



**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 ( <i>Fagus sylvatica</i> ) 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.

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3 Running head: Warming and proximate mechanisms of masting

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## 21 **Summary**

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

38

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

41

## 42 **Introduction**

43           The capacity of future forests to support biodiversity and deliver ecosystem services  
44 depends on regeneration that tracks the 21st-century climate (Clark *et al.* 2020; McDowell *et*  
45 *al.* 2020). Many tree species regenerate through synchronized, highly variable variation in  
46 fruit production, termed masting (Pearse *et al.* 2016). Masting is beneficial for successful  
47 plant recruitment as large and synchronized flowering effort enhances pollination success  
48 though positive density-dependence, and decreases seed predation by starving predator  
49 populations in years of low seed production and satiating them in high seed years (Kelly *et al.*  
50 2001; Tachiki & Iwasa 2010; Conlisk *et al.* 2012). Climate change is now altering masting by  
51 changing interannual variation and synchrony in seed production among individuals  
52 (Redmond *et al.* 2012; Pearse *et al.* 2017; Bogdziewicz *et al.* 2020c; Shibata *et al.* 2020).  
53 Consequently, forests are facing lowered recruitment and migration potential (Crawley &  
54 Long 1995; Bogdziewicz *et al.* 2020c, b). The trends in seed production are often paralleled  
55 by warming, but our understanding of the underlying proximate mechanisms is incomplete.  
56 Closing this gap is essential to predict the effects of warming that is underway on forest  
57 reproduction and vegetation dynamics.

58           The mechanisms responsible for masting determine the success of the transitions  
59 among seed development phases and thus population-wide variability and synchrony  
60 (Bogdziewicz *et al.* 2020a). In high seed years, plants in a population initiate many flowers,  
61 and these flowers are pollinated at a high rate. As flower initiation is an endogenous process  
62 that is often determined by an environmental cue, plants should all respond similarly to  
63 changes in the cue, resulting in population-level synchrony if regulatory networks are  
64 conserved (Bogdziewicz *et al.* 2020a). For example, seasonal deviations from mean weather  
65 values trigger changes in flowering hormone synthesis responsible for flower bud formation  
66 and explain interannual variation in masting grasses (Turnbull *et al.* 2012; Kelly *et al.* 2013).  
67 This process is likely to interact further with plant resource state, such that depleted resource  
68 pools after bumper crops limit flower production in subsequent years (Monks *et al.* 2016; Le  
69 Roncé *et al.* 2020). Once flowers are initiated, pollen limitation can enforce synchrony and  
70 interannual variation in seed production through pollen coupling, another endogenous process  
71 in which pollination success increases with flower density (Satake & Iwasa 2000; Kelly *et al.*  
72 2001).

73           Understanding the proximate mechanisms by which climate change is altering masting  
74 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 masting 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 masting 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 masting has 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.

108

## 109 **Methods**

### 110 **Study species**

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

116

### 117 **Data collection**

118 We sampled seed production in 139 beech trees located at 12 sites spaced across  
119 England annually between 1980 and 2018 (Bogdziewicz *et al.* 2020b, c). The ground below  
120 each tree was searched for seeds for 7 min and seeds were later classified as sound, or empty  
121 with formed pericarps (not pollinated), or damaged by *Cydia* sp. moth. Detailed descriptions  
122 of sites and procedures are given in Packham *et al.* (2008). Monthly weather data for each site  
123 were obtained from the corresponding 0.25° grid cell of the E-OBS dataset (Cornes *et al.*  
124 2018).

125

### 126 **Data analysis**

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

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

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

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

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

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



177 factors included the density of conspecific initiated seeds (flowers) at a given site and year,  
178 the within-year, within-site coefficient of variation of seed initiation among trees as an inverse  
179 proxy for flowering synchrony, and the interaction between these two terms. Next, we  
180 explored temporal changes in seed set effects on synchrony and interannual variation of beech  
181 reproduction by dividing the dataset into three equal parts: 1980-1992, 1993-2005, and 2006-  
182 2018. While binning our timeseries to these three periods is somehow subjective, it was based  
183 on the observation that both synchrony and interannual variability clearly broke-down in mid-  
184 2000s (see Fig. S1). We calculated the synchrony of seeds initiated and matured between  
185 individuals within sites using correlation coefficients (mean Pearson pairwise correlation  
186 coefficient for all pairs of trees within each site through each of the three time periods). This  
187 allowed us to test if among-tree synchrony of seed production was greater for matured than  
188 initiated seeds, as might be expected if pollen coupling enhances synchrony, and whether that  
189 changed over time. We also compared CV of seeds initiated and seeds matured for each tree  
190 averaged for all trees per site through each of the three time periods, to test if factors during  
191 seed set enhance the interannual variation of reproduction. All statistics were run in R, and we  
192 fitted models via the glmmTMB package (Brooks *et al.* 2017).

