

Mechanisms driving interspecific variation in regional synchrony of trees reproduction

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Data availability statement

The data supporting the results are archived and accessible at DOI: 10.17605/OSF.IO/27YUG.

Authorship statement

All authors designed the study. JSz, AHP, VJ analysed the data. MB drafted the manuscript. All authors contributed critically to the interpretation of the results and text revisions.

28 Summary

29 Seed production in many plants is characterized by large interannual variation, which is synchro-
30 nized at subcontinental scales in some species but restricted to local scales in others. The extent
31 of reproductive synchrony affects animal migrations, trophic responses to resource pulses, and
32 the planning of management and conservation. Spatial synchrony of reproduction is typically
33 attributed to the Moran effect, but this alone is unable to explain interspecific differences in syn-
34 chrony. We show that interspecific differences in the conservation of seed production-weather
35 relationships combine with the Moran effect to explain variation in reproductive synchrony.
36 Conservative timing of weather cues that trigger masting allows populations to be synchronized
37 at distances > 1000km. Conversely, if populations respond to variable weather signals, syn-
38 chrony cannot be achieved. Our study shows that species vary in the extent to which their weather
39 cueing is spatiotemporally conserved, with important consequences, including an interspecific
40 variation of masting vulnerability to climate change.

42 Introduction

43 Populations fluctuate in synchrony over large areas, which affects regional ecosystem functioning
44 (Bjørnstad *et al.*, 2002; Ostfeld & Keesing, 2000; Earn *et al.*, 2000; Liebhold *et al.*, 2004).
45 One ecological phenomenon often associated with subcontinental spatial synchrony is seed
46 production in perennial plants, especially those that mast (LaMontagne *et al.*, 2020; Koenig
47 & Knops, 2000). Masting is synchronous and interannually variable seed production by a
48 population of perennial plants (Kelly, 1994; Pesendorfer *et al.*, 2021). The variable allocation
49 of resources associated with masting affects plant growth, population dynamics of plants and
50 animals, carbon stocks, and disease risk (Clark *et al.*, 2019; Lauder *et al.*, 2019; Pearse *et al.*,
51 2021; Bregnard *et al.*, 2021). Synchrony in seed production can extend between populations,
52 in some cases to subcontinental scales (LaMontagne *et al.*, 2020; Bogdziewicz *et al.*, 2021a).
53 However, large interspecific differences exist. In some species masting synchrony extends
54 across entire ranges (>1500 km), but in others synchrony is local (<100 km) (Koenig & Knops,
55 2000; Suzuki *et al.*, 2005; Masaki *et al.*, 2020). While the among-species variation in regional
56 seed production synchrony is well evidenced (Fig. 1), the mechanisms behind these differ-
57 ences remain unknown. Yet, the variation in synchrony is important as it affects the spatial
58 scale of population outbreaks and collapses (Curran & Webb, 2000; Ostfeld & Keesing, 2000),
59 animal migrations (Zuckerberg *et al.*, 2020), enhances gene flow promoting adaptation (Kremer
60 *et al.*, 2012; Dale *et al.*, 2021), affects regional forecasting of risk from Lyme disease and
61 hantavirus by rodents dependent on mast (Bregnard *et al.*, 2021; Rubel & Brugger, 2021), and
62 the planning of management and conservation in forests (Pearse *et al.*, 2021). Our study presents
63 new mechanisms responsible for interspecific differences in the extent of spatial synchrony in
64 masting.

