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

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Abstract

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 breakdown 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 breakdown 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
mast seeding, phenology, pollen limitation, proximate mechanisms, reproduction, seed production, synchrony, warming

1 | INTRODUCTION

The capacity of future forests to support biodiversity and deliver ecosystem services depends on regeneration that tracks 21st-century climate (Clark et al., 2021; McDowell et al., 2020). Many tree species regenerate through synchronized, highly variable variation in fruit production, termed masting (Fernández-Martínez et al., 2019; Norden et al., 2007; 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; Schermer et al., 2019; Steven & Wright, 2002; Zwolak et al., 2016). Climate change is now altering masting by changing interannual variation and synchrony in seed production among individuals (Bogdziewicz et al., 2020; Pearse et al., 2017; Redmond et al., 2012; Shibata et al., 2020). Consequently, forests are facing lowered recruitment and migration potential (Bogdziewicz, Kelly, Thomas, et al., 2020; Clark et al., 2021). 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, Ascoli, et al., 2020). 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, Ascoli, et al., 2020). 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 (Kelly et al., 2013; Turnbull et al., 2012). 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 (Crone et al., 2009; Le Roncé et al., 2020; Monks et al., 2016). 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 (Kelly et al., 2001; Satake & Iwasa, 2000).

Understanding the proximate mechanisms by which climate change is altering masting requires closely tracking the seed developmental cycle. Long-term datasets that can pinpoint how climate change has changed seed initiation, seed set, and ultimately seed production, are almost non-existent. Here, we used a unique 39-year study of 139 individuals of European beech (*Fagus sylvatica* L.) to disentangle the mechanisms that cause masting in this species and tested how climate change has affected the transitions among seed development phases. Our past work on these beech populations showed that interannual variability and synchrony of beech masting declined by ~30% over the last four decades as the climate has warmed by 1°C (Bogdziewicz, Kelly, Tanentzap, et al., 2020; Figure S1). These declines increased pollen limitation and seed predation, indicating that tree reproduction has been reduced by climate change because masting has become less effective (Bogdziewicz, Kelly, Tanentzap, et al., 2020). However, we do not know the underlying mechanisms for these changes. Studying these mechanisms in beech is important because the species is a major forest-forming species across temperate Europe. Beech also represents a model system for studying the reproductive traits of many other globally important forest-forming species such as *Picea*, *Abies*, and *Nothofagus*. These traits include density-dependent wind pollination that determines seed set, and occasional mass flowering driven by a combination of temperature cues. Thus, our results may allow careful generalization to other key forest species.

We expected seed production in European beech to be driven by the following process. In European beech, warmer-than-average summers that follow cooler-than-average summers lead to years with large and synchronized flowering (Piovesan & Adams, 2001; Vacchiano et al., 2017). A rapidly warming climate can decrease the frequency of negative summer temperature anomalies, and increase the frequency of positive anomalies, thereby weakening the reinforcing dynamics of stored resources on synchrony and interannual variation of reproduction (Bogdziewicz et al., 2018; Rees et al., 2002). In short, the effect of increasing mean temperatures, at least in the short term, would be to increase the fraction of years when flowering is triggered. This will decrease individual interannual variation, since each plant will have less time between flowering efforts to accumulate reserves (Bogdziewicz et al., 2018; Rees et al., 2002). If true, the relationship between weather signals and seed production may weaken over time as climate warming progresses, lowering the synchrony of flowering. Moreover, pollen coupling should generally increase synchrony of seed production (Rapp et al., 2013), but progressively asynchronous flowering may limit pollination success leading to declines in synchrony. If true, synchrony of production of matured seeds should initially be larger than that of initiated seeds (flowers), but this should fade as climate warming makes flowering less synchronous.

2 | METHODS

2.1 | Study species

European beech (*F. sylvatica* L.) flowers are induced in summer one year before seed set. Flower buds overwinter, 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.

2.2 | Data collection

We sampled seed production in 139 beech trees located at 12 sites spaced across England annually between 1980 and 2018 (Bogdziewicz, Kelly, Tanentzap, et al., 2020; Bogdziewicz, Kelly, Thomas, et al., 2020). 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. While such data are potentially subject to biases caused by post-dispersal seed predation, it proved robust and easy-to-implement tool in methodological studies (Tattoni et al., 2021; Touzot et al., 2018). 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).

