

1 Summer solstice orchestrates the
2 subcontinental-scale synchrony of mast seeding

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18 **High interannual variation in seed production in perennial plants, can**
19 **be synchronized at subcontinental scales with wide consequences for**
20 **ecosystem functioning, but how such synchrony is generated is unclear**
21 **[1–3]. We investigated the factors contributing to masting synchrony in**
22 **European beech (*Fagus sylvatica*), that extends to the 2000 km geographic**
23 **range. Maximizing masting synchrony via spatial weather coordination,**
24 **known as the Moran effect, requires a simultaneous response to weather**
25 **conditions across distant populations. A celestial cue that occurs si-**
26 **multaneously across the entire Hemisphere is the longest day (summer**
27 **solstice). We show that European beech abruptly opens its temperature-**
28 **sensing window on the solstice, hence widely separated populations all**
29 **start responding to weather signals in the same week. This celestial**
30 **"starting gun" generates ecological events with high spatial synchrony**
31 **across the continent.**

32 Main

33 Subcontinental synchronization of interannual variation in seed production by trees means
34 that, in a large-seeding year, a large pulse of resources is made available to wildlife over the
35 majority of the continent by virtue of the synchronous reproduction by millions of trees [1–3].
36 Such large-seeding years are usually followed by reproductive failures, creating subsequent
37 famine [4, 5]. This synchronized cycle of abundance and shortage triggers far-reaching dis-
38 ruptions in food webs, including rodent outbreaks [6], migration of ungulates and birds [7–
39 11], and spikes in wildlife-borne human diseases [12, 13]. Moreover, in some species tree
40 and leaf growth is reduced in years of high seed production, creating large-scale fluctua-
41 tions in carbon sequestration [14–16]. The spatial scale of synchrony is a key aspect that
42 amplifies the ecological importance of year-to-year variation in seed production [17–19].
43 However, several key questions on how plants synchronize masting over such extensive
44 spatial scales remain unanswered.

45 Masting is synchronous and highly variable reproduction among years by a population
46 of perennial plants [20]. Synchrony often exceeds among populations and decades of in-
47 vestigation have demonstrated that the regional synchronization of masting stems from the
48 Moran effect, i.e. it is driven by spatially synchronized environmental signals [1, 2, 7, 21–
49 25]. A major mechanism that governs the annual allocation of resources to seed produc-
50 tion is weather variation [26–28]. These so-called weather cues are employed by plants
51 to maintain synchronized reproductive fluctuations within populations [29]. The mecha-
52 nisms underpinning weather cues exhibit species-specific variation, with a major example
53 being the influence of summer temperature on the promotion of flower production [30, 31].
54 Masting plants have evolved to be remarkably responsive to temperature fluctuations [29,
55 32]. Consequently, substantial flowering effort, or masting, is triggered when the temper-
56 ature meets some species-specific criteria. For example, one common link is that warm
57 summers are associated with a high subsequent seed crop [33–36]. If individuals and pop-
58 ulations collectively respond to the same cue across extensive regions, the spatial scale of
59 masting synchrony aligns with the broad-scale synchronization of weather patterns [2, 21,
60 23, 24]. Crucially, the highest regional synchrony is achieved if the cue window is tempo-
61 rally conserved [3]. For instance, if the cue window shifts among populations to be earlier in
62 the year in warmer climates, akin to the advancement of bud break or flowering in warmer
63 climate [37, 38], regional synchrony deteriorates [3].

64 A global comparison of the Moran effect in masting showed that European beech (*Fagus*
65 *sylvatica*) has stronger spatial synchrony than any other species in Europe (matched only
66 by white spruce, *Picea glauca*, in North America). Both species have very large ranges,
67 including latitudinally (north-south), which makes their ability to maintain significant masting
68 synchrony exceeding 1500 km especially puzzling [2, 3]. New evidence has demonstrated
69 that the timing of the cue window is exceptionally well conserved across the range of Euro-
70 pean beech [3], but the mechanism facilitating this stability remains unknown.