193

## 194 **Results**

195 **Temporal trends in climate.** Our sites experienced significant warming over the last  
196 four decades. The mean maximum June to July temperature increased by  $\sim 1$  °C from  $\sim 14.5$  in  
197 1980 to  $\sim 15.5$ °C in the 2010s (Table S1A, Fig. 1A). The change in mean maximum  
198 temperature was accompanied by a dramatic increase in the probability of occurrence of a  
199 positive summer temperature anomaly (1SD above the long-term mean) from  $\sim 7\%$  early in  
200 the study to  $\sim 38\%$  at the end of it (Table S1B, Fig. 1B). Concurrently, the probability of the  
201 occurrence of negative summer anomalies decreased from  $\sim 25\%$  to  $\sim 6\%$  (Table S1C, Fig.  
202 1C).

203 **Proximate mechanisms of masting: weather cueing.** In early years, summer weather  
204 anomalies effectively led to mast flowering. Seed initiation (i.e. overall number of seeds  
205 produced, both matured and not, which represents the number of female flowers) was highest  
206 when relatively cold summers were followed by warm ones (Table S2, Fig. 2A). Seed  
207 production increased non-linearly from about 5 seeds per tree (per 7 minute search) the year  
208 after cold summers ( $T_{\max} \sim 13$  °C) to 150 seeds tree<sup>-1</sup> following hot ones ( $\sim 17$  °C). This  
209 increase was stronger if summer two years before seed fall was cold, increasing from 40 to  
210 390 seeds tree<sup>-1</sup> over the same temperature range. However, the response of trees to the

211 combination of cold followed by hot years weakened with time. By the end of the monitoring  
212 period, seed initiation was no longer significantly related to that combination of weather cues  
213 (Table S2, Fig. 2A). For example, the effect size (logit slope of the relationship between  
214 flowering per tree and temperature) of cold summer two years before seedfall faded by 0.01  
215 each year from  $\beta$  (SE) = -0.53 (0.06) estimated for 1980 (Table S2, Fig 2a). Similarly, the  
216 effect size of warm summer one year before seedfall faded by 0.01 each year from  $\beta$  (SE) =  
217 0.63 (0.05) estimated for 1980 (Table S2). Previous year seed production limited seed  
218 initiation in later year, but we detected no temporal change in that effect (Table S2).

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

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

233 **Proximate mechanisms of masting: density-dependent seed set.** Pollination  
234 efficiency was positively density-dependent. The probability of successful maturation of  
235 seeds increased with the number of initiated seeds (logit slope:  $\beta = 0.91$ ,  $z = 7.94$ ,  $p < 0.001$ ),  
236 decreased as seed initiation was more variable among trees (high CV is an inverse proxy of  
237 synchrony;  $\beta = -0.58$ ,  $z = -7.93$ ,  $p < 0.001$ ), and was highest when high seed initiation density  
238 coincided with low CV/high synchrony (CV of seed initiation by density interaction:  $\beta = -$   
239  $0.69$ ,  $z = -9.96$ ,  $p < 0.001$ ). Density-dependent seed set subsequently maintained, rather than  
240 increased, synchrony from seed initiation to seed maturation, as measured by comparing the  
241 mean cross-correlation of seed initiation and seed maturation among trees (Fig. 4A). The  
242 mean synchrony of seed initiation (pairwise correlation among trees within each site) in the  
243 first decades of the study (1980-1993), equaled 0.81 and was similar to that of matured seeds  
244 (0.82,  $z = -1.49$ ,  $p = 0.14$ ). Similarly, we detected no difference in synchrony between seed

245 initiation and maturation in 1994-2005 ( $z = 1.09$ ,  $p = 0.28$ ). However, in recent years (2006-  
246 2018), the synchrony of seed maturation was significantly reduced (mean = 0.46) compared to  
247 the synchrony of seed initiation (0.54,  $z = 2.96$ ,  $p = 0.003$ ).