2.3 | Data analysis

2.3.1 | 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 (T_{max}) across June and July as this is a widely reported summer cue for European beech, including in our populations (Bogdziewicz, Kelly, Tanentzap, et al., 2020; Piovesan & Adams, 2001; Vacchiano et al., 2017). Another two models tested whether the probability that summer temperatures were higher or lower than 1 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 T_{max} but were fitted with a binomial error structure. We used ±1 SD because the flower cueing analysis presented below best predicted years of large and synchronized seed production if a cold summer (1 SD below the mean) was followed by a hot one (1 SD above the mean).

2.3.2 | 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 1 and 2 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, that is, 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.

2.3.3 | Proximate mechanisms of masting: Phenology of weather cues

We explored temporal stability of the weather-seed production relationships 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 2 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 T_{max} 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 1 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, that is, 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.

2.3.4 | Proximate mechanisms of masting: Density-dependent seed set

In the second step of our analysis, we modeled determinants of seed set using binomial generalized linear mixed models 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 time series 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 Figure 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 whether 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 whether 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).

3 | RESULTS

3.1 | 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; Figure 1A).

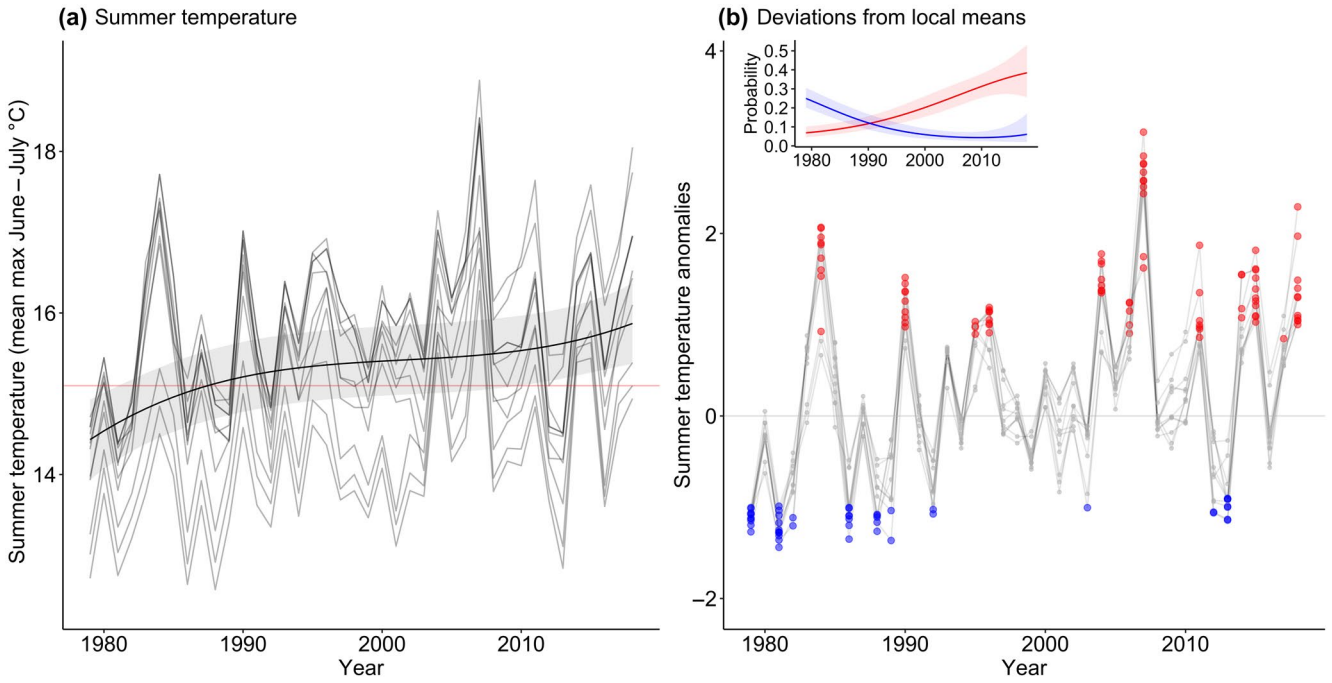

FIGURE 1 Temperature trends. (a) Mean maximum June–July temperature at each site. (b) The occurrence of positive (red points) and negative (blue points) summer temperature anomalies (1 SD above and below the long-term mean) at each study site. Horizontal lines in each graph show the long-term (1950–2018) 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% CIs. For longer perspective, Figure 2S shows the trends extended to 1960 [Colour figure can be viewed at wileyonlinelibrary.com]

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 ~7% early in the study to ~38% at the end of it (Table S1B; Figure 1B). Concurrently, the probability of the occurrence of negative summer anomalies decreased from ~25% to ~6% (Table S1C; Figure 1C).