71 Recently, Zohner *et al.* [39] showed that temperature has opposite effects on leaf senes-

72 cence phenology before and after the summer solstice, demonstrating that trees can time
73 their physiology using maximum day length. Similarly, wood formation in trees switches
74 from a focus on cell division to secondary wall thickening once days start to shorten [40,
75 41]. The capacity to sense the timing of solstice might explain the remarkable consistency
76 of the temporal window during which beech trees are receptive to cues triggering masting
77 events [3, 42]. Right across the European continent, the cues are anchored to June and
78 July temperatures despite great differences in climate and day length among studied sites
79 (mean summer annual temperature range across sites: 7.7 – 16.6 °C, maximum day length
80 15 hr 25 mins to 16 hr 50 mins) [3], and a significant warming trend (1 °C over 40 years)
81 [42], resulting in substantial variation in the growing season onset and duration. Here, we
82 show that European beech achieves high synchrony across very large scales by anchoring
83 the weather cue window to the summer solstice - the longest day of the year that occurs
84 simultaneously across the whole Northern Hemisphere. The solstice alignment enables
85 cohesive timekeeping across distant beech populations inhabiting diverse climatic regions.

86 We used a moving window analysis and observed an abrupt rise in the correlation be-
87 tween European beech seed production and temperatures at the summer solstice, showing
88 that the longest day coincides with the opening of the cue window. We ran a moving win-
89 dow correlation between annual seed production and mean temperatures in 61 populations
90 of European beech sampled across the species' range (Fig. 1a, mean number of annual
91 observations per site = 35, max = 68), across which masting synchrony reaches 2000 km
92 (Fig. 1b). The correlation coefficients displayed two distinct peaks, consistent among pop-
93 ulations independent of latitude or local climate (Fig. 1c). The first was a negative peak
94 occurring two years before seed fall, and the second was a positive peak arising one year
95 before seed fall, both following the summer solstice (Fig. 1c). The correlations' directions
96 between European beech masting and temperature in the summers before seed fall, one
97 (T1), and two (T2) years prior align with previous research [33, 42, 43]. Here, however, we
98 discover that the June-July period is not a mere consequence of physiological processes
99 operating at that time in the plant (such as resource priming in year T2; cf. [43]), but the cue
100 anchoring to the solstice. According to our hypothesis, European beech uses the solstice as
101 a trigger to open the cue window. In support of this, correlation coefficient values between
102 seed production and temperature rapidly increased after the solstice, compared to before
103 it (Fig. 2). To test that, we fitted a generalized additive model (GAM), in which a response
104 was the correlation between annual seed production and mean temperature in the 7-day
105 rolling window. The predictors were relative day length (with maximum happening at the
106 summer solstice) and the summer solstice as a categorical variable (before and after the
107 solstice) with their interaction. The interaction was significant (Table S1), showing that Eu-
108 ropean beech abruptly starts responding to temperature after, but not before, the solstice.
109 The predicted correlation between masting and temperature was ~4-fold higher one day
110 after the solstice compared to one day before (correlation before the solstice, 0.095; after
111 the solstice, 0.37, Fig. 2). Comparing the correlations in bins, defined as 0.95 - 1 (max)
112 day length, before (mean correlation = 0.02) and after the solstice (0.35) shows an even

113 greater magnitude of difference (Fig. 2b). We rejected the null hypothesis that the highest
114 difference in correlations at the solstice would emerge by chance ($p = 0.02$) (Fig. 2c) (see
115 Methods for details). Similar anchoring at solstice was observed for the temperature effects
116 in year T2 (Fig. S2).