65 The current consensus is that the driver of the regional synchrony of masting is the Moran
66 effect, i.e. spatial synchrony results from environmental entrainment (Haynes *et al.*, 2013; Ascoli
67 *et al.*, 2017; Koenig & Knops, 2013; Wion *et al.*, 2020). Specifically, annual reproductive in-
68 vestment is regulated by weather cues which plants use to maintain synchronous variation in
69 reproduction within populations (Kelly *et al.*, 2013). The mechanisms underpinning the cues
70 vary between species, but examples include temperature-related regulation of flowering effort
71 and weather-dependent pollination success during flowering (Smaill *et al.*, 2011; Koenig *et al.*,
72 2015). The spatial synchrony of reproductive effort then results from the spatial synchrony

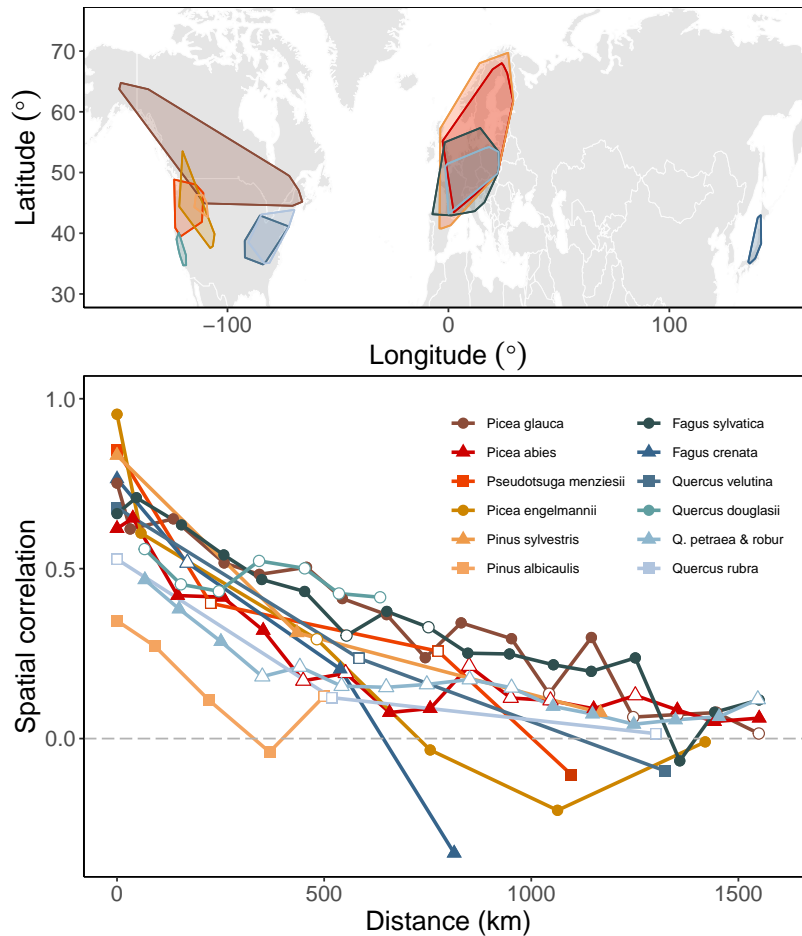


Figure 1: Interspecific variation in regional synchrony of seed production in the northern hemisphere. Polygons at a) are drawn based on the spatial distribution of the seed production data for each species; color codes shown on b). Lines at b) are Mantel correlograms for each species. Full shapes indicate significant Mantel correlations. **This figure is intended to present among species variation in the spatial synchrony of masting, and is not part of the analysis of the current study.** A subset of species with the highest spatiotemporal resolution of seed production data was selected for further analysis (see Methods). Data derived from MASTREE+.

