

1 Climate warming causes mast seeding to break down by reducing sensitivity to weather cues

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3 Running head: Warming and proximate mechanisms of masting

4
5 Michał Bogdziewicz^{1*}, Andrew Hacket-Pain², Dave Kelly³, Peter Thomas⁴, Jonathan Lageard⁵,
6 Andrew J. Tanentzap⁶

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8 1 Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University,
9 Umutłowska 89, 61-614 Poznań, Poland

10 2 Department of Geography and Planning, School of Environmental Sciences, University of
11 Liverpool, Liverpool L69 7ZT, UK

12 3 Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury,
13 Private Bag 4800, Christchurch 8140, New Zealand

14 4 School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK

15 5 Department of Natural Sciences, Manchester Metropolitan University, Manchester M1
16 5GD, UK

17 6 Ecosystems and Global Change Group, Department of Plant Sciences, University of
18 Cambridge, Downing Street, Cambridge CB2 3EA, UK

19
20 *corresponding author: michalbogdziewicz@gmail.com

Summary

Climate change is altering patterns of seed production worldwide with consequences for population recruitment and migration potential. For the many species that regenerate through synchronized, quasiperiodic reproductive events termed masting, these changes include decreases in the synchrony and interannual variation in seed production. This break-down in the occurrence of masting features harms reproduction by decreasing the efficiency of pollination and increasing seed predation. Changes in masting are often paralleled by warming temperatures, but the underlying proximate mechanisms are unknown. We used a unique 39-year study of 139 European beech (*Fagus sylvatica*) trees that experienced masting break-down to track the seed developmental cycle and pinpoint phases where weather effects on seed production have changed over time. A cold followed by warm summer led to large coordinated flowering efforts among plants. However, trees failed to respond to the weather signal as summers warmed and the frequency of reproductive cues changed fivefold. Less synchronous flowering resulted in less efficient pollination that further decreased the synchrony of seed maturation. As global temperatures are expected to increase this century, perennial plants that fine-tune their reproductive schedules based on temperature cues may suffer regeneration failures.

Keywords: proximate mechanisms, pollen limitation, phenology reproduction, seed production, warming

Introduction

The capacity of future forests to support biodiversity and deliver ecosystem services depends on regeneration that tracks the 21st-century climate (Clark *et al.* 2020; McDowell *et al.* 2020). Many tree species regenerate through synchronized, highly variable variation in fruit production, termed masting (Pearse *et al.* 2016). Masting is beneficial for successful plant recruitment as large and synchronized flowering effort enhances pollination success though positive density-dependence, and decreases seed predation by starving predator populations in years of low seed production and satiating them in high seed years (Kelly *et al.* 2001; Tachiki & Iwasa 2010; Conlisk *et al.* 2012). Climate change is now altering masting by changing interannual variation and synchrony in seed production among individuals (Redmond *et al.* 2012; Pearse *et al.* 2017; Bogdziewicz *et al.* 2020c; Shibata *et al.* 2020). Consequently, forests are facing lowered recruitment and migration potential (Crawley & Long 1995; Bogdziewicz *et al.* 2020c, b). The trends in seed production are often paralleled by warming, but our understanding of the underlying proximate mechanisms is incomplete. Closing this gap is essential to predict the effects of warming that is underway on forest reproduction and vegetation dynamics.

The mechanisms responsible for masting determine the success of the transitions among seed development phases and thus population-wide variability and synchrony (Bogdziewicz *et al.* 2020a). In high seed years, plants in a population initiate many flowers, and these flowers are pollinated at a high rate. As flower initiation is an endogenous process that is often determined by an environmental cue, plants should all respond similarly to changes in the cue, resulting in population-level synchrony if regulatory networks are conserved (Bogdziewicz *et al.* 2020a). For example, seasonal deviations from mean weather values trigger changes in flowering hormone synthesis responsible for flower bud formation and explain interannual variation in masting grasses (Turnbull *et al.* 2012; Kelly *et al.* 2013). This process is likely to interact further with plant resource state, such that depleted resource pools after bumper crops limit flower production in subsequent years (Monks *et al.* 2016; Le Roncé *et al.* 2020). Once flowers are initiated, pollen limitation can enforce synchrony and interannual variation in seed production though pollen coupling, another endogenous process in which pollination success increases with flower density (Satake & Iwasa 2000; Kelly *et al.* 2001).

Understanding the proximate mechanisms by which climate change is altering masting requires closely tracking the seed developmental cycle. Long-term datasets that can pinpoint

75 how climate change has changed seed initiation, seed set, and ultimately seed production, are
76 almost non-existent. Here, we used a unique 39-year study of 139 individuals of European
77 beech (*Fagus sylvatica* L.) to disentangle the mechanisms that cause mastings in this species
78 and tested how climate change has affected the transitions among seed development phases.
79 Our past work on these beech populations showed that interannual variability and synchrony
80 of beech mastings declined by ~30% over the last four decades as the climate has warmed by
81 1°C (Bogdziewicz *et al.* 2020b, Fig. S1). These declines increased pollen limitation and seed
82 predation, indicating that tree reproduction has been reduced by climate change because
83 mastings have become less effective (Bogdziewicz *et al.* 2020b). However, we do not know the
84 underlying mechanisms for these changes. Studying these mechanisms in beech is important
85 because the species is a major forest-forming species across temperate Europe. Beech also
86 represents a model system for studying the reproductive traits of many other globally
87 important forest-forming species such as *Picea*, *Abies*, and *Nothofagus*. These traits include
88 density-dependent wind pollination that determines seed set, and occasional mass flowering
89 driven by a combination of temperature cues. Thus, our results may allow careful
90 generalization to other key forest species.

91 We expected seed production in European beech to be driven by the following
92 process. In European beech, warmer-than-average summers that follow cooler-than-average
93 summers lead to years with large and synchronized flowering (Vacchiano *et al.* 2017). A
94 rapidly warming climate can decrease the frequency of negative summer temperature
95 anomalies, and increase the frequency of positive anomalies, thereby weakening the
96 reinforcing dynamics of stored resources on synchrony and interannual variation of
97 reproduction (Rees *et al.* 2002; Bogdziewicz *et al.* 2018). In short, the effect of increasing
98 mean temperatures, at least in the short term, would be to increase the fraction of years when
99 flowering is triggered. This will decrease individual interannual variation, since each plant
100 will have less time between flowering efforts to accumulate reserves (Rees *et al.* 2002;
101 Bogdziewicz *et al.* 2018). If true, the relationship between weather signals and seed
102 production may weaken over time as climate warming progresses, lowering the synchrony of
103 flowering. Moreover, pollen coupling should generally increase synchrony of seed production
104 (Rapp *et al.* 2013), but progressively asynchronous flowering may limit pollination levels
105 leading to declines in synchrony. If true, synchrony of production of matured seeds should
106 initially be larger than that of initiated seeds (flowers), but this should fade as climate
107 warming makes flowering less synchronous.

