Climate warming flattens masting-driven resource pulses

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, creating years of low or high resource availability that structure food webs. Mast seeding is a major example, yet climate warming is disrupting the synchrony that underpins these fluctuations. Ecological consequences depend on whether populations fail together or produce large seed crops together across space.

- We tested how warming-driven changes in European beech (*Fagus sylvatica*) masting affect spatial synchrony in failure and high-seeding years, and how these changes arise from altered links between weather cues and reproduction. We analysed 45 years of individual-tree seed production data from the United Kingdom and 33 years of seed harvest records from Poland.

- Synchrony declined strongly in high-seeding years, by 45% locally and 54% regionally. Synchrony in failure years also declined, although less strongly, by 34% locally and 19% regionally. The decline coincided with a restructuring of weather-cue responses: strong warm-summer T1 cues no longer generated uniform reproductive amplification, while unfavourable cue conditions that previously suppressed reproduction were associated with heterogeneous outcomes among trees.

- Declining synchrony weakened both the spatially coherent seed shortages generated by widespread reproductive failure and the resource surges generated by mast peaks. The flattening of masting-driven pulses is likely to reduce the strength, spatial extent, and predictability of consumer responses and food-web effects.

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 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 (Pearse *et al.*, 2017; 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; Jantzen *et al.*, 2026). 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 appear to lose their coordinating function (Bogdziewicz *et al.*, 2021; Hacket-Pain *et al.*, 2025). Masting desynchronization is now evident across much of the European beech 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 cue values 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 cue values are high, reproduction lies on the steeper part of the cue-response relationship. Then, small spatial differences in weather among trees or sites can be amplified into large differences in seed production, reducing synchrony in mast peaks (Szymkowiak *et al.*, 2024).

In this study, we ask whether the climate-change-induced disruption of European beech masting (Bogdziewicz *et al.*, 2020; Foest *et al.*, 2025b) weakens synchrony differently in seed failures and mast peaks. Previous work showed that warming increased the frequency of reproductive cues and progressively weakened the effects of both summer temperature cues on reproduction, consistent with increasingly frequent flowering depleting internal resources and limiting their recovery between reproductive events (Bogdziewicz *et al.*, 2021; Hacket-Pain *et al.*, 2025; Kelly *et al.*, 2025). However, it remains unknown how the cue-reproduction function has changed and whether this restructuring differentially affects the processes generating seed failures and mast peaks. We predicted a stronger decline in upper-tail synchrony, because resource limitation should weaken the amplification of reproduction under favourable cue conditions. In contrast, if unfavourable cue conditions continued to suppress reproduction consistently, 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 the UK (Hacket-Pain *et al.*, 2025). 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; Jantzen *et al.*, 2026). 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 (average size 13,9 ha). 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 seed production time series are provided in Figure 1.