117 More than a mere outcome of the Moran effect, the regional synchrony in European
118 beech masting stems from a mechanism that effectively harnesses weather variation for
119 synchronization. The negative correlation of European beech masting with temperatures
120 in summer T2 has been proximally associated with enhanced resource accumulation in
121 cooler years [43, 44], and the positive correlation in summer T1 with enhanced flower pri-
122 mordia differentiation [30, 33, 43]. Of course, the positive effect of resource accumulation
123 on seed production does not only appear after the longest day, and flower primordia can
124 begin differentiating in response to high temperatures before the celestial event. Theoretical
125 predictions suggest that masting can be triggered by any weather cue, yet cues are most
126 likely to evolve from weather variation that affects reproduction-related processes [20, 29,
127 45]. This sensitivity of such reproduction-related physiological processes is then reinforced
128 by natural selection when variable and synchronized reproduction enhances plant fitness,
129 as documented in a previous study on European beech [46]. However, to ensure ecological
130 synchrony through weather-based alignment, cue-sensing phenology must be harmonized
131 across populations. In species in which the cue-sensing is not harmonized, such as *Picea*
132 *abies* or *Quercus robur*, synchrony deteriorates [3]. Temperatures are highly synchronized
133 across space, but not necessarily over time. If one population opens its weather cue win-
134 dows in July, but another in August, they will likely be responding to different temperature
135 conditions, and their subsequent masting patterns will diverge, reducing synchrony [3]. The
136 problem is that plants at more northern latitudes have much longer days (by more than an
137 hour) near midsummer than plants further south, so using absolute day length to open the
138 weather cue window would result in a spread of cue windows by latitude, and consequently
139 large-scale asynchrony. A celestial cue that happens simultaneously across the entire con-
140 tinent, capable of transcending environmental diversity among very distant populations is
141 the annual maximum day length at the summer solstice. European beech responds to the
142 solstice to open the cue window on the same day at all latitudes, which creates a high
143 precision timing of the Moran effect.

144 In addition to summer temperatures, beech masting is correlated with summer (June/July)
145 precipitation (in T1 and T2), and with spring weather [16, 43]. We thus run a similar, 7-days
146 moving window analysis for precipitation. Consistent with past work, precipitation in June
147 and July was positively (in T2) and negatively (in T1) correlated with seed production (Fig.
148 S3). That effect was, however, not anchored to the solstice. Based on that, we hypoth-
149 esize that temperature is the primary weather cue for beech masting, while precipitation
150 during these periods may modulate the strength of temperature effects. That is supported
151 by generally weaker and less spatially consistent correlations between beech masting and
152 precipitation compared to temperature effects reported in past studies [43, 47]. Analyses
153 based on gene expression levels will shed more light on these mechanisms. The effects of

154 weather during pollination appear generally negligible compared to summer weather [43],
155 even if important locally [16]. In support, the peaks in correlations during the flowering sea-
156 son are not distinguishable from fluctuations along the two-year period that precedes seed
157 fall (Fig. 1, Fig. S3).

158 The observation that seed production in European beech is highly correlated with tem-
159 peratures around the solstice reinforces the theory that weather cues can serve as a prox-
160 imate mechanism enabling masting plants to synchronize patterns of seed production at
161 supra-annual and regional scales. The pivotal role of weather variation in driving seed
162 production in masting plants is not controversial [32]. However, the precise translation of
163 weather variation into seed production variability remains a topic of debate [29, 48–50].
164 On one hand, weather conditions may influence the transition from flowers to fruits by, for
165 example, disrupting pollination success or hindering resource uptake [44, 51, 52]. On the
166 other hand, gene regulatory networks might integrate various signals, such as temperature
167 and photoperiod, allowing flowering to occur only when all these cues are received [53].
168 In the latter scenario, hormones and genes that control flowering exhibit hypersensitivity
169 to environmental signals, thus granting masting a degree of independence from resource-
170 and pollen-related mechanisms [29]. The fact that European beech responsiveness to tem-
171 perature is prominent only as the days begin to shorten suggests that weather's influence
172 on masting extends beyond mere effects on flower development stages. Rather, it implies
173 the presence of a strongly conserved regulatory network that enables all plants to respond
174 uniformly to the cue. Future research should involve monitoring gene expression levels,
175 such as the FLOWERING LOCUS T, at the fine temporal scales disclosed in this study,
176 to understand how the negative (two years before seed fall, T2) and positive (in year T1)
177 correlations with temperature are translated into genetic and hormonal processes [30, 31,
178 54, 55].