3.2 | 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; Figure 2A). Seed production increased nonlinearly from about five seeds per tree (per 7-min search) the year after cold summers (T_{max}~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; Figure 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; Figure 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; Figure 2B). In early years, hot summers effectively reduced within-site, within-year CV of seed production to near-0 values—that is, high between-tree synchronization. By the end of the monitoring period, the relationship between CV and temperature was no longer statistically significant (Table S3; Figure 2B).

3.3 | Proximate mechanisms of masting: Phenology of weather cues

Moving-window correlations revealed little variation in seed production–weather relationships in space and time (Figure 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 (Figure 3). Importantly, we detected no apparent advance or delay in cue phenology over the four decades of the study. Seasonal peaks in relationships between seed

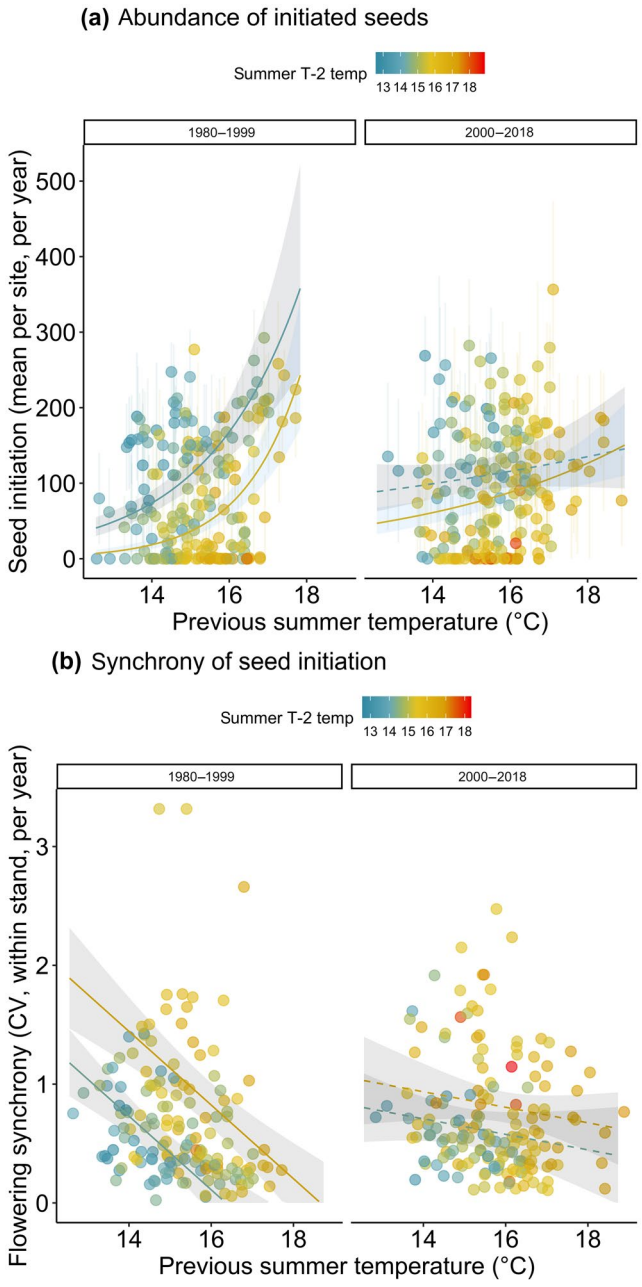

FIGURE 2 Interannual variation and synchrony of seed initiation versus weather cues. (a) The number of seeds initiated each year versus weather cues, and (b) synchrony (within-year, within-site coefficient of variation [CV]) of seed initiation in each year versus weather cues. Cues were June–July mean 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 2 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 generalized linear mixed models predictions, dashed lines show non-significant slopes while shading indicate 95% CIs. Vertical lines on points are SDs [Colour figure can be viewed at wileyonlinelibrary.com]

production and seasonal weather cues were temporally conserved (Figure 3).

3.4 | 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 (Figure 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 (Figure 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: $p = 0.31$).