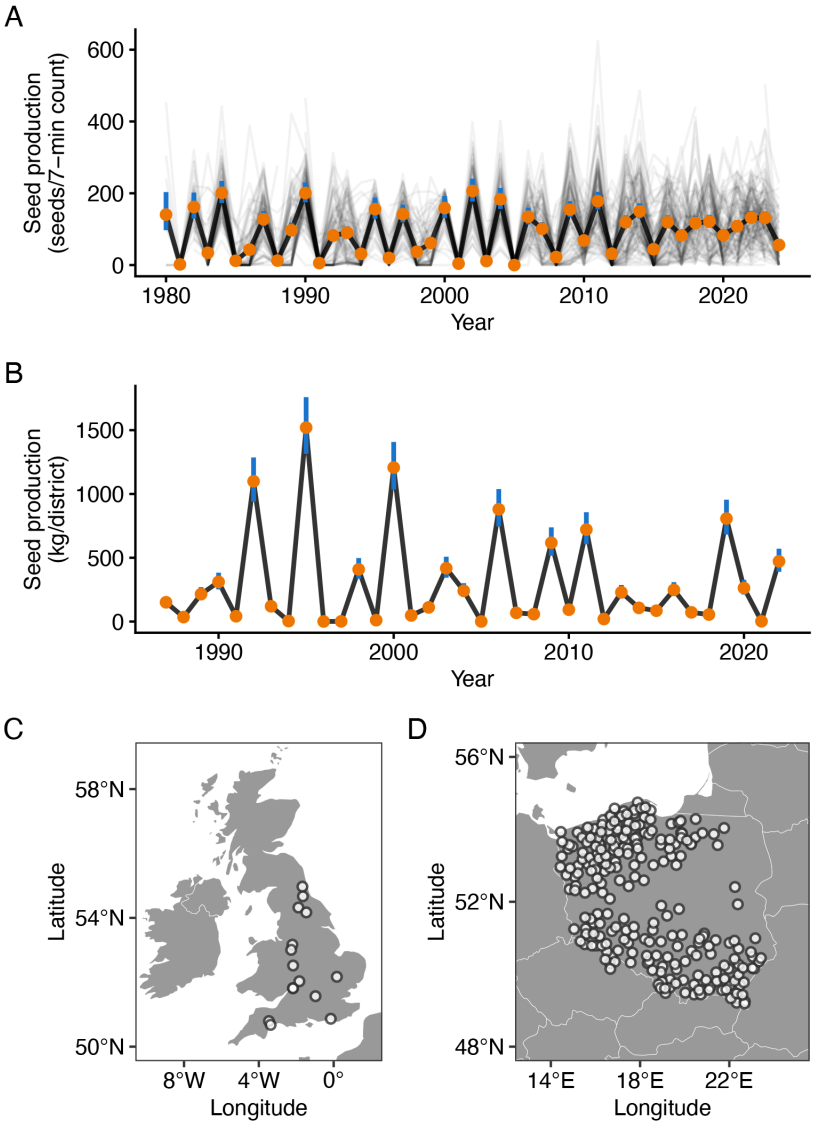

Figure 1: Seed production patterns of European beech in UK and Poland. A) For the UK, each line shows individual tree seed production (213 trees, 17 sites, 1980-2024), while a black thick line shows the country-level mean (orange points) and associated 95% confidence intervals (blue whiskers). Note that 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 (1987-2022). 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 analysed individual-tree observations from the UK dataset using a

generalized linear mixed models fitted via glmmTBM package (Brooks *et al.*, 2017). Annual seed production was fitted with a Tweedie error distribution and log link function. Fixed effects included study period, mean June–July maximum temperatures one and two years before seedfall (T1 and T2), their interactions with period (see below), the T1 × T2 interaction, and log-transformed seed production in the previous year. T1 and T2 were standardized before analysis. We divided the time series into 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). Tree identity was included as a random intercept with uncorrelated random slopes for T1 and T2. This structure accounted for repeated measurements of individual trees and allowed cue sensitivity to vary among trees. Site identity was included as a random intercept. We used a diagonal covariance structure for the tree-level random effects, avoiding estimation of correlations among the random intercept and cue slopes. The analysis included 3551 annual observations from 213 trees and 17 sites.

We initially fitted the full period × T1 × T2 interaction to test whether the joint relationship between the two temperature cues differed between periods. Adding the three-way interaction did not improve model fit relative to a model containing period × T1, period × T2 and T1 × T2 interactions ($\chi^2 = 0.20, p = 0.66$). We therefore retained the simpler model without the three-way interaction.

We then tested whether the functional forms of the relationships between seed production and the temperature cues changed between periods. Starting from the reduced interaction model, we added quadratic terms for standardized T1 and T2. We first fitted a common-curvature model in which the quadratic effects were constrained to be equal between periods. We used likelihood-ratio tests to evaluate period-specific changes in T1 and T2 curvature individually and then tested their combined contribution in a model allowing the curvature of both cues to vary between periods.

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 the 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. Examples, using 0.2/0.8 (Fig. S1) and 0.8/0.2 (Fig. S2) are provided in the Appendix.

Our use of "tails" follows recent work on tail-dependent spatial synchrony, where tails refer to lower and upper portions of a distribution rather than only to extreme quantiles (Walter *et al.*, 2022; Ghosh *et al.*, 2024, 2025; Reuman *et al.*, 2025). Thus, in the ecological context of masting, the lower tail represents low-seeding or failure years, whereas the upper tail represents high-seeding.

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).

We did not apply the simulation-based test for tail dependence proposed by Walter *et al.* (2022), because this procedure requires complete lower- and upper-tail correlation matrices to generate null datasets with the same overall Spearman correlation structure. Our modified partial Spearman analysis allows missing pairwise estimates arising from incomplete temporal overlap among sites within a given tail, which prevents construction and eigen-decomposition of the covariance matrix required by that test. Because our aim was to quantify tail-specific synchrony and its temporal change, rather than to test the existence of tail dependence per se, we interpreted tail dependence from the estimated lower- and upper-tail synchrony values and their temporal shifts.

