels in systems already undergoing change (Shibata *et al.*, 2020; Yukich-Clendon *et al.*, 2023; Bush *et al.*, 2020; Foest *et al.*, 2025b). Second, determining how general this restructuring is across masting species, climates, and reproductive strategies.

We expected climate warming to decrease masting synchrony, particularly in the upper tail, by increasing heterogeneity in individual responses to the warm-summer cue preceding flowering (T1). Instead, our results indicate a shift in the relative importance of cues: reproductive dynamics became increasingly governed by the priming effect of cold summers two years before seedfall (T2), while modulation by T1 weakened substantially. Past work has focused primarily on T1, showing that the responses to this cue are strongly contingent on internal resource levels: when resources have accumulated over several years since the last reproductive event, even moderate T1 warming can trigger large flowering, whereas depleted reserves suppress reproduction despite strong cues (Kelly *et al.*, 2025). As summer warming has increased the frequency of T1 cueing, repeated flowering has led to chronic resource depletion (Hacket-Pain *et al.*, 2025), reducing the sensitivity of trees to T1 and flattening the response that previously structured mast peaks. In contrast, the T2 cue is not expected to depend on resource state, as it precedes seedfall by three growing seasons and therefore cannot reliably index resource availability at the time of reproduction (Kelly *et al.*, 2025). Instead, T2 likely acts through developmental priming or epigenetic “summer memory”, initiating regulatory pathways that condition the plant’s subsequent response to later cues (Samarth *et al.*, 2020, 2021; Satake & Kelly, 2021). We hypothesize that because this mechanism is decoupled from short-term resource depletion, the effectiveness of T2 has been less eroded by warming. As a result, reproduction increasingly occurs following cold T2 summers even when T1 conditions are weak, producing seed crops under negative ΔT values. What remains unresolved is why reproduction is no longer consistently suppressed when internal resources are depleted, as predicted by resource–cue interaction models in which a low resource state constrains flowering responses (Kelly *et al.*, 2025). Resolving that issue will require experimental and molecular approaches that track resource state alongside cue perception.

The reweighting of cues provides a mechanistic explanation for why synchrony declined in both tails of the masting distribution. Under the former cue structure, reproduction was largely vetoed across wide areas whenever ΔT was negative, because cold T2 summers not followed by warm T1 conditions suppressed flowering. This produced high synchrony in the lower tail, as spatial variation in weather had little effect as long as ΔT remained negative. In contrast, cold T2 summers have increasingly become sufficient to induce reproduction regardless of T1, allowing some trees and populations to reproduce under conditions that previously produced synchronized failure. The consequence is a loss of spatially coherent seed scarcity. At the same time, the weakening of T1 reduced the amplification of reproductive effort under favourable conditions, replacing steep, nonlinear responses with flatter ones. This diminished the spatial coherence of mast peaks and led to a stronger decline in upper-tail synchrony.

The same logic suggests that climate-driven flattening of tail-dependent synchrony may extend beyond European beech. Masting systems differ in how strongly reproductive cues are coupled to internal resource dynamics; as suggested by variation in sensitivity to cues across species (Kelly *et al.*, 2013; Journé *et al.*, 2025). Species in which flowering responses are strongly gated by resource accumulation and amplified by rare, high-magnitude cues should be particularly sensitive to increases in cue frequency, as chronic depletion will weaken cue responsiveness. In contrast, systems dominated by relative cues, such as differential-temperature cues (Kelly *et al.*, 2013; LaMontagne *et al.*, 2021), may retain stronger non-linear behaviour and more stable tail dependence under warming. Testing this prediction across species will be required for understanding when climate change will reorganize the synchrony structure that underpins resource pulses and their ecological effects.