179 Across the entire continent, the summer solstice serves as a celestial "starting gun" that
180 enables cohesive timekeeping across far-distant beech populations, highlighting how evo-
181 lution may have capitalized on this astronomical event to maximize ecological synchrony.
182 A prime fitness benefit of masting lies in predator satiation [20, 32]. The synchronized,
183 substantial year-to-year variation in seed production effectively starves seed consumers in
184 low-seeding years, making it easier to satiate these consumer populations in mast years
185 [56]. High regional synchrony of masting appears to have a selective advantage as it al-
186 lows to satiate mobile seed consumers, such as highly mobile vertebrates [9, 18], that can
187 prevent regeneration if mast years are localized [57]. Large-scale synchrony also increases
188 the likelihood of seed release into disturbed areas [18]. Variation in day length provides a
189 reliable signal of seasonal shifts and is unaffected by climatic changes in space and time
190 [58]. To increase masting synchrony under the Moran effect, populations separated by hun-
191 dreds of kilometers align their cue window with the moment when day length reaches its
192 longest duration once a year.

193 Anchoring to solstice means that the timing of cue sensing withstands climate variation
194 and generates a high scale of regional synchrony. However, the climate changes of the

195 twenty-first century generate novel challenges that may prove the solstice-anchoring sub-
196 optimal. In European beech, increasing temperatures lead to a decrease in interannual
197 variation and synchrony of seed production, a process called masting breakdown [59]. The
198 consequence is inefficient predator satiation and decreased pollination efficiency that to-
199 gether lead to a collapse in viable seed production [60]. The breakdown follows from higher
200 summer temperatures and therefore more frequent triggering of reproduction [42]. If sum-
201 mer cues would not be anchored to the solstice, shifting the sensitive periods to earlier in
202 the season would perhaps compensate for the change in cueing frequency. Second, cli-
203 mate change leads not only to trends in mean weather conditions but also to changes in
204 large-scale weather patterns [61]. Long-lasting blocking weather patterns that create ex-
205 treme conditions over certain regions, appear to change in frequency [61]. For example,
206 high-pressure areas sandwiched between low-pressure systems called an omega block,
207 can bring long-lasting heat to the high-pressure area [61, 62]. Transition probabilities to-
208 wards omega in summer over the Northern Hemisphere increase over time, which may
209 create repeated periods of masting asynchrony between low- and high-pressure blocks.
210 Similarly, the among-site variation in correlation values between temperatures and masting
211 could be associated with omega blocking. The consequences of such disruptions in the
212 large-scale patterns of synchrony appear as an interesting avenue for future research.

213 Recent discovery indicated that solstice triggers a shift in trees' responsiveness to tem-
214 perature, enabling plants to anticipate the approaching end of the growing season [39]. Our
215 study shows that the solstice also serves as a continent-wide "starting gun" to which plants
216 respond simultaneously from southern France to Sweden, and orchestrates the multiyear-
217 long process that determines reproductive investment in European beech, generating eco-
218 logical events marked by the unparalleled spatial synchrony across the continent.

219 **Materials and Methods**

220 **Study system and data** European beech (*Fagus sylvatica* L.) is a major forest-forming
221 species in temperate Europe. Beech is a model masting species, with seed production
222 characterized by large interannual variation and synchrony of seed production [16, 22, 63].
223 Beech masting allows to escape seed predation and increases pollination efficiency [59,
224 63]. Subsequent cold (two years before seed fall) and hot (one year before seed fall) sum-
225 mers trigger large seed production in European beech [33, 43].

226 **Seed production and environmental data** Annual observations of seed production of
227 European beech were extracted from MASTREE+, an open-access database of annual
228 records of population-level reproductive effort [64]. For our analysis, we restricted the Eu-
229 ropean beech time series to the continuous observations of seed production that covered
230 more than 14 years, observed after 1952. We excluded pollen-based and ordinal records.
231 We used a conservative, relatively high number of years per time series, to ensure that

232 enough mast years had a chance to happen and optimize the signal-to-noise ratio. The
 233 cut-off in 1952 was motivated by limited climatic data availability before that year. That re-
 234 sulted in 61 time series available for the analysis (averaged length time series, 35 years;
 235 maximum length time series, 68 years). The number of years per time series is given in
 236 Fig. S1. We extracted daily climate data for each site from the corresponding 0.1° grid cell
 237 of the E-OBS dataset [65].