73 of these weather cues (the Moran effect), and the spatial decay in masting synchrony often
 74 parallels the spatial decay in synchrony of its cues (Koenig & Knops, 2013; LaMontagne *et al.*,
 75 2020; Bogdziewicz *et al.*, 2021a; Wion *et al.*, 2020). **Another potential driver of synchrony in**
 76 **masting is pollen coupling, but it does not appear to play a major role as a driver of regional**
 77 **(among-populations) masting synchrony** (Koenig & Knops, 2013; Bogdziewicz *et al.*, 2021a;
 78 Wion *et al.*, 2020; LaMontagne *et al.*, 2020). The extent of regional synchrony in reproduction
 79 varies greatly among species, and this interspecific variation remains unexplained. For example,
 80 the spatial synchrony of seed production in *Fagus sylvatica* and *Picea glauca* shows spatial
 81 decay that parallels spatial decay in synchrony of summer temperatures at distances up to 1500
 82 km (LaMontagne *et al.*, 2020; Bogdziewicz *et al.*, 2021a; Vacchiano *et al.*, 2017). In contrast,
 83 in other, often sympatric species such as oaks *Quercus petraea*, seed production synchrony can
 84 disappear at distances less than 400 km (Bogdziewicz *et al.*, 2019; Fernández-Martínez *et al.*,
 85 2017). If the regional synchrony of weather conditions is largely similar, then what drives the
 86 interspecific variation in the spatial synchrony of seed production?

87 We propose that the spatiotemporal variation in weather cues that determine annual repro-

88 ductive investment across populations drives the interspecific differences in regional synchrony
89 of masting. Our logic has the following steps. First, the Moran effect drives the regional syn-
90 chrony of masting (Vacchiano *et al.*, 2017; LaMontagne *et al.*, 2020). Second, species differ in
91 the spatiotemporal variation of seed production-weather relationships. A recent study detected
92 remarkable stability of the temporal window when beech trees are sensitive to cues that trigger
93 reproduction (Bogdziewicz *et al.*, 2021b). Despite great differences in climate among sites
94 (mean summer temperatures range: 13.84 – 15.77 °C), and a significant warming trend (1°C
95 over 40 years) the timing when beech trees were responding to weather cues was generally
96 consistent across populations and decades (Bogdziewicz *et al.*, 2021b). We suggest that the
97 conserved temporal window when populations of beech sense the environment to determine
98 the extent of annual reproduction allows distant populations to remain highly synchronous. In
99 species with lower regional synchrony, the timing of when trees are sensitive to environmental
100 signals will change among populations. For example, the temporal window of the weather cue
101 may shift towards earlier in the year in warmer climates, similar to the advance in bud break
102 or flowering with warming (Fu *et al.*, 2015; Zohner *et al.*, 2016). Due to the temporal vari-
103 ation that we hypothesize exists in such species, the regional synchrony deteriorates, because
104 the temperature is well correlated in space but less so in time. For example, across a region,
105 unusually hot temperatures in March can trigger masting in populations that are sensing cues
106 at that time. Simultaneously, low temperatures in April will translate to small seed production
107 in populations whose sensitive period was delayed to that month, creating asynchrony among
108 those populations.

109 To test our theory, we used beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), and
110 oaks (*Quercus robur* and *Q. petraea*). We first examined the extent of regional synchrony of
111 masting and the synchrony of weather cues previously recognized to be important for these
112 focal species, i.e. temperature in summer in beech and spruce, and temperature in spring for
113 oaks (Vacchiano *et al.*, 2017; Caignard *et al.*, 2017; Moreira *et al.*, 2021). We predicted that
114 regional synchrony of temperature in all populations should be similarly high (Koenig & Knops,
115 2013). Masting synchrony should be high in beech (Bogdziewicz *et al.*, 2021a), and lower in
116 oaks (Bogdziewicz *et al.*, 2019; Fernández-Martínez *et al.*, 2017), and remains to be determined
117 in Norway spruce. We explored the spatiotemporal stability of the weather-seed production
118 relationships by searching for the periods when the correlation between seed production and
119 temperature was the highest. According to our theory, the period should be relatively stable
120 across populations in beech, but not in oaks. In Norway spruce, the spatiotemporal conservation
121 of the weather-seed production relationships should be either high (if regional masting synchrony
122 is high) or low (if regional masting synchrony is low). In the final step, we estimated the spatial
123 synchrony of the cues actually used by each population, i.e., the synchrony of the weather-
124 sensitive period revealed for each population in our moving window correlation analysis. That
125 temporally-adjusted synchrony of weather should reassemble the synchrony of seed production
126 across species, which should be especially relevant for less synchronous species like oaks. **By
127 uncovering the spatiotemporal variation in weather cueing and its role in creating regional mast-
128 ing synchrony, our study adds a key new brick to our understanding of proximate mechanisms
129 of mast seeding.**