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). In each period, we included only trees with at least 10 years of seed-production records, which resulted in 84 trees (11 sites) in 1980-2006, and 96 trees (11 sites) in 2007-2024. 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. At the local scale in the UK, mean upper-tail synchrony decreased by approximately 45%, from 0.38 (± 0.07 SD; mean partial Spearman correlation among trees within sites) in 1980-2006 to 0.21 (± 0.14) in

2007-2024 (Fig. 2). Lower-tail synchrony also declined substantially, although less strongly, decreasing by approximately 34%, from 0.56 (± 0.09) to 0.37 (± 0.16).

Regional synchrony in Poland showed the same asymmetric temporal pattern. Upper-tail synchrony declined by approximately 54%, from 0.26 (± 0.005; mean partial Spearman correlation among sites) in 1987-1998 to 0.12 (± 0.007) in 2011-2022 (Fig. 3). In contrast, lower-tail synchrony declined by approximately 19%, from 0.37 (± 0.01) to 0.30 (± 0.02). Thus, the stronger decline in synchrony during mast peaks matched our prediction, although synchrony also weakened substantially during low-seeding years at both local and regional scales.

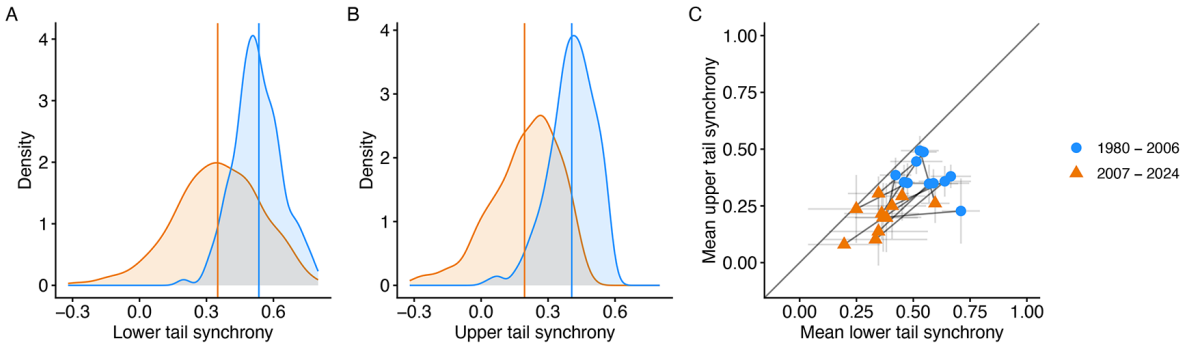

Figure 2: The temporal decline in local (within-site) masting synchrony is stronger in upper-tail (high-seeding years) years than in lower-tail (poor-seeding years). Density plots show local (among trees, within-site) synchrony in A) lower, and B) upper tail of masting, estimated separately for two periods, 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).