To summarize, our results show that climate warming is altering the nonlinear cue structures that generate masting-driven pulsed resources, reducing synchrony in both seed failures and mast peaks, with a stronger decline in the latter. Pulsed-resource systems shape ecological dynamics because strong environmental events trigger synchronized biological responses, creating predictable booms and busts that spread through food webs (Yang *et al.*, 2010). By flattening cue–reproduction relationships, warming weakens this alignment, replacing spatially coherent pulses with weaker and less predictable dynamics. This shift has implications for ecological processes, including for ecological forecasting (Dietze *et al.*, 2018; Pearse *et al.*, 2021). When relationships between climatic cues, masting, and consumer responses are preserved, climate information can be used to anticipate downstream effects such as bird irruptions, zoonotic disease outbreaks, and to plan conservation and management actions (Pearse *et al.*, 2021; Journé *et al.*, 2023; Oberklammer *et al.*, 2025). Our results suggest that such forecasting frameworks may become less reliable as cue responses and synchrony decline, because weather signals lose predictive power. Determining whether similar cue reweighting and synchrony asymmetric synchrony decline occur in other masting species is important for assessing how broadly climate change is reshaping pulsed-resource dynamics and their predictability.

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Author Contributions Statement

MBogdziewicz, JJF, and JSz conceived and designed the study. AHP, RG, PAT, JGAL SJ, MKD, JJF and JSz collected and curated the data. JSz and MBogdziewicz conducted the analysis. MBogdziewicz wrote the first draft of the manuscript. All authors contributed to the interpretation of the analysis, revised the draft, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data availability statement

The data supporting the results are archived in the Open Science Framework and are available at: `https://osf.io/c59rf/overview?view_only=c659c7a7ba0944d1becccbd765b1173d` .

References

Anderson, T.L., Sheppard, L.W., Walter, J.A., Rolley, R.E. & Reuman, D.C. (2020). Synchronous effects produce cycles in deer populations and deer-vehicle collisions. *Ecology Letters*, 24, 337–347.

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.

Bjørnstad, O. & Falck, W. (2021). Nonparametric spatial covariance functions: estimation and testing. *Ecology Letters*, 8, 53–70.

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., Journé, V., Hacket-Pain, A. & Szymkowiak, J. (2023a). Mechanisms driving interspecific variation in regional synchrony of trees reproduction. *Ecology Letters*, 26, 754–764.

Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P., Foest, J., Lageard, J. *et al.* (2023b). 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. (2020). 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.

Bregnard, C., Rais, O. & Voordouw, M.J. (2021). Masting by beech trees predicts the risk of lyme disease. *Parasites and Vectors*, 14, 1–22.

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.

Dietze, M.C., Fox, A., Beck-Johnson, L.M., Betancourt, J.L., Hooten, M.B., Jarnevich, C.S. *et al.* (2018). Iterative near-term ecological forecasting: Needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 1424–1432.

Fernández-Martínez, M., Bogdziewicz, M., Espelta, J.M. & Peñuelas, J. (2017). Nature beyond linearity: Meteorological variability and jensen's inequality can explain mast seeding behavior. *Frontiers in Ecology and Evolution*, 5, 134.

Fidler, A.E., Lawrence, S.B. & McNatty, K.P. (2008). An hypothesis to explain the linkage between kakapo (strigops habroptilus) breeding and the mast fruiting of their food trees. *Wildlife Research*, 35, 1–7.

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., Bogdziewicz, M., Caignard, T., Hadad, M., Thomas, P.A. & Hacket-Pain, A. (2025a). Comparing two ground-based seed count methods and their effect on masting metrics. *Forest Ecology and Management*, 581, 122551.

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

Ghosh, S., Cottingham, K.L. & Reuman, D.C. (2021). Species relationships in the extremes and their influence on community stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200343.

Ghosh, S., Sheppard, L.W., Reid, P.C. & Reuman, D. (2020). A new approach to interspecific synchrony in population ecology using tail association. *Ecology and Evolution*, 10, 12764–12776.

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.

Hansen, B.B., Grøtan, V., Herfindal, I. & Lee, A.M. (2020). The moran effect revisited: spatial population synchrony under global warming. *Ecography*, 43, 1591–1602.