4 | DISCUSSION

Altered seed production induced by anthropogenic global change is occurring worldwide (Bogdziewicz, Kelly, Thomas, et al., 2020; Buechling et al., 2016; Pearse et al., 2017; Pesendorfer et al., 2020; Redmond et al., 2012; 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 (Clark et al., 2021; Ibáñez et al., 2008; Zhu et al., 2012). 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

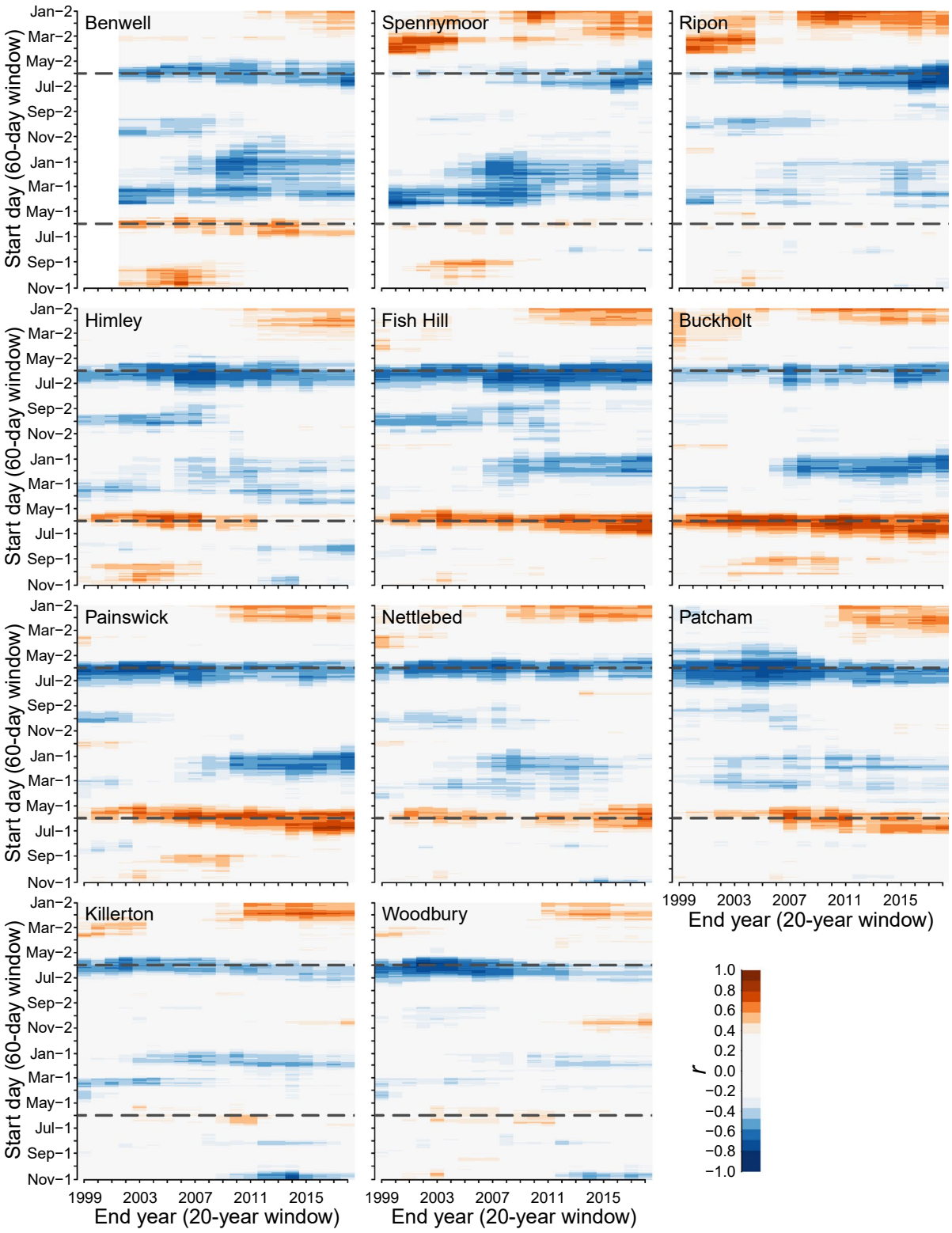

FIGURE 3 Spatiotemporal variation in seed production–weather cues correlations. Correlations are reported as the start DOY (day of the year) for the seasonal cues (*y*-axis) either T-2 or T-1 years before seed production, and the end year for the moving 20-year window (*x*-axis). The dashed lines in 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) [Colour figure can be viewed at wileyonlinelibrary.com]