Methods

Study species

European beech (*F. sylvatica* L.) flowers are induced in summer one year before seed set. Flower buds overwinter then flowers open in the spring, and are pollinated and develop into mature fruit in summer. Because fruit and seed coats develop if pollination occurs, while unpollinated fruits lack a seed (kernel) (Nilsson & Wastljung 1987), pollination and seed initiation (flowering) can be separately estimated from seed production data.

Data collection

We sampled seed production in 139 beech trees located at 12 sites spaced across England annually between 1980 and 2018 (Bogdziewicz *et al.* 2020b, c). The ground below each tree was searched for seeds for 7 min and seeds were later classified as sound, or empty with formed pericarps (not pollinated), or damaged by *Cydia* sp. moth. Detailed descriptions of sites and procedures are given in Packham *et al.* (2008). Monthly weather data for each site were obtained from the corresponding 0.25° grid cell of the E-OBS dataset (Cornes *et al.* 2018).

Data analysis

Temperature trends. Temperature trends were analyzed with three models. The first was a linear mixed model (LMM) that tested for a general temporal trend in mean maximum summer temperatures as a response. Year was included as a continuous fixed effect and site as a random intercept. We used mean maximum temperature (Tmax) across June and July as this is a widely reported summer cue for European beech, including in our populations (Piovesan & Adams 2001; Vacchiano *et al.* 2017; Bogdziewicz *et al.* 2020b). Another two models tested whether the probability that summer temperatures were higher or lower than one standard deviation (SD) from the long-term (1950-2018) mean at each site (i.e. the summer weather anomaly) changed over time. These models had the same predictors as for Tmax but were fitted with a binomial error structure. We used ± 1 SD because the flower cueing analysis presented below best predicted large and synchronized mast years if a cold summer (1SD below the mean) was followed by a hot one (1SD above the mean).

Proximate mechanisms of masting: weather cues. We first tested whether a combination of cold and hot summers caused population-level mast flowering. We fitted a zero-inflated, negative binomial mixed model to the annual number of initiated seeds in each tree, with fixed factors that included summer temperatures in one and two years before

seedfall, their interaction term, and seed production in the previous year to account for possible resource depletion. We also included the interaction of all the above predictors with study year to test for temporal changes in tree behavior. We included tree ID and site ID as random intercepts and a first-order temporal autocorrelation structure.

We fitted another LMM to test whether the cue combination led to coordinated flowering. The response of this model was the CV for the abundance of initiated seeds among trees within each site in a particular year. Small CV values indicated similar reproductive investment among trees in a particular site-by-year combination, i.e. high synchrony. As CV is sensitive to counts smaller than 1 (McArdle & Gaston 1995), site-year combinations with this level of seed production were excluded from model fitting. This removed ~20% of observations, representing the years of population-wide masting failure. We also ran an alternative analysis where we added 1 to all seed production observations, which resulted in qualitatively the same results (not shown). Fixed factors included both summer cues in interaction with study year. We included site as a random intercept.

Proximate mechanisms of masting: phenology of weather cues. We explored temporal stability of the weather-seed production relationships by using a dual moving window approach. For each site, we tested mast-weather relationships by calculating correlations between seed count and mean Tmax in 60-day windows for the two years prior to the year of seed production. We used the `daily_response()` function in the `dendroTools` package (Jevšenak & Levanič 2018), which slides a moving (60-day) window through the daily climate data, calculating the mean of the 60 daily observations. The function then calculates the correlation between the calculated mean Tmax and the seed count time-series at daily time-steps. This method allowed us to investigate the seasonal peaks in the relationships between seed production and seasonal weather cues without being constrained by the timing of calendar months (i.e. monthly climate data). The mast-weather cue correlations were calculated for 20-year periods to test how they varied over time. Using another moving-window approach, we advanced the 20-year window by one year at a time to explore temporal evolution of the strength and seasonality of seed count-weather cue relationships. This dual approach was designed to explore whether the climate cues of masting were shifting over time, i.e. whether the apparent weakening between seed count and June-July temperatures was an artefact of the seasonal cue shifting to earlier or later in the year.

Proximate mechanisms of masting: density-dependent seed set. In the second step of our analysis, we modelled determinants of seed set using binomial generalized linear mixed models (GLMM) with the proportion of successfully matured seeds as a response. Fixed

factors included the density of conspecific initiated seeds (flowers) at a given site and year, the within-year, within-site coefficient of variation of seed initiation among trees as an inverse proxy for flowering synchrony, and the interaction between these two terms. Next, we explored temporal changes in seed set effects on synchrony and interannual variation of beech reproduction by dividing the dataset into three equal parts: 1980-1992, 1993-2005, and 2006-2018. While binning our timeseries to these three periods is somehow subjective, it was based on the observation that both synchrony and interannual variability clearly broke-down in mid-2000s (see Fig. S1). We calculated the synchrony of seeds initiated and matured between individuals within sites using correlation coefficients (mean Pearson pairwise correlation coefficient for all pairs of trees within each site through each of the three time periods). This allowed us to test if among-tree synchrony of seed production was greater for matured than initiated seeds, as might be expected if pollen coupling enhances synchrony, and whether that changed over time. We also compared CV of seeds initiated and seeds matured for each tree averaged for all trees per site through each of the three time periods, to test if factors during seed set enhance the interannual variation of reproduction. All statistics were run in R, and we fitted models via the glmmTMB package (Brooks *et al.* 2017).

Results

Temporal trends in climate. Our sites experienced significant warming over the last four decades. The mean maximum June to July temperature increased by ~ 1 °C from ~ 14.5 in 1980 to ~ 15.5 °C in the 2010s (Table S1A, Fig. 1A). The change in mean maximum temperature was accompanied by a dramatic increase in the probability of occurrence of a positive summer temperature anomaly (1SD above the long-term mean) from $\sim 7\%$ early in the study to $\sim 38\%$ at the end of it (Table S1B, Fig. 1B). Concurrently, the probability of the occurrence of negative summer anomalies decreased from $\sim 25\%$ to $\sim 6\%$ (Table S1C, Fig. 1C).

Proximate mechanisms of masting: weather cueing. In early years, summer weather anomalies effectively led to mast flowering. Seed initiation (i.e. overall number of seeds produced, both matured and not, which represents the number of female flowers) was highest when relatively cold summers were followed by warm ones (Table S2, Fig. 2A). Seed production increased non-linearly from about 5 seeds per tree (per 7 minute search) the year after cold summers ($T_{\max} \sim 13$ °C) to 150 seeds tree⁻¹ following hot ones (~ 17 °C). This increase was stronger if summer two years before seed fall was cold, increasing from 40 to 390 seeds tree⁻¹ over the same temperature range. However, the response of trees to the

combination of cold followed by hot years weakened with time. By the end of the monitoring period, seed initiation was no longer significantly related to that combination of weather cues (Table S2, Fig. 2A). For example, the effect size (logit slope of the relationship between flowering per tree and temperature) of cold summer two years before seedfall faded by 0.01 each year from β (SE) = -0.53 (0.06) estimated for 1980 (Table S2, Fig 2a). Similarly, the effect size of warm summer one year before seedfall faded by 0.01 each year from β (SE) = 0.63 (0.05) estimated for 1980 (Table S2). Previous year seed production limited seed initiation in later year, but we detected no temporal change in that effect (Table S2).