Holt, R.D. (2008). Theoretical perspectives on resource pulses. *Ecology*, 89, 671–681.

Jones, C.G., Ostfeld, R.S., Richard, M.P., Schauber, E.M. & Wolff, J.O. (1998). Chain reactions linking acorns to gypsy moth outbreaks and lyme disease risk. *Science*, 279, 1023–1026.

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., Hacket-Pain, A., Oberklammer, I., Pesendorfer, M.B. & Bogdziewicz, M. (2023). Forecasting seed production in perennial plants: identifying challenges and charting a path forward. *New Phytologist*, 239, 466–476.

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.

Koenig, W.D. (2019). Acorn production and california oaks in a changing world. *International Oaks*, 30, 45–52.

Koenig, W.D., Kelly, D., Sork, V.L., Duncan, R.P., Elkinton, J.S., Peltonen, M.S. *et al.* (2003). Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos*, 102, 581–591.

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

Koenig, W.D. & Knops, J.M.H. (2013). Large-scale spatial synchrony and cross-synchrony in acorn production by two california oaks. *Ecology*, 94, 83–93.

LaMontagne, J.M., Pearse, I.S., Greene, D.F. & Koenig, W.D. (2020). Mast seeding patterns are asynchronous at a continental scale. *Nature Plants*, 6, 460–465.

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.

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

Nilsson, S.G. & Wastljung, U. (1987). Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology*, 68, 260–265.

Oberklammer, I., Gratzer, G., Schueler, S., Konrad, Heino, Hacket-Pain *et al.* (2025). See(d)ing the seeds-toward weather-based forecasting of annual seed production in six european forest tree species. *Ecoevorxiv*, https://doi.org/10.32942/X2T05Z.

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., Lordon, M., Hipp, A.L. & Koenig, W.D. (2020). Biogeography and phylogeny of masting: do global patterns fit functional hypotheses? *New Phytologist*, 227, 1557–1567.

Pearse, I.S., Wion, A.P., Gonzalez, A.D. & Pesendorfer, M.B. (2021). Understanding mast seeding for conservation and land management. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 34657466.

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.

Pesendorfer, M.B., Bogdziewicz, M., Oberklammer, I., Nopp-Mayr, U., Szwagrzyk, J. & Gratzer, G. (2024). Positive spatial and temporal density-dependence drive early reproductive economy-of-scale effects of masting in a european old-growth forest community. *Journal of Ecology*, 112, 1872–1884.

Piovesan, G. & Adams, J.M. (2001). Masting behaviour in beech: Linking reproduction and climatic variation. *Canadian Journal of Botany*, 79, 1039–1047.

Reuman, D.C., Walter, J.A., Sheppard, L.W., Karatayev, V.A., Kadiyala, E.S., Lohmann, A.C. *et al.* (2025). Insights into spatial synchrony enabled by long-term data. *Ecology Letters*, 28, e70112.

Samarth, Kelly, D., Turnbull, M.H. & Jameson, P.E. (2020). Molecular control of masting: An introduction to an epigenetic summer memory. *Annals of Botany*, 125, 851–858.

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.

Satake, A. & Kelly, D. (2021). Studying the genetic basis of masting. *Philosophical Transactions of the Royal Society B*, 376, 20210116.

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.

Sears, A.L.W., Holt, R.D. & Polis, G.A. (2004). Feast and famine in food webs: the effects of pulsed productivity. In: *Food Webs at the Landscape Level* (eds. Polis, G.A., Power, M.E. & Huxel, G.R.). University of Chicago Press, Chicago, pp. 359–386.

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.

Strong, C., Zuckerberg, B., Betancourt, J.L. & Koenig, W.D. (2015). Climatic dipoles drive two principal modes of north american boreal bird irruption. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 2795–2802.

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. (2024). Tail-dependence of masting synchrony results in continent-wide seed scarcity. *Ecology Letters*, 27, e14474.