130 **Material and Methods**

131 **Data**

132 **Seed production data: MASTREE+** We extracted data from the MASTREE+, a database of
133 annual variation in plant reproductive effort from six continents. **A key step of our analysis is**

134 data-hungry, as it requires long, temporally overlapping time series that do not include missing
 135 values. We, therefore, limited the analysis to species for which appropriate data were available:
 136 European beech (*Fagus sylvatica*), common oak (*Quercus robur*), sessile oak (*Q. petraea*) and
 137 Norway spruce (*Picea abies*) (Fig.2). We pooled acorn production data for (*Q. robur* and *Q.*
 138 *petraea*) and analyzed the data on *Quercus* at the community level. We pooled them because, for
 139 a number of populations, the specific oak species was not reported. Both species have similar
 140 biology and ecology, seed production is expected to be correlated with spring temperatures, and
 141 their seed production in our data was highly correlated (sympatric populations synchrony: $r =$
 142 0.77). Separating the two oak species provides qualitatively the same results (Table S4).

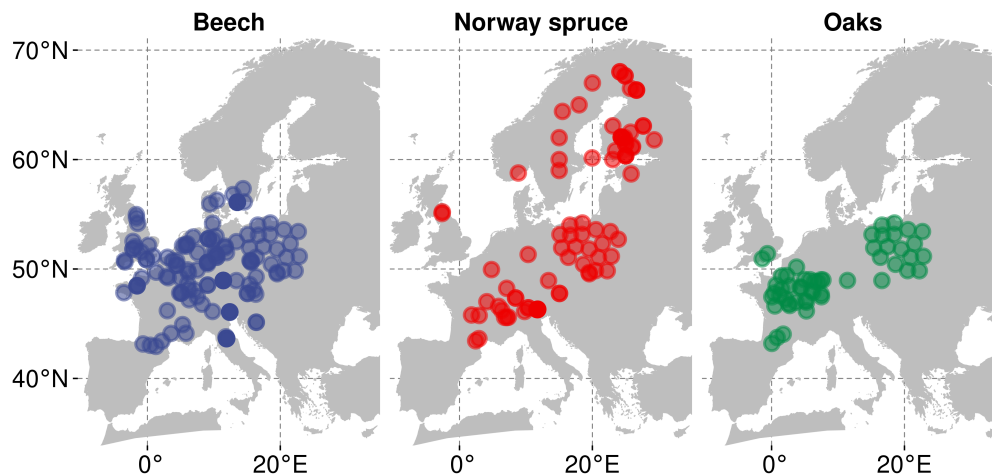


Figure 2: Sites location for beech, Norway spruce, and oaks from MASTREE+. A subset of that data was used in the moving window analysis (see Figure S1).

143 When characterizing the scale of synchrony in seed production, we used time series from
 144 the period 1954-2020 (beech) or 1954-2019 (oaks and spruce), while for all other analyses we
 145 used time series limited to 10-years (1995-2004) that included continuous, overlapping data
 146 records that provided highest possible spatial coverage. We used records of reproductive output
 147 measured on a continuous scale and excluded records of annual flower or pollen production,
 148 or tree-ring-based mast year reconstructions. The data used in this study are summarised in
 149 Table S1, and presented in Fig.2 and Fig.S1.

150 **Weather data** Daily weather data for each site were obtained from the corresponding 0.1°
 151 grid cell of the E-OBS dataset (Cornes *et al.*, 2018).