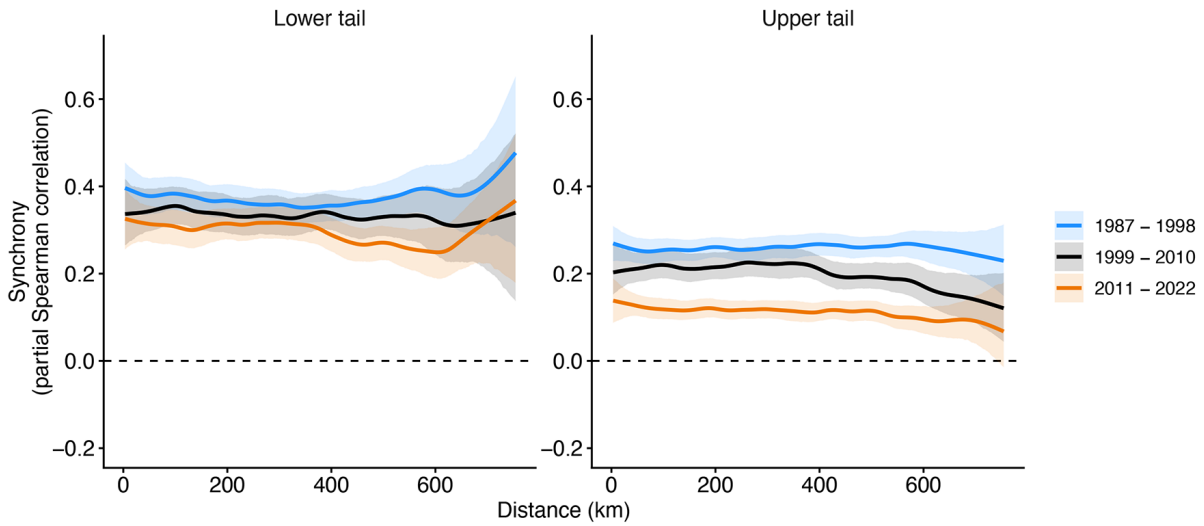

Figure 3: The temporal decline in regional (among-sites) masting synchrony is stronger in upper-tail (high-seeding) years than in lower-tail (poor-seeding years). Distance decay of beech masting synchrony in the upper and lower tail, estimated separately for the three periods (1987-1998, 1999-2010, and 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 coincided with substantial changes in the relationships between seed production and both weather cues (Fig. 4, Table S1). At the median values of T1 and T2, seed production during 1980–2006 was strongly positively associated with summer T1 temperature ($\beta = 0.75 \pm 0.036$ SE) and negatively associated with summer T2 temperature ($\beta = -0.79 \pm 0.036$ SE). During 2007–2024, the corresponding local slopes were 0.36 ± 0.033 for T1 and -0.33 ± 0.028 for T2. Thus, the magnitudes of the local T1 and T2 effects declined by approximately 52% and 58%, respectively.

The temporal change extended beyond a reduction in the magnitude of the cue effects and also involved changes in their functional forms. Adding quadratic T1 and T2 terms improved model fit relative to the model containing only linear cue effects on the log-link scale ($\chi^2_2 = 37.40$, $p < 0.001$). Allowing curvature to differ between periods produced a further improvement in model fit ($\chi^2_2 = 45.91$, $p < 0.001$). Period-specific changes in curvature were supported for both T1 ($\chi^2_1 = 13.63$, $p < 0.001$) and T2 ($\chi^2_1 = 29.91$, $p < 0.001$).

Model predictions revealed changes in both the population-level cue response and the diversity of responses among trees (Fig. 4, Fig. S3). During 1980–2006, predicted seed production increased continuously and rapidly with T1. After 2006, this relationship became hump-shaped.

Seed production peaked at approximately 22°C and subsequently declined, so increasingly strong T1 cues no longer produced continued amplification of reproductive output. This truncation of the response under strong T1 cues provides a potential mechanism for the pronounced decline in upper-tail synchrony, because weather conditions that previously generated large, coordinated seed crops produced weaker and more variable reproductive responses after 2006.

Predictions also revealed changes relevant to the synchrony of reproductive failures. Under weak T1 cues, reproduction was consistently suppressed during 1980–2006 (Fig. 4), whereas after 2006 the same conditions were associated with a broader range of tree-level responses, including relatively large seed production by some trees (Fig. 4). A similar change occurred for T2. High T2 temperatures, representing weak priming conditions, produced uniformly low seed production before 2007, but the post-2006 relationship was shallower and tree-level predictions were more variable (Fig. 4). Consequently, weather conditions that formerly suppressed reproduction in most trees no longer consistently caused failure.

Discussion

Our analyses show that masting synchrony in European beech declined in both tails of the seed-production distribution, with a stronger decline in the upper tail. This pattern was consistent across spatial scales and datasets. Contrary to our expectations, climate-driven disruption extended to both mast peaks and reproductive failures. These changes in synchrony coincided with a weakening and restructuring of the relationships between weather cues and reproduction. Reproductive sensitivity to T1 and T2 declined after 2006, while the functional forms of both cue responses changed. Before 2007, high T1 temperatures produced continued amplification of seed production, whereas after 2006 the relationship became hump-shaped. Weak T1 cues and high T2 temperatures consistently suppressed reproduction before 2007, but were associated with a wider range of tree-level outcomes after 2006. The reduced amplification under favourable conditions and less consistent suppression under unfavourable conditions offer a plausible explanation for declining synchrony in both tails.

The weakening of synchrony in both seed failures and mast peaks has consequences for ecosystems structured by pulsed seed resources. Desynchronization of failures weakens the