248 Interannual variation of seed maturation was larger than that of seed initiation,  
249 suggesting that seed set amplified interannual variation of seed production. This effect was  
250 maintained through time (Fig. 4B). The mean coefficient of variation (CV) of initiated seeds  
251 equaled 1.17 in the first decades (1980-1993) and was smaller than that of matured seeds that  
252 equaled 1.46 ( $z = -7.09$ ,  $p < 0.001$ ). Similarly, in 1994-2005 the mean CV of seed limitation  
253 equaled 1.15, while that of matured seeds 1.40 ( $z = 6.29$ ,  $p < 0.001$ ). In 2006-2018, the CV of  
254 initiated seed (mean = 0.94) was also lower than that of matured seeds (1.29,  $z = -7.02$ ,  $p <$   
255  $0.001$ ). The difference in CV between seed initiation and seed maturation was similar in all  
256 periods (seed phase by time interaction:  $p = 0.31$ ).

257

## 258 Discussion

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

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

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

288         The weakening of seed count—June-July temperature relationships were not an  
289 artefact of a temporal shift in the cue to earlier or later in the year. Rather, despite the  
290 warming trend, we detected remarkable stability of the temporal window when beech trees  
291 appear sensitive to environment signals both among sites and over time. This result may seem  
292 surprising given that an earlier onset of both spring bud break and growth has been observed  
293 in temperate forests worldwide during recent decades (Fu *et al.* 2015). Moreover, our study  
294 sites differ notably in climate, including in mean max summer temperatures (range: 13.84 –  
295 15.77 °C). One hypothesis for why warming does not translate into earlier cue-sensing  
296 phenology is that photoperiod may play a leading role in determining temperature-sensitive  
297 periods for reproductive phenology in European beech. European beech phenology is well-  
298 known for its high photoperiod sensitivity (Vitasse *et al.* 2009; Ettinger *et al.* 2020).  
299 Experiments in the mast-seeding grass *Chionochloa rigida* indicated that promotion of  
300 flowering by high temperatures only occurred in long days (>14 hours) (Mark 1965). Future  
301 studies that would examine the temperature-sensitive periods that plant use to fine-tune their  
302 flowering intensity and seed production appear to be a promising avenue for future research.  
303 One interesting question is whether species with any plasticity in temperature-sensitive  
304 periods for reproductive phenology are better suited to withstand the effects of a rapidly  
305 warming climate (Vitasse *et al.* 2010; Ettinger *et al.* 2020). By shifting the sensitive periods to  
306 earlier in the season, trees may be able to compensate for the change in cueing frequency.  
307 Understanding the mechanisms by which weather affects seed production is challenging, but  
308 critical if we are to understand how climate change will affect masting behavior.

309         Widely available data on forest growth and mortality has allowed a good  
310 understanding of how tree growth and survival responds to climate fluctuations (McMahon *et*  
311 *al.* 2010; Berdanier & Clark 2016; Young *et al.* 2017; Brien *et al.* 2020; Manzanedo *et al.*  
312 2020). By contrast, an understanding of climate change impacts on fecundity is less

313 developed, as seed production is not directly observed for most species and habitats, and data  
314 accumulate slowly and with substantial investment (Clark *et al.* 2020; Kunstler *et al.* 2020).  
315 Thus, realistic estimates of tree fecundity and population growth rate are basically absent  
316 from most vegetation models (Vacchiano *et al.* 2018; McDowell *et al.* 2020; Kunstler *et al.*  
317 2020). Our study starts to fill this gap by identifying mechanisms by which climate change  
318 breaks down masting patterns. Climate change will not only affect mean seed production, but  
319 also interannual variability and synchrony, which has important consequences for plant  
320 fecundity and fitness (Bogdziewicz *et al.* 2020c). Our findings that the proximate mechanisms  
321 of masting are vulnerable to climate warming may apply widely to taxa that rely on similar  
322 physiological approaches as European beech to fine-tune their reproductive schedules.  
323 Consequently, population recruitment may be widely compromised as forests rapidly warm.