The strong synchronizing effect of the summer cues on seed initiation from the 1980s also faded over time (Table S3, Fig 2B). In early years, hot summers effectively reduced within-site, within-year CV of seed production to near-0 values – i.e. high between-tree synchronization. By the end of the monitoring period, the relationship between CV and temperature was no longer statistically significant (Table S3, Fig 2B).

Proximate mechanisms of masting: phenology of weather cues. Moving window correlations revealed little variation in seed production – weather relationships in space and time (Fig. 3). The strongest relationships between seed production and seasonal weather cues occurred in the June-July period at all sites. This was especially clear for the negative correlation with June-July temperature in year T-2. The positive correlation with summer temperature in year T-1 was generally weaker compared to T-2, and some sites were less responsive than others (Fig. 3). Importantly, we detected no apparent advance or delay in cue phenology over the four decades of the study, i.e. seasonal peaks in relationships between seed production and seasonal weather cues were temporally conserved (Fig. 3).

Proximate mechanisms of masting: density-dependent seed set. Pollination efficiency was positively density-dependent. The probability of successful maturation of seeds increased with the number of initiated seeds (logit slope: $\beta = 0.91$, $z = 7.94$, $p < 0.001$), decreased as seed initiation was more variable among trees (high CV is an inverse proxy of synchrony; $\beta = -0.58$, $z = -7.93$, $p < 0.001$), and was highest when high seed initiation density coincided with low CV/high synchrony (CV of seed initiation by density interaction: $\beta = -0.69$, $z = -9.96$, $p < 0.001$). Density-dependent seed set subsequently maintained, rather than increased, synchrony from seed initiation to seed maturation, as measured by comparing the mean cross-correlation of seed initiation and seed maturation among trees (Fig. 4A). The mean synchrony of seed initiation (pairwise correlation among trees within each site) in the first decades of the study (1980-1993), equaled 0.81 and was similar to that of matured seeds (0.82, $z = -1.49$, $p = 0.14$). Similarly, we detected no difference in synchrony between seed

initiation and maturation in 1994-2005 ($z = 1.09$, $p = 0.28$). However, in recent years (2006-2018), the synchrony of seed maturation was significantly reduced (mean = 0.46) compared to the synchrony of seed initiation (0.54, $z = 2.96$, $p = 0.003$).

Interannual variation of seed maturation was larger than that of seed initiation, suggesting that seed set amplified interannual variation of seed production. This effect was maintained through time (Fig. 4B). The mean coefficient of variation (CV) of initiated seeds equaled 1.17 in the first decades (1980-1993) and was smaller than that of matured seeds that equaled 1.46 ($z = -7.09$, $p < 0.001$). Similarly, in 1994-2005 the mean CV of seed limitation equaled 1.15, while that of matured seeds 1.40 ($z = 6.29$, $p < 0.001$). In 2006-2018, the CV of initiated seed (mean = 0.94) was also lower than that of matured seeds (1.29, $z = -7.02$, $p < 0.001$). The difference in CV between seed initiation and seed maturation was similar in all periods (seed phase by time interaction: $p = 0.31$).

Discussion

Altered seed production induced by anthropogenic global change is occurring worldwide (Redmond *et al.* 2012; Buechling *et al.* 2016; Pearse *et al.* 2017; Bogdziewicz *et al.* 2020c; Shibata *et al.* 2020). The changes in seed production will determine the capacity of trees to disperse seed to the novel habitats they may occupy in the future (Ibáñez *et al.* 2008; Zhu *et al.* 2012, Clark *et al.* 2020). Furthermore, changes in masting patterns have tremendous ecosystem consequences as masting acts as pacemaker for trophic interactions (Ostfeld & Keesing 2000; Touzot *et al.* 2020). Understanding the mechanistic drivers of changes in seed production is therefore necessary to predict how ongoing climate change will influence future forest dynamics and their food webs. Our study now uncovers that changes in European beech seed production are associated with a breakdown in the weather cueing process that leads to asynchronous flowering. This, in turn, increases pollination failure which further decreases synchrony of seed maturation (summarized in Table 1).

Synchrony of interannual variation in reproduction in European beech was achieved through a common response to the weather cue, which became less efficient with climate change. During the last four decades trees experienced dramatic change in climate regime: the occurrence of positive summer temperature anomalies increased fivefold, with negative summer anomalies decreasing at a similar magnitude. As cueing became more frequent, the relationship between seed production and the weather cues weakened. Moreover, our data indicate that density-dependent pollen limitation is not the synchronizing mechanism of masting in European beech. However, pollen coupling still amplifies the negative

consequences of warming on masting once a rapid increase in cueing frequency leads to desynchronized flowering. Other plant species may similarly experience disruptions in their reproductive schedules as warming progresses if they rely on temperature cues to coordinate their reproduction and have density-dependent seed set. If increasing temperatures reduce interannual variation and synchrony in seed production through disrupting weather-seed production relationships, the resulting increases in potential seed predator populations and elevated pollen limitation, as already reported for European beech (Bogdziewicz *et al.* 2020b, c), raise doubts about the ability of plant species to migrate rapidly in response to global climate change (Zhu *et al.* 2012).

The weakening of seed count—June-July temperature relationships were not an artefact of a temporal shift in the cue to earlier or later in the year. Rather, despite the warming trend, we detected remarkable stability of the temporal window when beech trees appear sensitive to environment signals both among sites and over time. This result may seem surprising given that an earlier onset of both spring bud break and growth has been observed in temperate forests worldwide during recent decades (Fu *et al.* 2015). Moreover, our study sites differ notably in climate, including in mean max summer temperatures (range: 13.84 – 15.77 °C). One hypothesis for why warming does not translate into earlier cue-sensing phenology is that photoperiod may play a leading role in determining temperature-sensitive periods for reproductive phenology in European beech. European beech phenology is well-known for its high photoperiod sensitivity (Vitasse *et al.* 2009; Ettinger *et al.* 2020). Experiments in the mast-seeding grass *Chionochloa rigida* indicated that promotion of flowering by high temperatures only occurred in long days (>14 hours) (Mark 1965). Future studies that would examine the temperature-sensitive periods that plant use to fine-tune their flowering intensity and seed production appear to be a promising avenue for future research. One interesting question is whether species with any plasticity in temperature-sensitive periods for reproductive phenology are better suited to withstand the effects of a rapidly warming climate (Vitasse *et al.* 2010; Ettinger *et al.* 2020). By shifting the sensitive periods to earlier in the season, trees may be able to compensate for the change in cueing frequency. Understanding the mechanisms by which weather affects seed production is challenging, but critical if we are to understand how climate change will affect masting behavior.