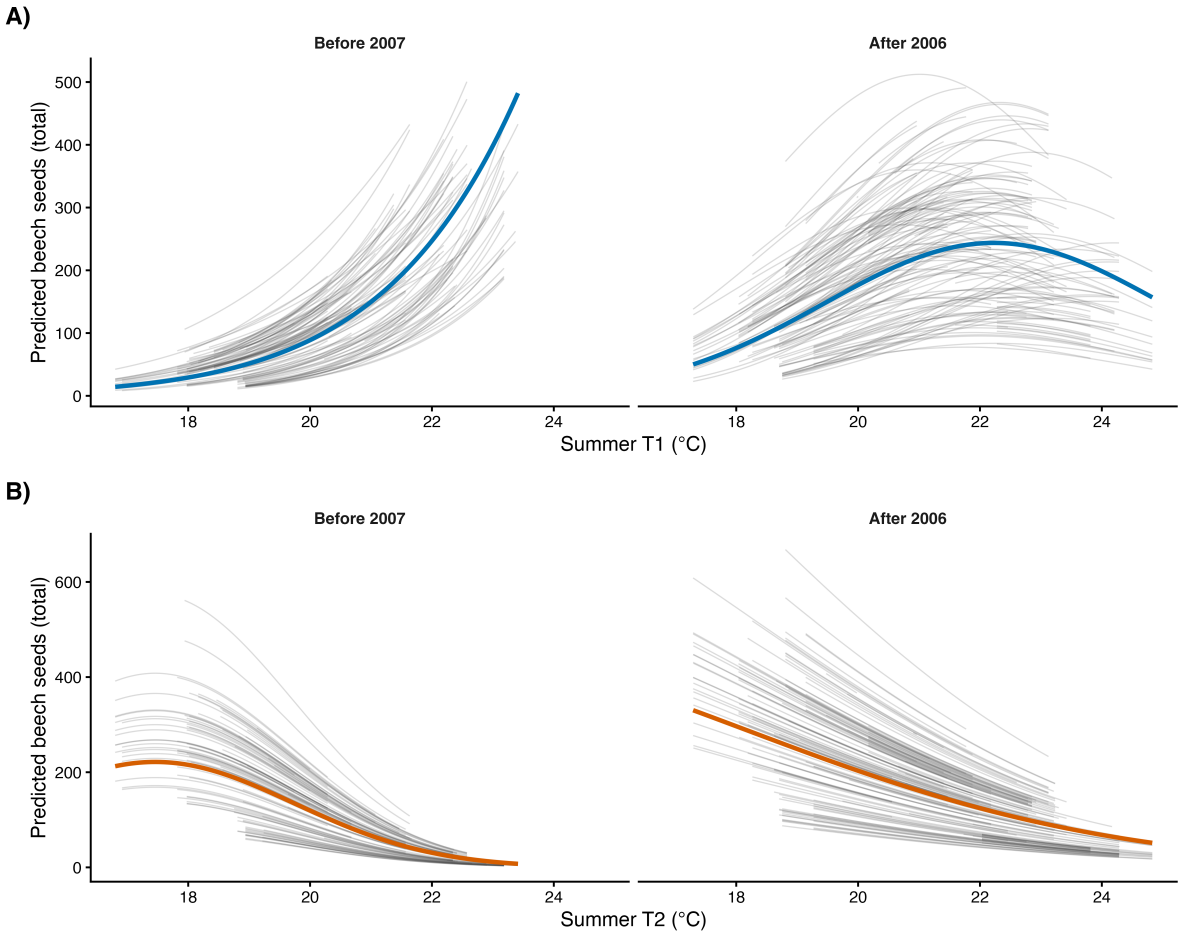

Figure 4: Weather-cue dependence of seed production weakened and changed shape after 2006. Predicted beech seed production in relation to maximum summer temperature one year (A; T1) and two years (B; T2) before seed fall, during 1980–2006 and 2007–2024. Thin grey curves show tree-specific predictions incorporating fitted random effects, whereas thick coloured curves show population-level predictions based on fixed effects. The complementary temperature cue was held at its median and previous-year seed production at its 10th percentile. Curves are restricted to the temperature ranges observed for each tree or period. Predictions were derived from 3,551 annual observations of 213 trees across 17 sites. Model summary is provided in Table S1.

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 become weaker or less spatially extensive, 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 (Dri *et al.*, 2025). 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 predicted that upper-tail synchrony would decline because resource limitation would reduce reproductive amplification under the warm-summer T1 cue. The shift from a continuously increasing T1 response before 2007 to a hump-shaped response after 2006 was consistent with this prediction: a shared warm-summer cue became less capable of generating coordinated mast peaks. At the other end of the response, the relaxation of reproductive suppression under weak T1 and high T2 conditions, together with greater variation in tree-level predictions, provides a possible explanation for declining lower-tail synchrony. Shared unfavourable weather became

less likely to produce failure across all trees. Thus, the altered cue-response functions could weaken synchrony in both tails by making reproductive outcomes less consistent among trees exposed to similar weather. Increasingly frequent reproductive induction and chronic resource depletion may explain these patterns (Hacket-Pain *et al.*, 2025). Resource limitation could constrain reproductive amplification under favourable conditions (Kelly *et al.*, 2025), while differences among trees in resource availability and reproductive history could generate different outcomes under the same weather conditions (Barringer *et al.*, 2013). Measurements of cue perception, flowering induction, resource state, and seed production within the same trees will be needed to test these mechanisms.