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

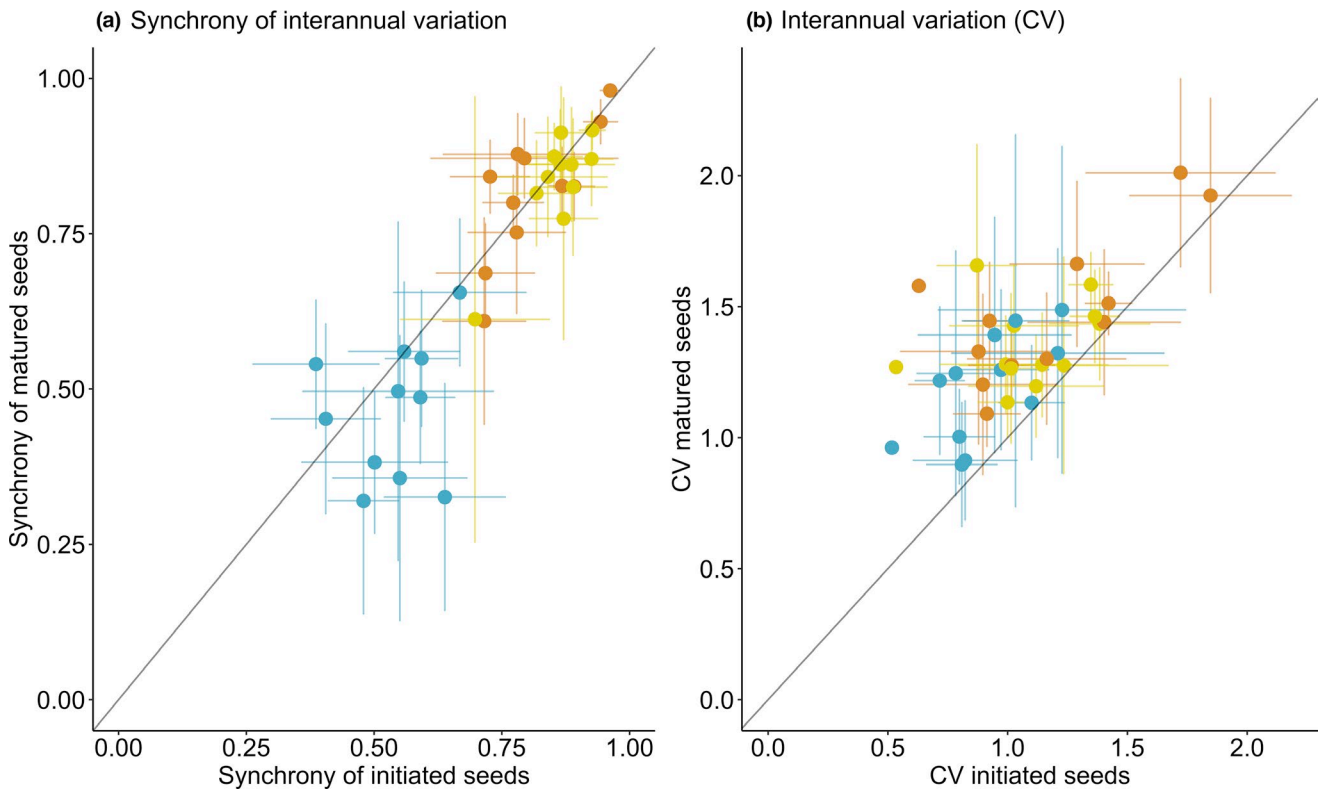

FIGURE 4 Effects of seed set on synchrony and interannual variation of seed production. (a) Mean ± SD for pairwise correlations between trees within each site for seed initiated and matured. Synchrony was significantly reduced between seed initiation and maturation in the most recent years (2006–2018, blue points). (b) Mean ± SD for tree level coefficient of variation (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 [Colour figure can be viewed at wileyonlinelibrary.com]

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	Observed 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

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,

Kelly, Tanentzap, et al., 2020; Bogdziewicz, Kelly, Thomas, et al., 2020), raise doubts about the ability of plant species to migrate rapidly in response to global climate change (Zhu et al., 2012).

The weakening relationships between seed count and June–July temperature 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 (Ettinger et al., 2020; Vitasse et al., 2009). Experiments in the mast-seeding grass *Chionochloa rigida* indicated that promotion of flowering by high temperatures only occurred in long days (>14 h; 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 (Ettinger et al., 2020; Vitasse et al., 2010). 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 have allowed a good understanding of how tree growth and survival respond to climate fluctuations (Berdanier & Clark, 2016; Brienen et al., 2020; Manzanedo et al., 2020; McMahon et al., 2010; Young et al., 2017). 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., 2021; Kunstler et al., 2021). Thus, realistic estimates of tree fecundity and population growth rate are basically absent from most vegetation models (Kunstler et al., 2021; McDowell et al., 2020; Vacchiano et al., 2018). 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, Kelly, Thomas, et al., 2020). 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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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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