Widely available data on forest growth and mortality has allowed a good understanding of how tree growth and survival responds to climate fluctuations (McMahon *et al.* 2010; Berdanier & Clark 2016; Young *et al.* 2017; Brien *et al.* 2020; Manzanedo *et al.* 2020). By contrast, an understanding of climate change impacts on fecundity is less

developed, as seed production is not directly observed for most species and habitats, and data accumulate slowly and with substantial investment (Clark *et al.* 2020; Kunstler *et al.* 2020). Thus, realistic estimates of tree fecundity and population growth rate are basically absent from most vegetation models (Vacchiano *et al.* 2018; McDowell *et al.* 2020; Kunstler *et al.* 2020). Our study starts to fill this gap by identifying mechanisms by which climate change breaks down masting patterns. Climate change will not only affect mean seed production, but also interannual variability and synchrony, which has important consequences for plant fecundity and fitness (Bogdziewicz *et al.* 2020c). Our findings that the proximate mechanisms of masting are vulnerable to climate warming may apply widely to taxa that rely on similar physiological approaches as European beech to fine-tune their reproductive schedules. Consequently, population recruitment may be widely compromised as forests rapidly warm.

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Literature

- Berdanier, A.B. & Clark, J.S. (2016). Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecological Applications*, 26, 17–23.
- Bogdziewicz, M., Ascoli, D., Hacket-Pain, A., Koenig, W.D., Pearse, I., Pesendorfer, M., *et al.* (2020a). From theory to experiments for testing the proximate mechanisms of mast seeding: an agenda for an experimental ecology. *Ecology Letters*, 23, 210–220.
- Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P.A., Lageard, J.G.A. & Hacket-Pain, A. (2020b). Climate Change Strengthens Selection for Mast Seeding in European Beech. *Current Biology*.
- Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A. & Hacket-Pain, A. (2020c). Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants*, 6, 88–94.
- Bogdziewicz, M., Steele, M.A., Marino, S. & Crone, E.E. (2018). Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytologist*, 219, 98–108.
- Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., *et al.* (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications*, 11, 1–10.

351 Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., *et*
352 *al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated
353 generalized linear mixed modeling. *The R journal*, 9, 378–400.

354 Buechling, A., Martin, P.H., Canham, C.D., Shepperd, W.D. & Battaglia, M.A. (2016).
355 Climate drivers of seed production in *Picea engelmannii* and response to warming
356 temperatures in the southern Rocky Mountains. *Journal of Ecology*, 104, 1051–1062.

357 Conlisk, E., Lawson, D., Syphard, A.D., Franklin, J., Flint, L., Flint, A., *et al.* (2012). The
358 Roles of Dispersal, Fecundity, and Predation in the Population Persistence of an Oak
359 (*Quercus engelmannii*) under Global Change. *PLOS ONE*, 7, e36391.

360 Cornes, R.C., Schrier, G. van der, Besselaar, E.J.M. van den & Jones, P.D. (2018). An
361 Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. *Journal of*
362 *Geophysical Research: Atmospheres*, 123, 9391–9409.

363 Crawley, M.J. & Long, C.R. (1995). Alternate Bearing, Predator Satiation and Seedling
364 Recruitment in *Quercus Robur L.* *Journal of Ecology*, 83, 683–696.

365 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B.,
366 Savas, T., *et al.* (2020). Winter temperatures predominate in spring phenological
367 responses to warming. *Nature Climate Change*, 1–6.

368 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., *et al.* (2015). Declining global
369 warming effects on the phenology of spring leaf unfolding. *Nature*, 526, 104–107.

370 Ibáñez, I., Clark, J.S. & Dietze, M.C. (2008). Evaluating the Sources of Potential Migrant
371 Species: Implications Under Climate Change. *Ecological Applications*, 18, 1664–
372 1678.

373 Jevšenak, J. & Levanič, T. (2018). dendroTools: R package for studying linear and nonlinear
374 responses between tree-rings and daily environmental data. *Dendrochronologia*, 48,
375 32–39.

376 Kelly, D., Geldenhuys, A., James, A., Penelope Holland, E., Plank, M.J., Brockie, R.E., *et al.*
377 (2013). Of mast and mean: differential-temperature cue makes mast seeding
378 insensitive to climate change. *Ecology Letters*, 16, 90–98.

379 Kelly, D., Hart, D.E. & Allen, R.B. (2001). Evaluating the Wind Pollination Benefits of Mast
380 Seeding. *Ecology*, 82, 117–126.

381 Kunstler, G., Guyennon, A., Ratcliffe, S., Rüger, N., Ruiz-Benito, P., Childs, D.Z., *et al.*
382 (n.d.). Demographic performance of European tree species at their hot and cold
383 climatic edges. *Journal of Ecology*, n/a.

384 Le Roncé, I., Toïgo, M., Dardevet, E., Venner, S., Limousin, J.-M. & Chuine, I. (n.d.).
385 Resource manipulation through experimental defoliation has legacy effects on
386 allocation to reproductive and vegetative organs in *Quercus ilex*. *Ann Bot.*

387 Manzanedo, R.D., HilleRisLambers, J., Rademacher, T.T. & Pederson, N. (2020). Evidence
388 of unprecedented rise in growth synchrony from global tree ring records. *Nature*
389 *Ecology & Evolution*, 1–8.

390 Mark, A.F. (1965). Flowering, seeding, and seedling establishment of narrow-leaved Snow
391 Tussock, *Chionochloa Rigida*. *New Zealand Journal of Botany*, 3, 180–193.

392 McArdle, B.H. & Gaston, K.J. (1995). The Temporal Variability of Densities: Back to Basics.
393 *Oikos*, 74, 165–171.

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

397 McMahon, S.M., Parker, G.G. & Miller, D.R. (2010). Evidence for a recent increase in forest
398 growth. *PNAS*, 107, 3611–3615.