238 The day length for each location was calculated as

$$\cos \omega_0 = -\tan\left(\frac{\phi \times \pi}{180}\right) \times \tan \delta \quad (1)$$

239 where ω_0 is the solar hour angle, ϕ is latitude and δ is declination. Declination of the sun
 240 can be obtained with

$$\delta = \frac{\pi \times 23.45}{180} \times \sin\left(\frac{2 \times \pi \times (284 + \text{DOY})}{365}\right) \quad (2)$$

241 where DOY is Day of the Year. Day length in hours was obtained with

$$\text{DL} = \begin{cases} 0 & \omega_0 > 1 \\ 24 & \omega_0 < -1 \\ \frac{24}{\pi \times \arccos(\omega_0)} & \text{otherwise} \end{cases} \quad (3)$$

242 For each site, the relative day length was normalized to the 0 - 1 range.

243 **Moving window correlation** To determine how correlations between mast seeding and
 244 temperature fluctuate at a fine temporal scale, we ran a moving window correlation analysis.
 245 Specifically, we ran a moving Spearman correlation between log-transformed annual seed
 246 production and mean daily temperature. The window size was set as 7 days, with a 1-day
 247 step. The moving window size was set relatively small to ensure the detection of fine-
 248 scale temporal changes in the correlation between masting and temperature. Correlations
 249 were run over year T2 (two years before seed fall) and T1 (one year before seed fall), as
 250 we expected the June-July summer cues [33, 43] to be fine-tuned to the summer solstice.
 251 Moving window correlations were run for each site separately. We computed the standard
 252 error of the Spearman correlation (cor_{se}) as

$$\text{cor}_{\text{se}} = \sqrt{(1 - \text{cor}^2)^2 \times \frac{(1 + \text{cor}^2/2)}{(n - 3)}} \quad (4)$$

253 with cor being the estimated Spearman correlation value and n the sample size [66].

254 **Cue window and the solstice**

255 To test whether the change in Spearman correlations be-
256 tween masting and temperature changes abruptly at solstice we used generalized additive
257 models (GAM). We included the correlation coefficients as a response, while the relative day
258 length, the summer solstice as a categorical variable (before or after the solstice), and their
259 interaction were used as predictors. If the cue window opens at the solstice, we expected
260 the interaction to be significant, with the correlation abruptly increasing at the solstice. We
261 fitted GAMs with a beta distribution family, by using the `mgcv` package (v1.8-42, [67]), and
262 specified the restricted maximum likelihood (REML) method to estimate smoothing param-
263 eters. We fitted models using the beta distribution because fitting a model with a Gaussian
264 distribution of errors, given our response type, would have been inappropriate and result
265 in biased parameter estimates. Because the beta distribution requires the response to be
266 bounded between 0 and 1, we rescaled the Spearman correlations to 0-1 range. The scal-
267 ing was done for each site separately and is a simple mathematical transformation that does
268 not affect the distribution of a variable. We used the inverse of the standard error of corre-
269 lation coefficients (i.e. $1/\text{cor}_{se}$) as weights in the GAM models, to ensure that observations
270 with higher error had lower weight on parameter estimates [68]. The site was included as a
271 random intercept. We tested for spatial autocorrelation of model residuals using the `DHARMA`
272 package (v0.4.6) [69], and detected none. The test was run separately for correlations in
273 one (T1) and two (T2) years before seed fall.

274 As an additional test, we also binned the moving window correlations between masting
275 and temperature changes into two categories, i.e. before and after the solstice. For each
276 bin, we used a number of days that included 5% of change in day length at each side of
277 the solstice (24 days). We tested for the difference between the period (i.e. before/after the
278 solstice) using the GAM model with correlations in these bins as a response, while including
279 group (before/after the solstice) as a predictor fitted as a parametric term.

280 Furthermore, we used a null model to explicitly test whether the observed increase in the
281 values of correlation coefficients between masting and temperature just after solstice could
282 emerge by chance also if any other day of the year was considered instead of the solstice.
283 For each day of the year between 25th January and 6th December we compared correlation
284 coefficients for 24 days before and 24 days after that day using analogous GAM models as
285 described above. From these models, we extracted the beta coefficients for the “after”
286 category, showing how correlation coefficients differ as compared to the “before” category.
287 This procedure resulted in a distribution of beta coefficients under the null hypothesis i.e.
288 the before-after difference in correlation coefficients if any other day of the year would have
289 been considered instead of the solstice. Then, to test for the significance of the solstice
290 effect (i.e. whether the increase in the values of correlation coefficients we observed at the
291 solstice is more probable than given purely by chance), we calculated the p-value as the
292 number of times an absolute value of randomized beta coefficients was greater than, or
293 equal to, the absolute value of a beta coefficient from GAM model comparing correlations
binned around the solstice, divided by the number of tests.