324

325

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332

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For Review Only



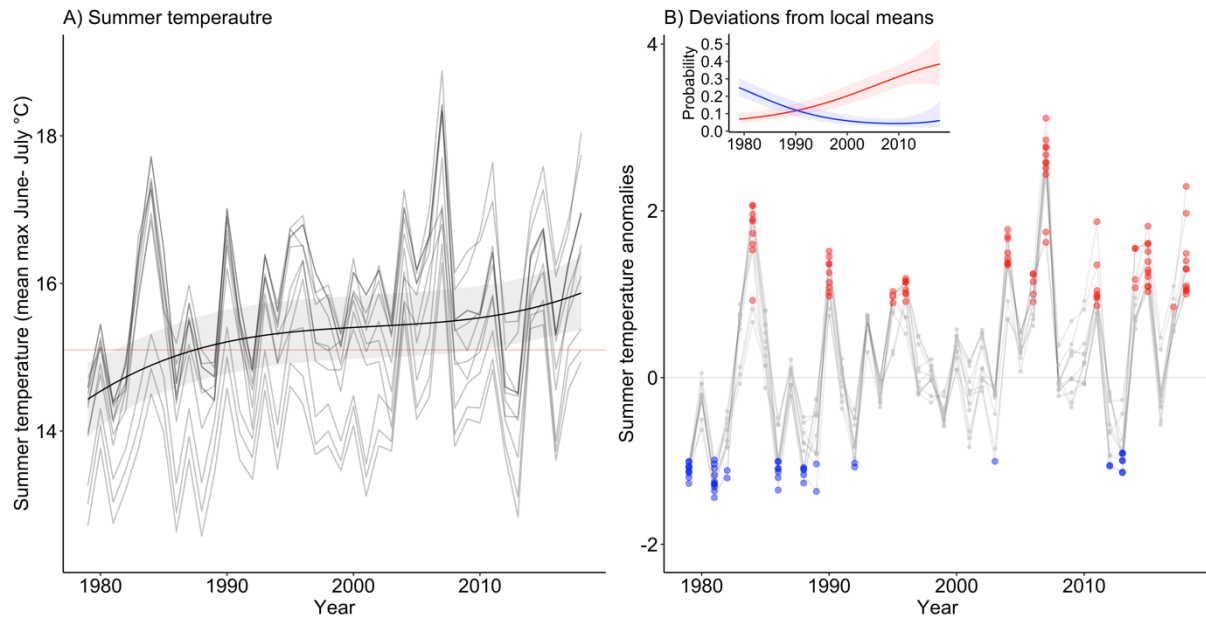
456 Table 1. Summary of proximate mechanisms driving seed production patterns in European  
 457 beech and warming-related temporal changes tested in this study.

458

<b>Developmental phase</b>	<b>Theoretical mechanism</b>	<b>General pattern</b>	<b>Observed temporal changes in mechanism</b>
<b>Flowering (seed initiation)</b>	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
<b>Flower maturation (seed set)</b>	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