- Monks, A., Monks, J.M. & Tanentzap, A.J. (2016). Resource limitation underlying multiple masting models makes mast seeding sensitive to future climate change. *New Phytologist*, 210, 419–430.
- Nilsson, S.G. & Wastljung, U. (1987). Seed Predation and Cross-Pollination in Mast-Seeding Beech (*Fagus Sylvatica*) Patches. *Ecology*, 68, 260–265.
- Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15, 232–237.
- Packham, J.R., Thomas, P.A., Lageard, J.G.A. & Hilton, G.M. (2008). The English Beech Masting Survey 1980–2007: Variation in the Fruiting of the Common Beech (*fagus Sylvatica* L.) and Its Effects on Woodland Ecosystems. *Arboricultural Journal*, 31, 189–214.
- Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212, 546–562.
- Pearse, I.S., LaMontagne, J.M. & Koenig, W.D. (2017). Inter-annual variation in seed production has increased over time (1900–2014). *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171666.
- Piovesan, G. & Adams, J.M. (2001). Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany*, 79, 1039–1047.
- Rapp, J.M., McIntire, E.J. & Crone, E.E. (2013). Sex allocation, pollen limitation and masting in whitebark pine. *Journal of Ecology*, 101, 1345–1352.
- Redmond, M.D., Forcella, F. & Barger, N.N. (2012). Declines in pinyon pine cone production associated with regional warming. *Ecosphere*, 3, art120.
- Rees, M., Kelly, D. & Bjørnstad, O.N. (2002). Snow tussocks, chaos, and the evolution of mast seeding. *The American Naturalist*, 160, 44–59.
- Satake, A. & Iwasa, Y. (2000). Pollen Coupling of Forest Trees: Forming Synchronized and Periodic Reproduction out of Chaos. *Journal of Theoretical Biology*, 203, 63–84.
- 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.
- Tachiki, Y. & Iwasa, Y. (2010). Both seedling banks and specialist seed predators promote the evolution of synchronized and intermittent reproduction (masting) in trees. *Journal of Ecology*, 98, 1398–1408.
- Touzot, L., Schermer, É., Venner, S., Delzon, S., Rousset, C., Baubet, É., *et al.* (2020). How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. *Ecological Applications*, 30, e02134.
- Turnbull, M.H., Pharis, R.P., Kurepin, L.V., Sarfati, M., Mander, L.N. & Kelly, D. (2012). Flowering in snow tussock (*Chionochloa* spp.) is influenced by temperature and hormonal cues. *Functional Plant Biol.*, 39, 38–50.
- Vacchiano, G., Ascoli, D., Berzaghi, F., Lucas-Borja, M.E., Caignard, T., Collalti, A., *et al.* (2018). Reproducing reproduction: How to simulate mast seeding in forest models. *Ecological modelling*, 376, 40–53.
- 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.
- Vitasse, Y., Bresson, C.C., Kremer, A., Michalet, R. & Delzon, S. (2010). Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology*, 24, 1211–1218.
- Vitasse, Y., Delzon, S., Dufrêne, E., Pontailier, J.-Y., Louvet, J.-M., Kremer, A., *et al.* (2009). Leaf phenology sensitivity to temperature in European trees: Do within-species

448 populations exhibit similar responses? *Agricultural and Forest Meteorology*, 149,
449 735–744.
450 Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., *et al.* (2017).
451 Long-term climate and competition explain forest mortality patterns under extreme
452 drought. *Ecology Letters*, 20, 78–86.
453 Zhu, K., Woodall, C.W. & Clark, J.S. (2012). Failure to migrate: lack of tree range expansion
454 in response to climate change. *Global Change Biology*, 18, 1042–1052.
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Table 1. Summary of proximate mechanisms driving seed production patterns in European beech and warming-related temporal changes tested in this study.

Developmental phase	Theoretical mechanism	General pattern	Observed temporal changes in mechanism
Flowering (seed initiation)	Coordinated response to a weather signal (endogenous)	Cold followed by warm summer leads to large synchronous flowering crops	Cue combination fails to initiate large synchronous flowering
	Resource depletion	Negative effect of previous year seed production on seed initiation	None
Flower maturation (seed set)	Seed set (density-dependent pollination efficiency) enhances synchrony and interannual variability of seeding	Seed set increases interannual variability, but not synchrony of seed production	No change in effects of seed set on interannual variability, seed set decreases synchrony in recent years

Figure 1. Temperature trends. A) Mean maximum June-July temperature at each site. B) The occurrence of positive (red points) and negative (blue points) summer temperature anomalies (1SD above and below the long-term mean) at each study site. Horizontal lines in each graph show the long-term (1950-2018) mean. The inset plot at B) shows the modeled probability of anomaly occurrence (red – positive; blue – negative anomaly). The prediction lines are based on significant mixed models, shading indicates the 95% confidence intervals. For longer perspective, Figure 2S shows the trends extended to 1960.

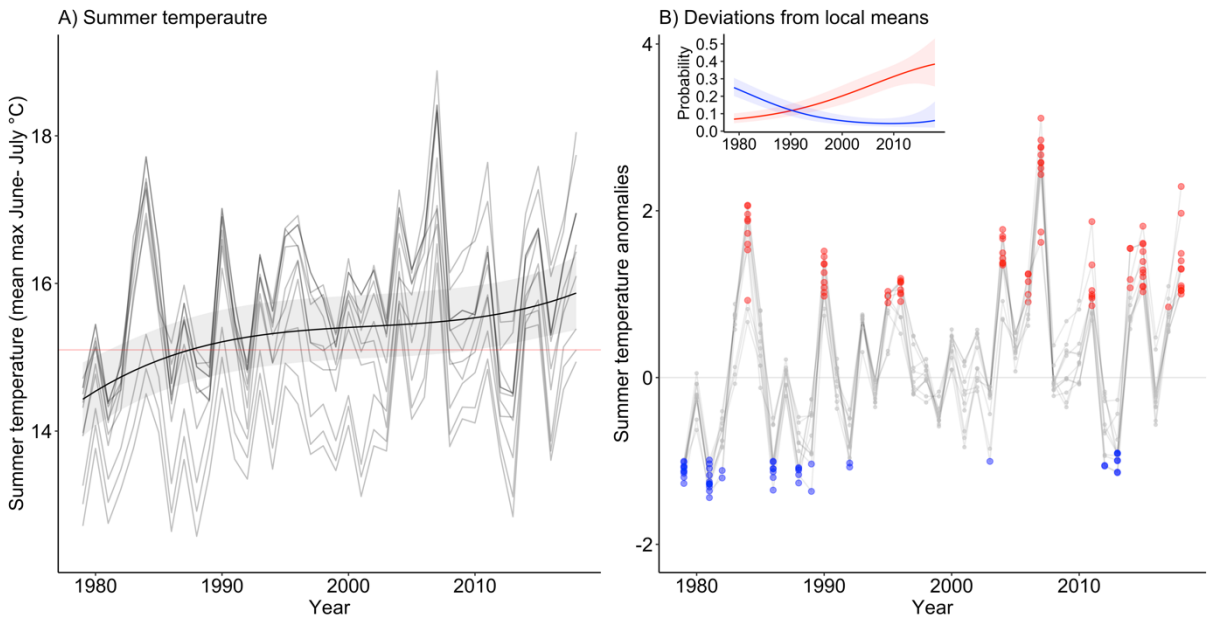


Figure 2. Interannual variation and synchrony of seed initiation vs. weather cues. A) The number of seeds initiated each year vs. weather cues, and B) synchrony (within-year, within-site CV) of seed initiation in each year vs. weather cues. Cues were June-July mean max temperature in years preceding seed fall. Summer temperature in the year preceding seed fall is given on the x-axis (T-1), while points are colored according to temperature two years preceding seed fall (T-2). Different colored lines show predictions for low (-1 SD, blue) and high (+1 SD, orange) temperatures in year T-2. Facets show data and predictions for early (1980-1999) and recent (2000-2018) years, but this categorization was only for visualization and year was included as a continuous predictor in the models. The solid lines are effects based on statistically significant binomial GLMMs predictions, dashed lines show non-significant slopes. Shading and vertical lines on points indicate 95% confidence intervals.