Tonelli, B.A., Youngflesh, C. & Tingley, M.W. (2026). An ecological cascade links climatic variability to avian irruptions and zoonotic salmonellosis outbreaks. *Proceedings of the National Academy of Sciences*, 123, e2511209123.

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.

Walter, J.A., Castorani, M.C., Bell, T.W., Sheppard, L., Cavanaugh, K.C. & Reuman, D.C. (2022). Tail-dependent spatial synchrony arises from nonlinear driver–response relationships. *Ecology Letters*, 25, 1189–1201.

Walter, J.A., Emery, K.A., Dugan, J.E., Hubbard, D.M., ID, T.W.B., Sheppard, L.W. *et al.* (2024). Spatial synchrony cascades across ecosystem boundaries and up food webs via resource subsidies. *PNAS*, 121, e2310052120.

Widick, I.V., Strong, C., LaMontagne, J.M., Young, M.A. & Zuckerberg, B. (2025). Continent-wide patterns of climate and mast seeding entrain boreal bird irruptions. *Global Change Biology*, 31, e70076.

Wion, A.P., Weisberg, P.J., Pearse, I.S. & Redmond, M.D. (2020). Aridity drives spatiotemporal patterns of masting across the latitudinal range of a dryland conifer. *Ecography*, 43, 569–580.

Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008). What can we learn from resource pulses. *Ecology*, 89, 621–634.

Yang, L.H., Edwards, K.F., Byrnes, J.E., Bastow, J.L., Wright, A.N. & Spence, K.O. (2010). A meta-analysis of resource pulse-consumer interactions. *Ecological Monographs*, 80, 125–151.

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.

Zwolak, R., Bogdziewicz, M., Wróbel, A. & Crone, E. (2016). Advantages of masting in european beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia*, 180, 749–758.

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

Climate warming flattens masting-driven pulsed resources

Table S1: Summary of the GLMMs testing the population-level relationship between a composite weather cue (ΔT) and annual variation in seed production, separately for the two periods, i.e., 1980-2006 and 2007-2024. The models were fitted with a Tweedie error distribution and a log link function, and included tree identity and site as random intercepts. The previous year's seed production was included as a covariate.

Model term	**Slope**	**Std. Error**	**z value**	**p value**
1980–2006 period				
Conditional part				
Intercept	4.60	0.12	39.56	< 0.001
ΔT	0.40	0.02	23.74	< 0.001
Seed production T−1	-0.15	0.01	-11.78	< 0.001
Zero-inflated part				
Intercept	-11.42	1.55	-7.35	< 0.001
Seed production T−1	2.07	0.29	7.03	< 0.001
2007–2024 period				
Conditional part				
Intercept	4.97	0.11	45.95	< 0.001
ΔT	0.19	0.01	15.77	< 0.001
Seed production T−1	-0.11	0.01	-8.21	< 0.001
Zero-inflated part				
Intercept	-4.81	2.258	-2.13	0.033
Seed production T−1	-16.16	1152.80	-0.01	0.989

Table S2: Summary of the GLMMs testing the population-level relationship between weather cues (summer temperatures in year T1 and T2) and annual variation in seed production, separately for the two periods, i.e., 1980-2006 and 2007-2024. The models were fitted with a Tweedie error distribution and a logit link function, and included tree identity and site as random intercepts. The previous year's seed production was included as a covariate. Summer temperature is the mean maximum temperature in June and July.