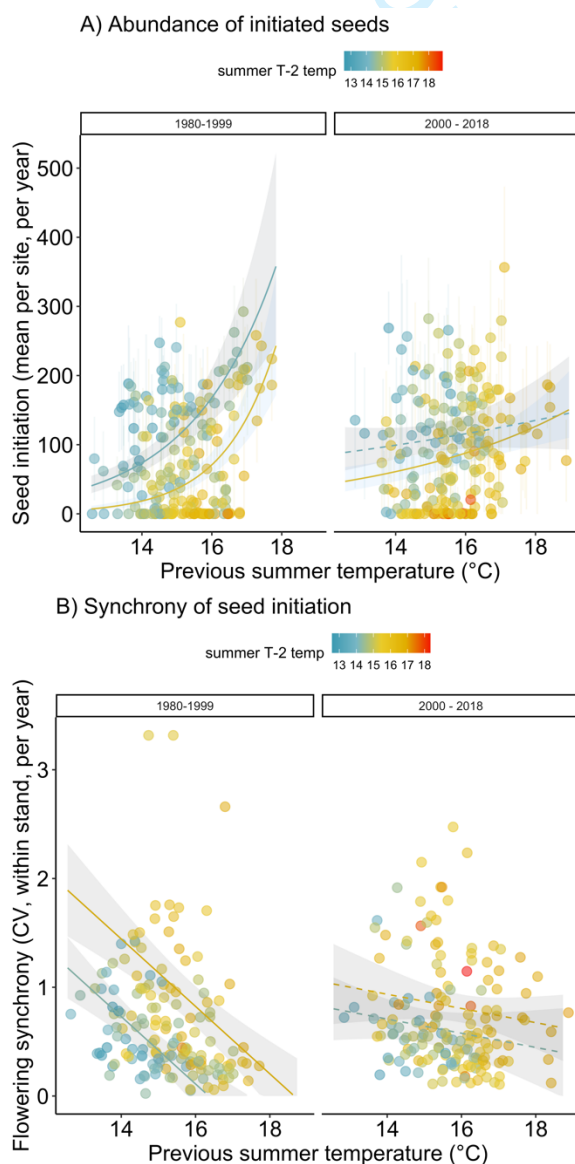
459

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



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472 **Figure 2. Interannual variation and synchrony of seed initiation vs. weather cues.** A) The  
 473 number of seeds initiated each year vs. weather cues, and B) synchrony (within-year, within-  
 474 site CV) of seed initiation in each year vs. weather cues. Cues were June-July mean max  
 475 temperature in years preceding seed fall. Summer temperature in the year preceding seed fall  
 476 is given on the x-axis (T-1), while points are colored according to temperature two years  
 477 preceding seed fall (T-2). Different colored lines show predictions for low (-1 SD, blue) and  
 478 high (+1 SD, orange) temperatures in year T-2. Facets show data and predictions for early  
 479 (1980-1999) and recent (2000-2018) years, but this categorization was only for visualization  
 480 and year was included as a continuous predictor in the models. The solid lines are effects  
 481 based on statistically significant binomial GLMMs predictions, dashed lines show non-  
 482 significant slopes. Shading and vertical lines on points indicate 95% confidence intervals.  
 483