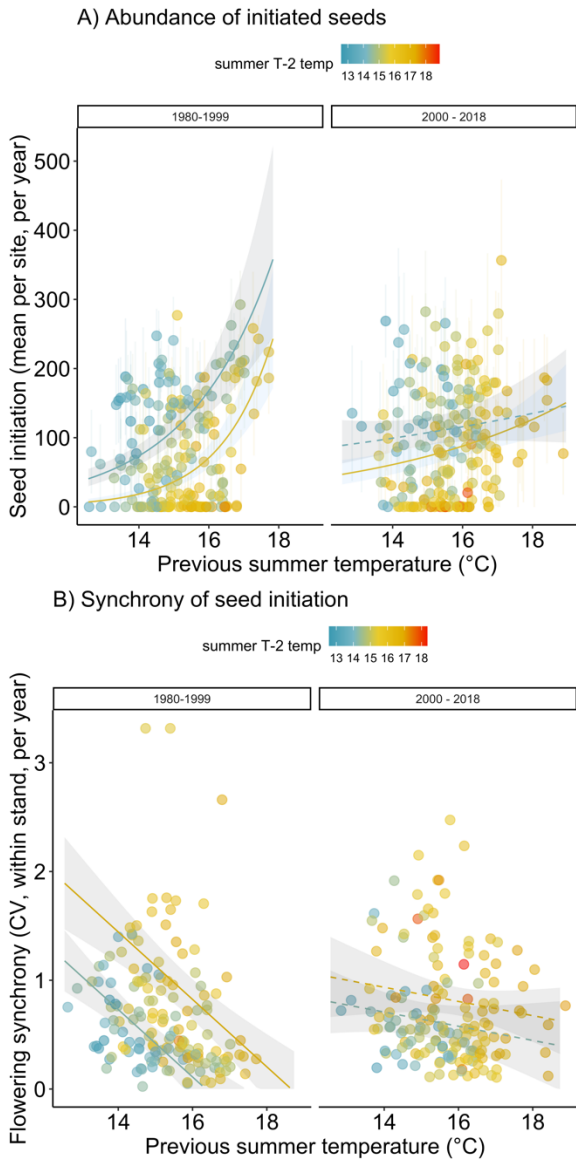


Figure 3. Spatiotemporal variation in seed production – weather cues correlations.

Correlations are reported as the start DOY for the seasonal cues (y-axis) either T-2 or T-1 years before seed production, and the end year for the moving 20-year window (x-axis). The dashed lines in the figures indicate the start of a 60-day window starting on June 1st, approximately equivalent to mean June-July data. Each panel shows one study site, ordered by latitude (moving left-to-right and then by rows).

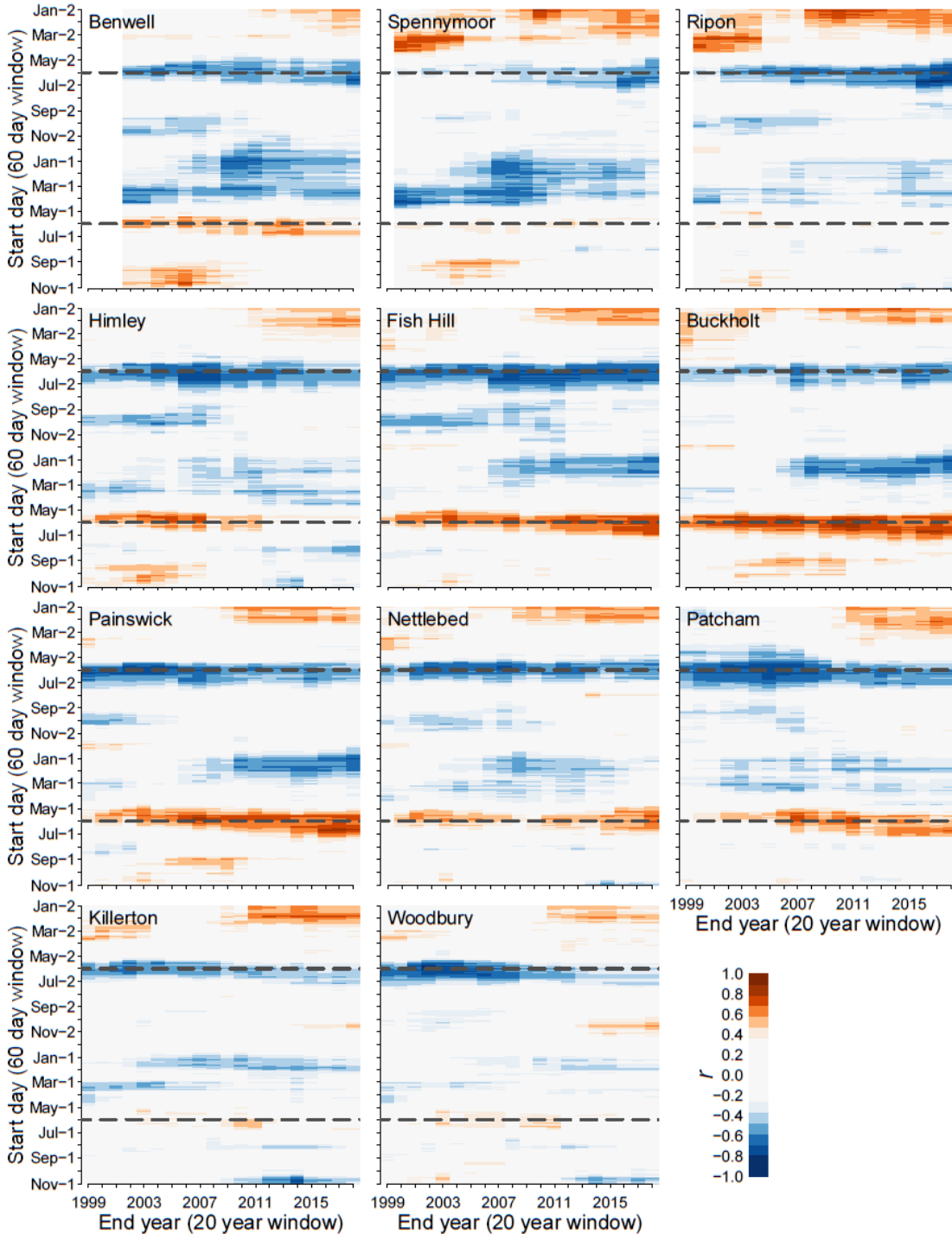
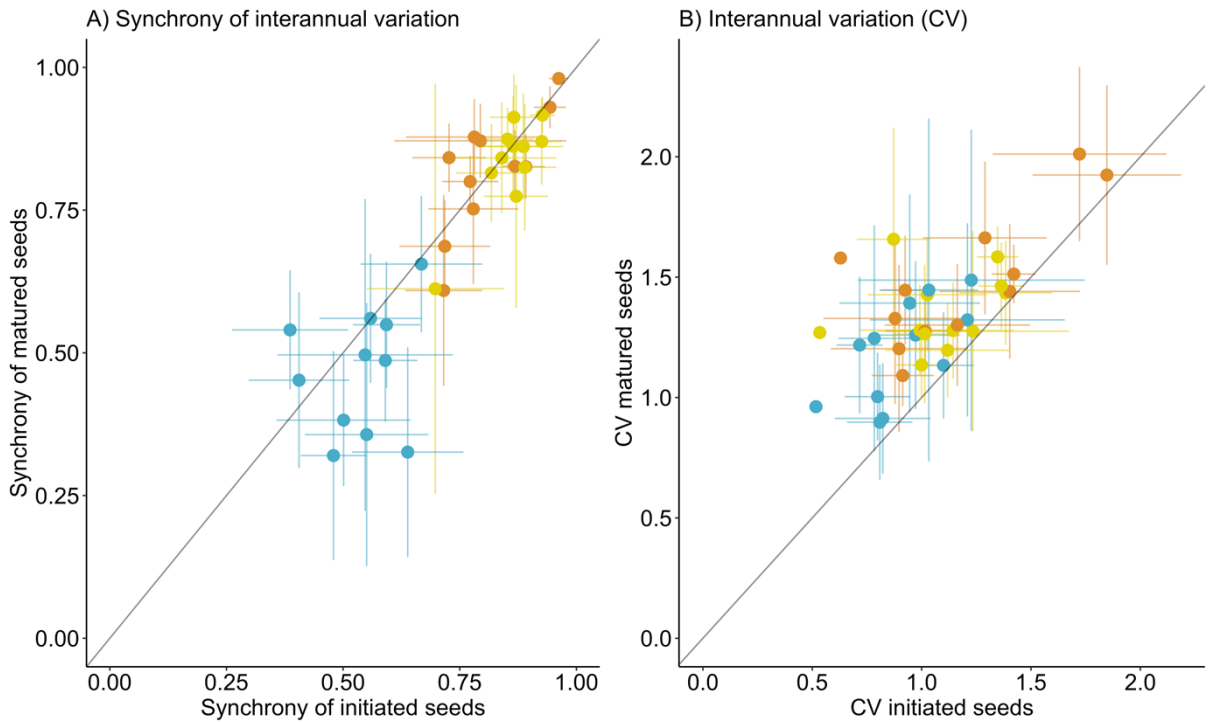