Similar changes in cue–reproduction relationships may occur in other masting systems where responses to weather cues depend on resource state. Species in which flowering is triggered by infrequent weather conditions and constrained by resource accumulation may be sensitive to increases in cue frequency (Journé *et al.*, 2025; Kelly *et al.*, 2025). Under warming, reproductive cues may recur before resources used during previous reproductive events have been replenished. This could limit reproductive amplification under favourable conditions and increase differences among individuals with different resource histories (Bogdziewicz *et al.*, 2024). These processes could affect both tails of the seed-production distribution. Reduced amplification under favourable conditions could weaken coordinated mast peaks, whereas less consistent suppression under unfavourable conditions could weaken synchronized failures (Bogdziewicz *et al.*, 2025). Comparative analyses across masting species, climates, and reproductive strategies are needed to determine how generally climate warming reorganizes the cue structures that generate pulsed seed resources.

In summary, our results show that climate warming is altering the cue–reproduction relationships underlying masting and weakening synchrony in both tails of the seed-production distribution. After 2006, warm T1 conditions no longer produced continued increases in seed production, while weak T1 and high T2 conditions no longer suppressed reproduction as consistently across trees. Comparable weather conditions were therefore associated with a wider range of reproductive outcomes. These changes provide a possible mechanism for declining synchrony in both seed failures and mast peaks, with a stronger decline in the latter. Pulsed-resource

systems depend on environmental conditions producing coordinated biological responses (Yang *et al.*, 2010). When the relationship between a shared environmental cue and the biological response changes, resource peaks and shortages may become less spatially coherent and less predictable. This has implications for ecological forecasting (Dietze *et al.*, 2018; Pearse *et al.*, 2021). Climate information can be used to anticipate bird irruptions, consumer outbreaks, and zoonotic-disease risk when relationships among weather, seed production, and consumer responses remain stable (Pearse *et al.*, 2021; Journé *et al.*, 2023; Oberklammer *et al.*, 2025). Such forecasts may become less reliable if similar weather conditions produce different reproductive outcomes across periods and individuals. Testing whether comparable changes occur in other masting species will help establish how generally climate change is altering pulsed-resource dynamics.

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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 .

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Supporting Information

Climate warming flattens masting-driven resource pulses

Table S1: Summary of the generalized linear mixed model testing temporal changes in the relationships between annual seed production and summer temperatures one (T1) and two (T2) years before seedfall. The model was fitted to 3,551 annual observations from 213 trees across 17 sites using a Tweedie error distribution and log link. The period 1980–2006 was the reference level. T1 and T2 were standardized before analysis, and linear and quadratic cue effects were allowed to differ between periods. Tree identity was included as a random intercept with uncorrelated random slopes for T1 and T2, and site identity was included as a random intercept. Previous-year seed production was included as a log-transformed covariate. Estimates are reported on the log-link scale.

Model term	**Estimate**	**Std. Error**	z **value**	p **value**
Intercept	4.614	0.131	35.18	< 0.001
Period (after 2006)	0.629	0.052	12.12	< 0.001
Summer temperature T1	0.769	0.036	21.16	< 0.001
Summer temperature $T1^2$	-0.023	0.025	-0.91	0.361
Summer temperature T2	-0.816	0.038	-21.69	< 0.001
Summer temperature $T2^2$	-0.208	0.029	-7.27	< 0.001
T1 $\times$ T2	0.208	0.026	8.13	< 0.001
T1 $\times$ Period (after 2006)	-0.405	0.039	-10.30	< 0.001
$T1^2$ $\times$ Period (after 2006)	-0.111	0.028	-4.01	< 0.001
T2 $\times$ Period (after 2006)	0.488	0.044	11.11	< 0.001
$T2^2$ $\times$ Period (after 2006)	0.178	0.031	5.65	< 0.001
Previous-year seed production (log)	-0.165	0.009	-18.36	< 0.001