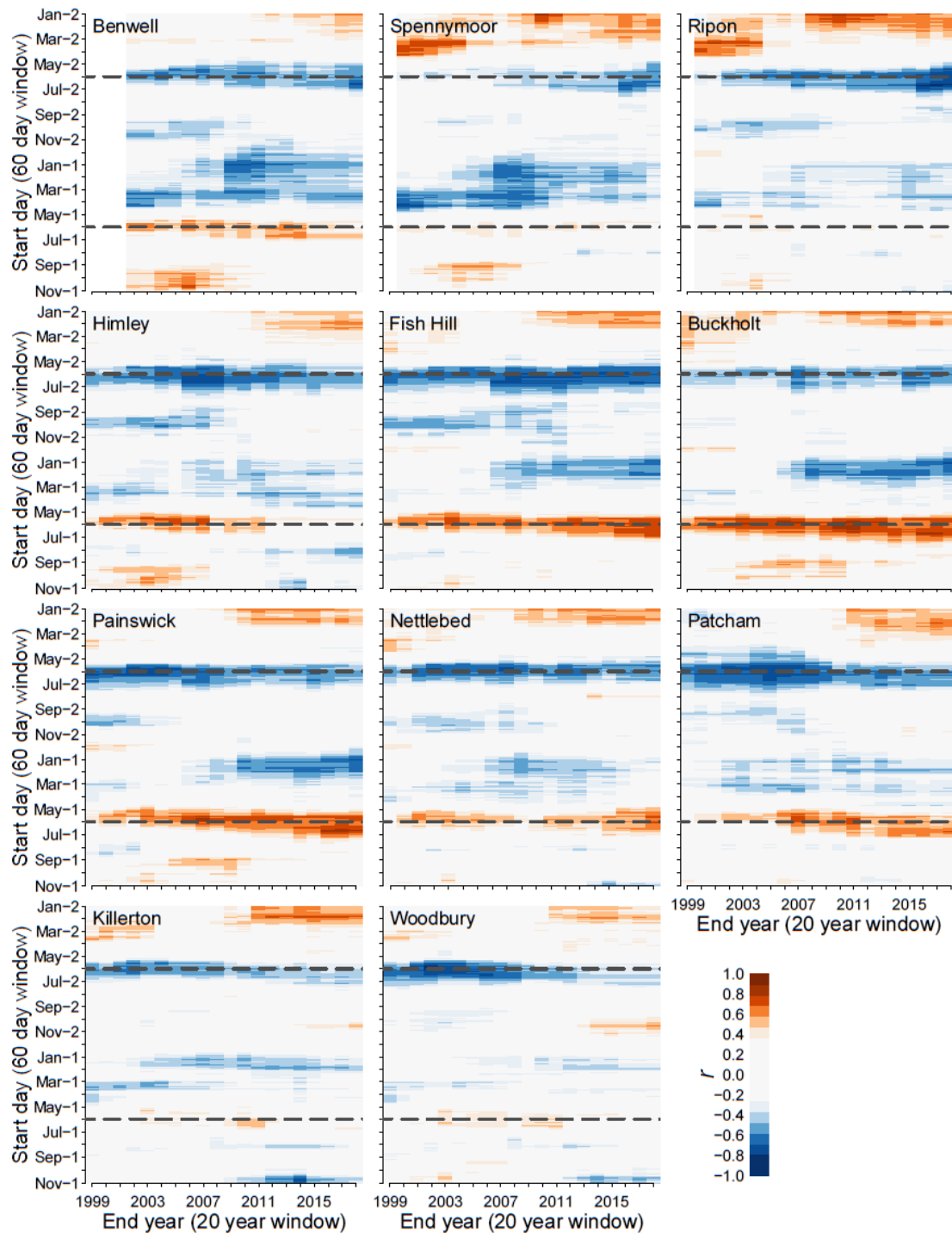


484

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

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

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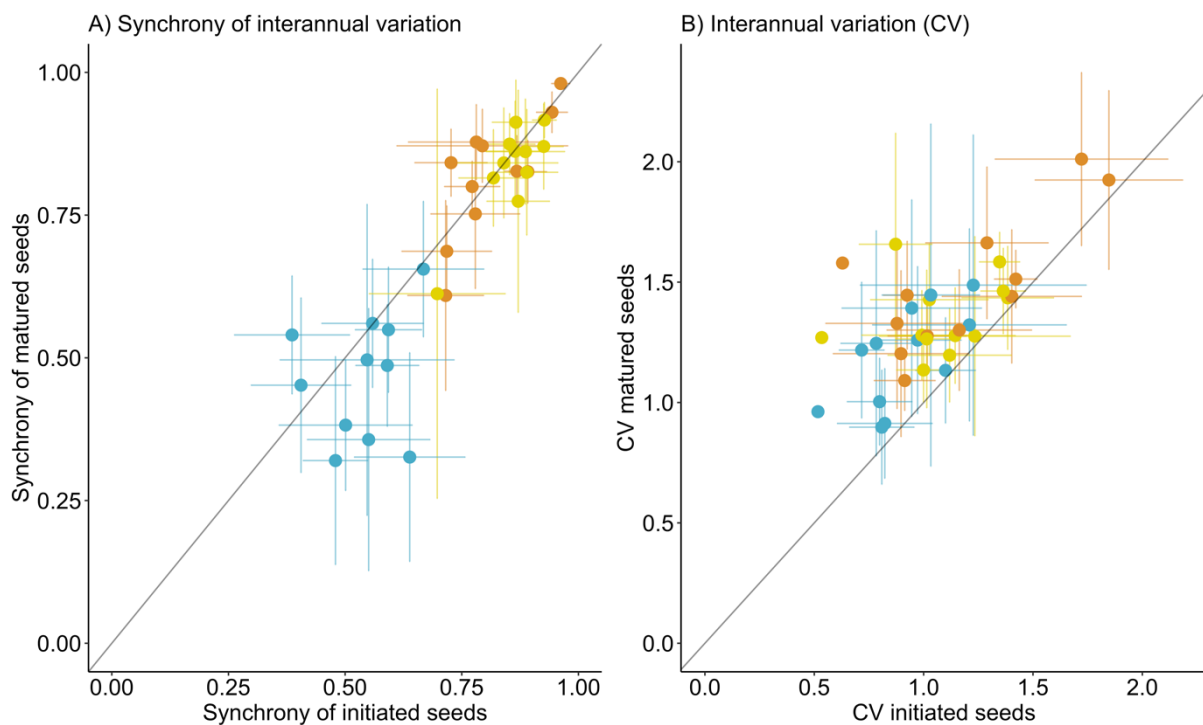