Figure 4. Effects of seed set on synchrony and interannual variation of seed production.

A) Mean \pm SD for pairwise correlations between trees within each site for seed initiated and matured. Synchrony was significantly reduced between seed initiation and maturation in the most recent years (2006-2018). B) Mean \pm SD for tree level CV of seeds initiated and matured. CV was significantly increased between seed initiation and maturation in all periods. Each point is one site during one time period: orange: 1980-1992, yellow: 1993-2005, blue: 2006-2018.



Trends in masting

As we showed previously (Bogdziewicz *et al.* 2020c), European beech mast seeding weakened over the last four decades (Fig. S1). The mean estimated interannual variability of seed production of individual trees measured by the coefficient of variation (CV) declined from ~ 1.20 in the first decades to ~ 0.90 in recent years (Fig. S1B). Synchrony, as measured by mean cross-correlation of seed production among trees, declined from ~ 0.85 to ~ 0.55 (Fig. S1C).

Figure S1. Observed seed production patterns. A) Tree-level seed production per 7 min searches. The blue line shows yearly means across all trees and sites. Probability density plots of (B) interannual variability and (C) among-tree synchrony of seed production divided into three time periods of the study. Inset plots show mean \pm 95% CIs of tree-level metrics estimated with GLMMs as a function of the time period.

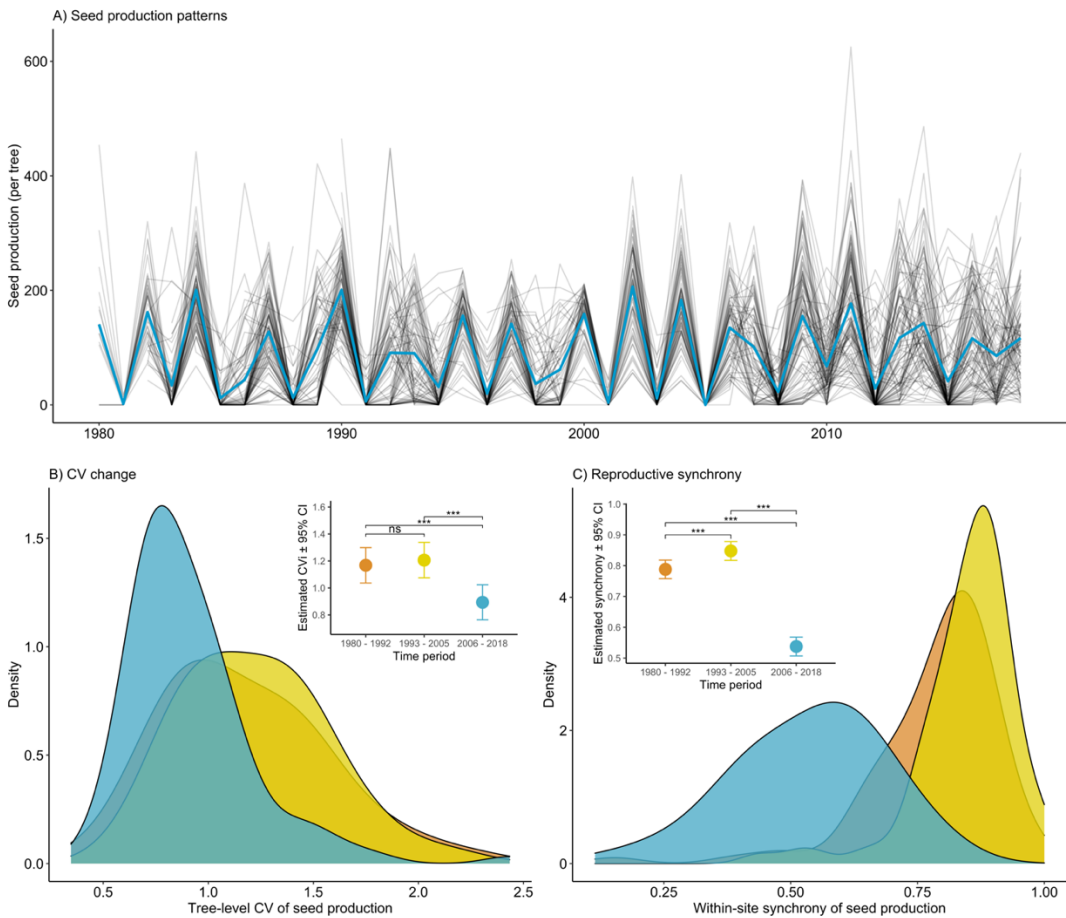


Figure S2. Temperature trends extended back to 1960. A) Mean maximum June-July temperature at each site. B) The occurrence of positive (red points) and negative (blue points) summer temperature anomalies (1SD above and below the long-term mean) at each study site. Horizontal lines in each graph show the long-term (1950-2018) mean. The inset plot at B) shows the modeled probability of anomaly occurrence (red – positive; blue – negative anomaly). The prediction lines are based on significant mixed models, shading indicates the 95% confidence intervals.