Model term	**Slope**	**Std. Error**	**z value**	**p value**
1980–2006 period				
Conditional part				
Intercept	3.17	0.67	4.72	< 0.001
Summer temperature T−1	0.43	0.02	19.62	< 0.001
Summer temperature T−2	-0.36	0.03	-14.14	< 0.001
Seed production T−1	-0.15	0.01	-11.97	< 0.001
Zero-inflated part				
Intercept	-11.32	1.51	-7.48	< 0.001
Seed production T−1	2.06	0.29	7.18	< 0.001
2007–2024 period				
Conditional part				
Intercept	6.02	0.50	11.94	< 0.001
Summer temperature T−1	0.17	0.02	9.04	< 0.001
Summer temperature T−2	-0.22	0.02	-13.00	< 0.001
Seed production T−1	0.10	0.01	-6.57	< 0.001
Zero-inflated part				
Intercept	-5.25	3.63	-1.45	0.147
Seed production T−1	-2.66	7.43	-0.36	0.720

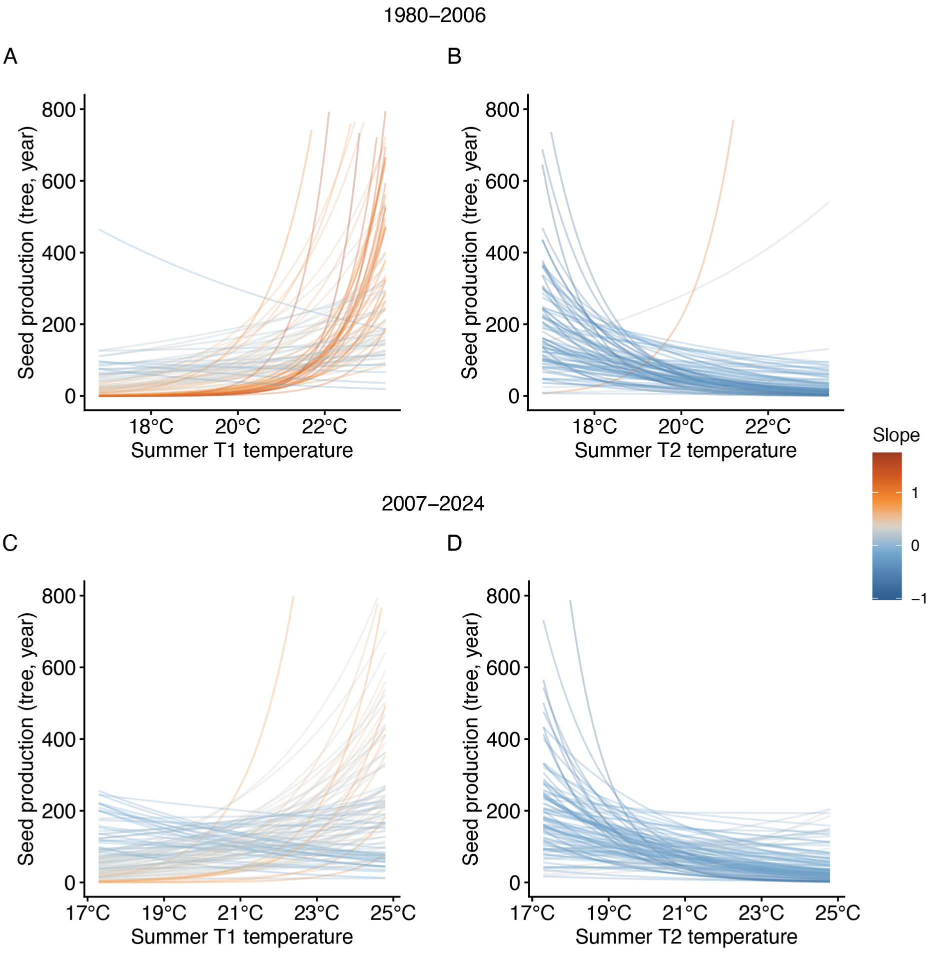

Figure S1: Tree-level weather-cue and seed production relationships indicate that sensitivity to T1 cue weakened more than to the T2 cue. Tree-level relationships between annual seed production and summer (June-July) mean maximum temperatures one (T1) and two years (T2) preceding seedfall. Relationships were estimated with tweedie models, separately for the two time periods, i.e., 1980–2006 (top row; n = 84 trees at 11 sites), and 2007–2024 (bottom row; n = 96 trees at 11 sites). Slopes of these relationships are summarized in Fig. 4.