492

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

494 A) Mean  $\pm$  SD for pairwise correlations between trees within each site for seed initiated and  
495 matured. Synchrony was significantly reduced between seed initiation and maturation in the  
496 most recent years (2006-2018). B) Mean  $\pm$  SD for tree level CV of seeds initiated and  
497 matured. CV was significantly increased between seed initiation and maturation in all periods.  
498 Each point is one site during one time period: orange: 1980-1992, yellow: 1993-2005, blue:  
499 2006-2018.

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503 Supplementary material

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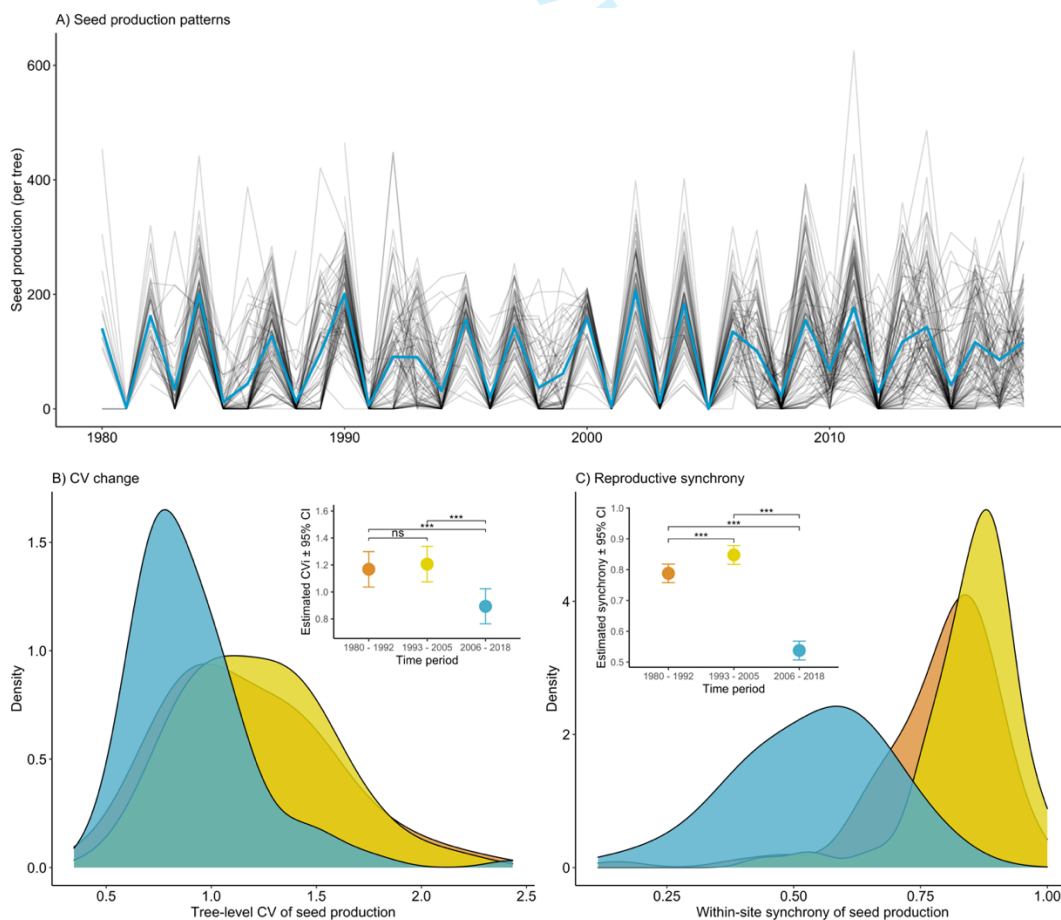
### 505 Trends in masting