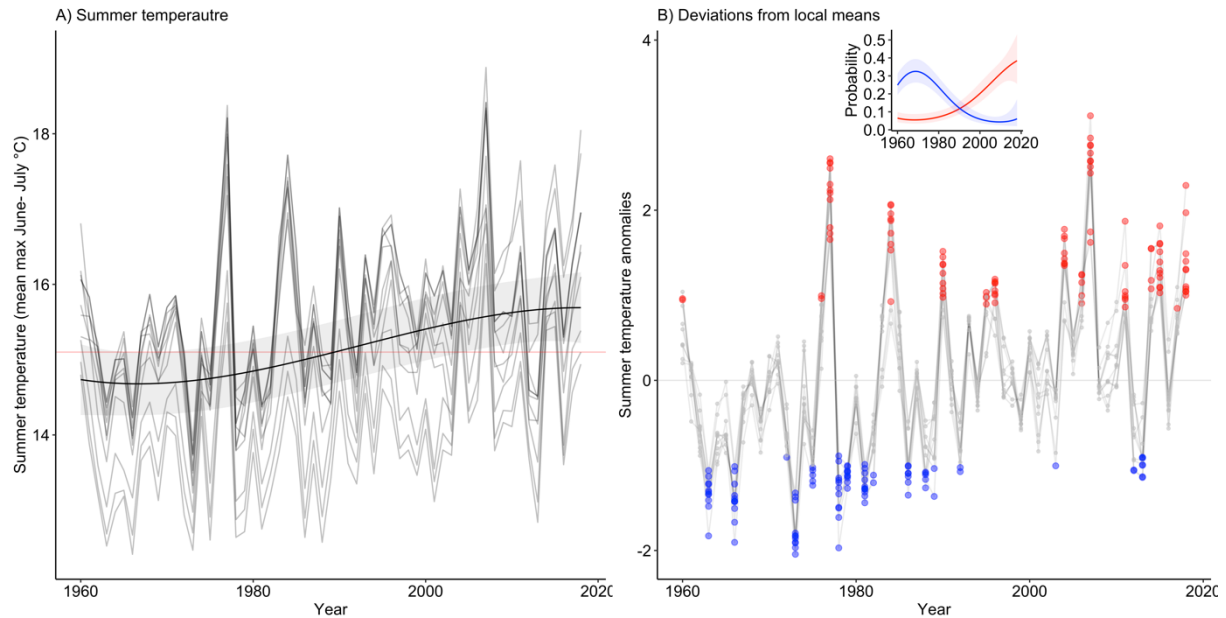


Table S1. Temperature trends.

A) Summer (mean max June-July) temperature was modeled using the Gaussian mixed model with the site included as a random intercept and year as a fixed factor.

Predictor	Effect size (SE)	z-value	p-value
Intercept	15.30 (0.21)	71.86	< 0.001
Year	6.60 (0.82)	8.08	< 0.001
Year ²	1.56 (0.82)	-1.91	0.05
Year ³	1.72 (0.82)	2.11	0.04

B) Probability of occurrence of positive summer anomaly (1SD above 1950-2018 mean) modeled using a binomial mixed model with the site included as a random intercept and year as a fixed factor.

Predictor	Effect size (SE)	z-value	p-value
Intercept	-1.52 (0.13)	-11.26	< 0.001
Year	13.61 (3.08)	3.08	< 0.001
Year ²	0.58 (3.10)	0.18	0.85
Year ³	6.03 (2.85)	2.11	0.03

C) The probability of occurrence of negative summer anomaly (1SD below 1950-2018 mean) was modeled using a binomial mixed model with the site included as a random intercept and year as a fixed factor.

Predictor	Effect size (SE)	z-value	p-value
Intercept	-2.53 (0.21)	-12.15	< 0.001
Year	-13.82 (3.50)	-3.95	< 0.001
Year ²	16.26 (3.89)	4.18	< 0.001
Year ³	3.85 (3.56)	-1.07	0.28

Table S2. Abiotic drivers of beech seed initiation and their temporal change. Seed initiation (yearly records per tree) was modeled using the zero-inflated negative binomial mixed model with tree ID and site used as random intercepts and temporal autoregressive order-1 autocorrelation structure. The logit part of the model included the same set of variables, but only count model results are presented. Fixed factors were standardized. Summer T1 is the mean Jun-July max temperature in the year prior seed fall; Summer T2 is the mean Jun-July max temperature two years before seed fall.

Predictor	Effect size (SE)	z-value	p-value
Intercept	4.34 (0.09)	45.21	< 0.001
Summer T1	0.63 (0.05)	11.63	< 0.001
Summer T2	-0.53 (0.06)	-8.35	< 0.001
Previous year seed production	-0.32 (0.05)	-6.16	< 0.001
Year	0.005 (0.002)	2.10	0.03
Summer T1 × Summer T2	0.15 (0.05)	3.02	0.002
Summer T1 × year	-0.01 (0.002)	-6.14	< 0.001
Summer T2 × year	0.01 (0.002)	4.05	< 0.001
Previous year seed production × year	0.001 (0.002)	0.56	0.58
Summer T1 × Summer T2 × year	-0.002 (0.002)	-1.26	0.21

Table S3. Abiotic drivers of within-site among-trees synchrony of seed initiation and their temporal change. Synchrony (within-year, within-site CV of seed initiation) was modeled using the Gaussian mixed model with and the site used as a random intercept. Fixed factors were standardized. Summer T1 is the mean Jun-July max temperature in the year prior seed fall; Summer T2 is the mean Jun-July max temperature two years before seed fall.

Predictor	Effect size (SE)	z-value	p-value
Intercept	0.70 (0.06)	10.86	< 0.001
Summer T1	-0.39 (0.067)	-5.50	< 0.001
Summer T2	0.41 (0.07)	5.59	< 0.001
Year	0.0005 (0.002)	0.18	0.86
Summer T1 \times year	0.008 (0.003)	2.96	0.003
Summer T2 \times year	-0.008 (0.003)	-2.73	0.006