294 **Data availability statement**

295 The data used in this study have been deposited in the Open Science Framework (OSF)
296 (DOI: [10.17605/OSF.IO/S2CD4](https://doi.org/10.17605/OSF.IO/S2CD4)). The full MASTREE+ dataset is available in [64]. Cli-
297 mate data have been extracted from E-OBS at [https://cds.climate.copernicus.eu/
298 cdsapp#!/dataset/insitu-gridded-observations-europe?tab=form](https://cds.climate.copernicus.eu/cdsapp#!/dataset/insitu-gridded-observations-europe?tab=form).

299
300 **Code availability statement**

301 R statistical software v4.3.0 was used in this work [70]. All analyses used published R pack-
302 ages.

303

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313

314 **Author Contributions Statement**

315 MB conceived the study, MB, VJ, JSz, JF, AHP, DK designed the study. VJ and JSz per-
316 formed the analysis, MB led the writing of the manuscript. All authors contributed critically
317 to the interpretation of the analysis and drafts, and gave final approval for publication.

318

319 **Competing Interests Statement**

320 None declared.

321

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Figure Captions

Figure 1: Studied populations, their masting synchrony, and response to temperature coordinated by the solstice. a) Locations of the 61 time series of annual seed production of European beech used in the study (average N years per series = 38). The yellow area highlights the species range (based on EUFORGEN, [71]). b) Spatial correlation between seed production over years and sites. The orange line represents the non-parametric spatial covariance function, with the shaded area showing 95% bootstrap confidence envelope. Hexes are pairwise Spearman correlations between sites, with the hex color scaled to the number of observations within each hex. Pairwise correlations were calculated for series with at least 5 years of overlap, that we deemed a minimum number of observations to calculate a correlation. c) Mean rolling Spearman correlation between temperature and masting averaged across all 61 sites. The graph shows correlations in two (T2) and one (T1) years before seed production, up until September when seed fall happens. The size of the temperature window is 7 days, with a 1-day step, and correlations are plotted according to the day of the year at the end of each 7-day window. Black dashed lines close to the sun icon indicate the summer solstice (21st June). Correlations are coded blue for positive, and red for negative. The black solid lines represent the standard error of the correlation coefficients across the sites for each window. Correlation for each site separately is reported in Fig S1.

Figure 2: Summer solstice as a celestial "starting gun". a) Correlations between European beech seed production and temperature at 7-day windows abruptly increase just after the summer solstice. The prediction lines and associated 95% confidence intervals are based on the GAM model with Spearman correlation coefficients as a response and interaction between relative day length (at the particular time window) and the time of the year (before vs. after the summer solstice (as a categorical variable) as predictors. Each point is the per site (N =61) per window correlation coefficient. b) Correlations shown at before and after the solstice shown at a) binned into 0.95 - 1 (max) day length before and after the solstice to help visualize abrupt change at the same day length at the two sides of the solstice. The asterisks (***) indicate a significant ($p < 0.0001$) difference between bins tested with GAM (see Methods). Box plots show medians (internal lines) and first and third quartiles (lower and upper hinges, respectively); whiskers show 1.5 times the interquartile range from the respective hinge and the points are outliers. c) Results of a null model testing whether the abrupt increase in the correlation coefficients (between masting and summer temperatures) is highest at the summer solstice or any other day in the year. Histogram shows the distribution of beta coefficients under the null hypothesis i.e. the before-after difference in correlation coefficients in any other day of the year considered instead of the solstice. The red dashed line shows the observed effect i.e., how correlation coefficients "after solstice" differ as compared to "before solstice". The null model was rejected ($p = 0.02$; the randomization procedure is described in Methods). All three graphs show the effects for summer T1 (one year before seedfall), effects for summer T2 are presented in Fig. S2 .