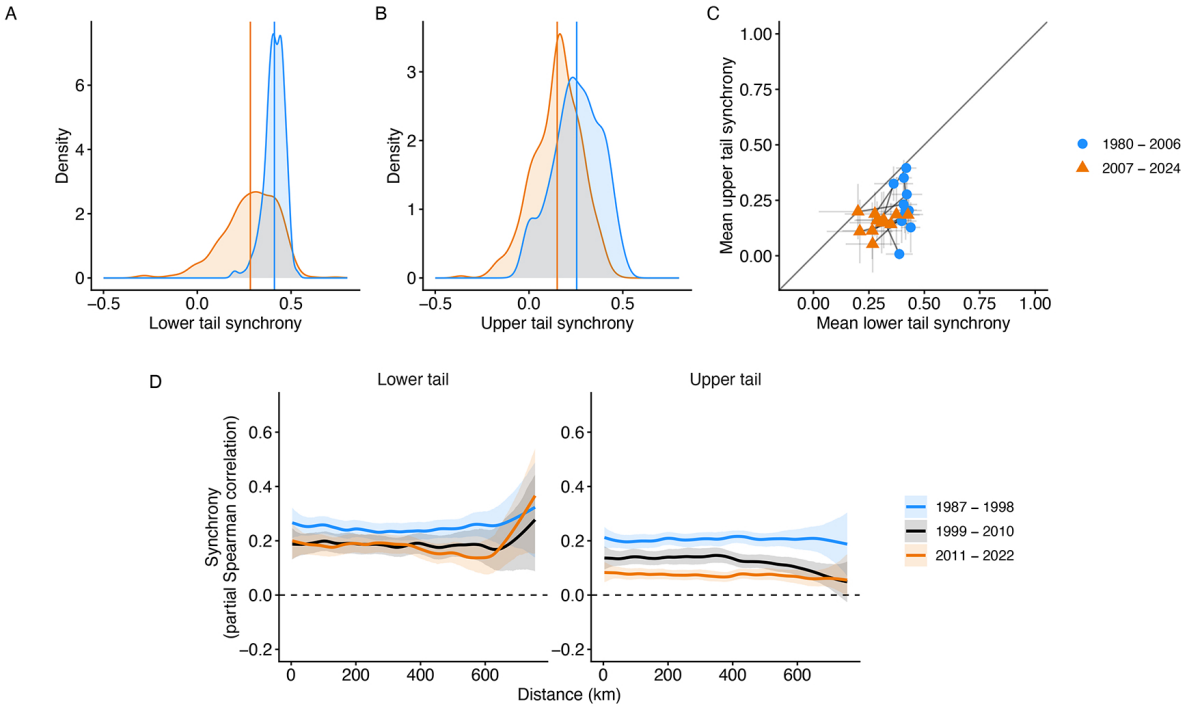

Figure S1: Sensitivity analysis of within-tail synchrony, with the lower and upper tail defined using 0.2 as a threshold. Density plots show local synchrony in the lower (A) and upper (B) tails of masting in the before (1980-2006) and after (2007-2024) masting breakdown period. Panel C shows site-level tail-dependence, with points showing site-level mean tail-dependent synchrony, while whiskers show SDs. Panel D shows the temporal decline in regional (between-sites) masting synchrony in lower and upper tails.