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

512

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

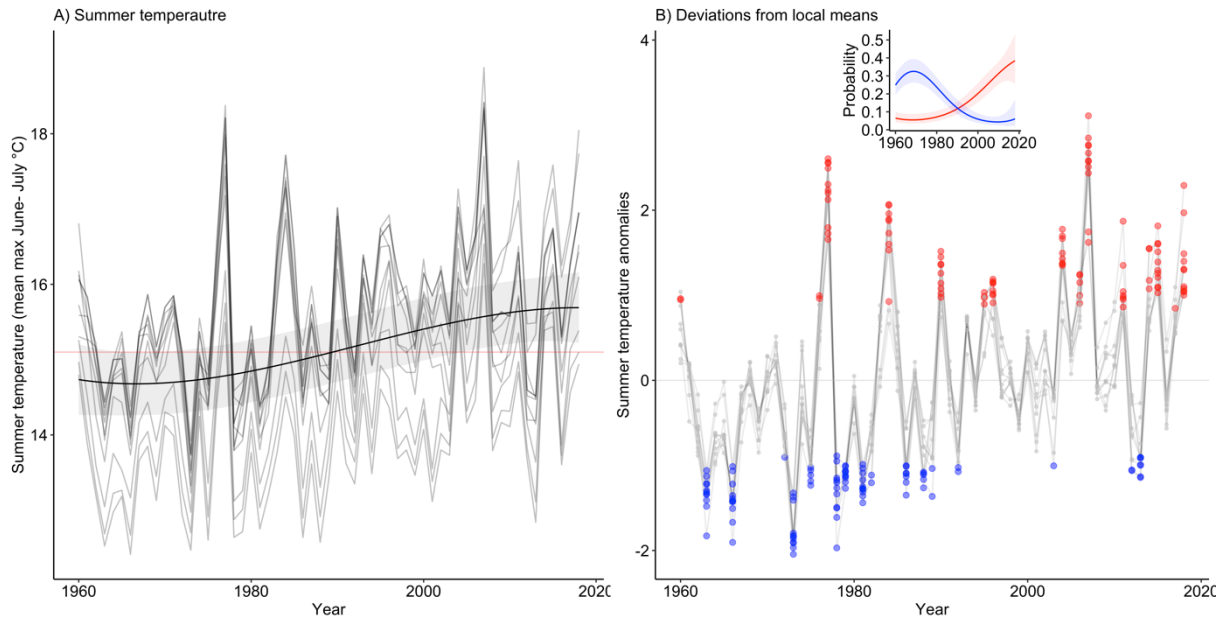
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521 **Figure S2. Temperature trends extended back to 1960.** A) Mean maximum June-July  
522 temperature at each site. B) The occurrence of positive (red points) and negative (blue points)  
523 summer temperature anomalies (1SD above and below the long-term mean) at each study site.  
524 Horizontal lines in each graph show the long-term (1950-2018) mean. The inset plot at B)  
525 shows the modeled probability of anomaly occurrence (red – positive; blue – negative  
526 anomaly). The prediction lines are based on significant mixed models, shading indicates the  
527 95% confidence intervals.  
528



529  
530

531 **Table S1. Temperature trends.**

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

534

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

535

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

539

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

540

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

544

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

545



546 **Table S2. Abiotic drivers of beech seed initiation and their temporal change.** Seed  
 547 initiation (yearly records per tree) was modeled using the zero-inflated negative binomial  
 548 mixed model with tree ID and site used as random intercepts and temporal autoregressive  
 549 order-1 autocorrelation structure. The logit part of the model included the same set of  
 550 variables, but only count model results are presented. Fixed factors were standardized.  
 551 Summer T1 is the mean Jun-July max temperature in the year prior seed fall; Summer T2 is  
 552 the mean Jun-July max temperature two years before seed fall.  
 553

<b>Predictor</b>	<b>Effect size (SE)</b>	<b>z-value</b>	<b>p-value</b>
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

554

555

556 **Table S3. Abiotic drivers of within-site among-trees synchrony of seed initiation and**  
 557 **their temporal change.** Synchrony (within-year, within-site CV of seed initiation) was  
 558 modeled using the Gaussian mixed model with and the site used as a random intercept. Fixed  
 559 factors were standardized. Summer T1 is the mean Jun-July max temperature in the year prior  
 560 seed fall; Summer T2 is the mean Jun-July max temperature two years before seed fall.  
 561

<b>Predictor</b>	<b>Effect size (SE)</b>	<b>z-value</b>	<b>p-value</b>
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 × year	0.008 (0.003)	2.96	0.003
Summer T2 × year	-0.008 (0.003)	-2.73	0.006

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