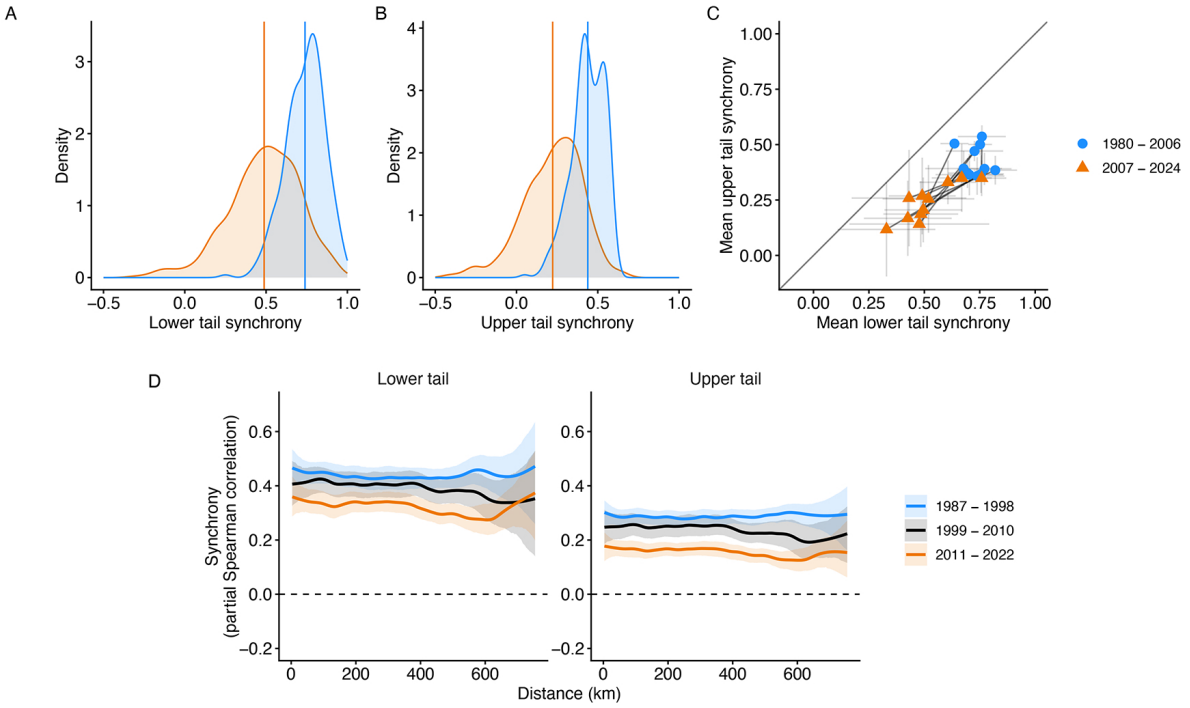

Figure S2: Sensitivity analysis of within-tail synchrony, with the lower and upper tail defined using 0.8 as a threshold. Density plots show local synchrony in the lower (A) and upper (B) tails of masting in the before (1980-2006)and after (2007-2024) masting breakdown period. Panel C shows site-level tail-dependence, with points showing site-level mean tail-dependent synchrony, while whiskers show SDs. Panel D shows the temporal decline in regional (between-sites) masting synchrony in lower and upper tails.

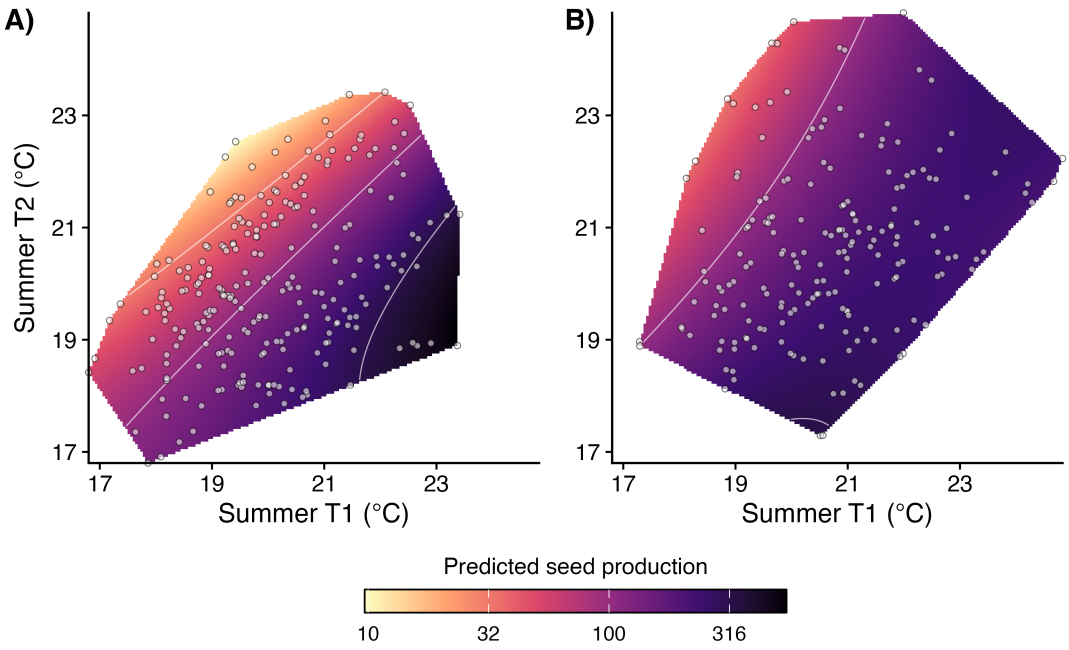

Figure S3: Weather-cue dependence of seed production weakened after 2006. Population-level predictions of annual seed production across summer temperatures one (T1) and two years (T2) before seedfall during A) 1980–2006 and B) 2007–2024. Predictions were generated from a Tweedie GLMM containing period × T1, period × T2 and T1 × T2 interactions, tree-level random intercepts, random T1 and T2 slopes, and a site random intercept. For predictions, previous-year seed production was held at 10th percentile. Predictions were restricted to the range of T1–T2 combinations represented in the observations. The analysis included 2639 annual observations from 143 trees. Tree-level predictions are provided in Fig. 4. Model summary is provided in Table S1.