152 Analysis

153 **Regional synchrony and its drivers** We started by characterizing the scale of regional syn-
 154 chrony in our populations with Mantel correlograms. That procedure was repeated for seed
 155 production and for the weather cues previously reported to be the main seed production drivers
 156 in each species, i.e. summer (June-July) mean max temperature for beech (Piovesan & Adams,
 157 2011; Vacchiano *et al.*, 2017), mean July temperature in Norway spruce (Moreira *et al.*, 2021),
 158 and mean April temperature in oaks (Caignard *et al.*, 2017).

159 To test the role of weather variation in driving the spatial synchrony of masting, we used the
 160 Multiple Regression Quadratic Assignment Procedure with Double-Semi-Partialing (MRQAP)

161 (Dekker *et al.*, 2007). The MRQAP is a modeling framework that allows investigation of the
162 relationship between a dependent matrix and independent matrices while considering the non-
163 independence of relational data by using permutation techniques to test the significance of effect
164 sizes (Dekker *et al.*, 2007). We first created relatedness matrices where the elements were the
165 synchrony in seed production and weather and spatial distance for all pair-wise combinations of
166 locations. Synchrony in seed production and weather was calculated as the Spearman pairwise
167 correlation coefficients for all time series with at least 5 years of overlap. Spatial distance
168 values were calculated as the geodesic distance between all sites on a WGS84 ellipsoid. Next,
169 we investigated the roles of environmental factors in driving spatial synchrony by fitting a
170 separate MRQAP model for each species where explanatory matrices were spatial proximity
171 and synchrony in weather cues. The models were fitted using the *asnipe* R package and statistical
172 significance was assessed based on t-statistics and 1000 permutations (Farine, 2013).

173 **Spatiotemporal stability of weather cues: moving window correlations** We explored the
174 spatiotemporal stability of the weather-seed production relationships using a moving-window
175 approach. For each site-species, we tested seed production–weather relationships by calculating
176 correlations between seed production and the focal weather cue in 60-day (beech) or 30-day
177 (Norway spruce, oaks) windows for one and two years prior to the year of seed production
178 (beech, Norway spruce), or the year of seed production (oaks). Timing of cues followed well-
179 established literature on the subject (Piovesan & Adams, 2011; Vacchiano *et al.*, 2017; Caignard
180 *et al.*, 2017; Zamorano *et al.*, 2018; Moreira *et al.*, 2021). We constructed an algorithm that
181 slides a moving window through the daily climate data, calculating the mean of the 30 or 60
182 daily observations. The function then calculated the correlation between the calculated mean
183 temperature at the window and the seed production at daily time steps. This method allowed
184 us to investigate the seasonal peaks in the relationships between seed production and seasonal
185 weather cues without being constrained by the timing of calendar months (i.e. monthly climate
186 data). This approach was designed to explore whether the weather cue of masting was shifting
187 over time and space.

188 **Spatiotemporal variability of weather cues and regional synchrony** To test if the spatiotem-
189 poral variability in the weather cues described for each species in the previous step is responsible
190 for interspecific variation in regional synchrony, we re-run the MRQAP models. Here, we re-
191 placed the matrices of weather synchrony calculated on weather anchored to a species-specific
192 calendar month with the population-specific cue revealed in the moving window correlations
193 analysis.

194 Results

195 The extent of regional masting synchrony clearly differed among the studied species. The spatial
196 synchrony was highest in beech (mean pairwise Spearman rank correlation and 95% CI: 0.33,
197 0.32 – 0.34) and noticeably lower in Norway spruce (0.21, 0.19 – 0.23) and oaks (0.20, 0.18 –
198 0.22) (Fig. 3). At the same time, spatial synchrony of the weather cues, i.e. of summer (in the
199 case of beech and spruce) and spring (oaks) temperatures, was uniformly high and similar in all
200 species (Fig. 3). Synchrony decreased with distance among sites. In all species, the MRQAP
201 indicated that the spatial synchrony in masting is higher among sites for which weather variation
202 is more synchronous (Table S2).

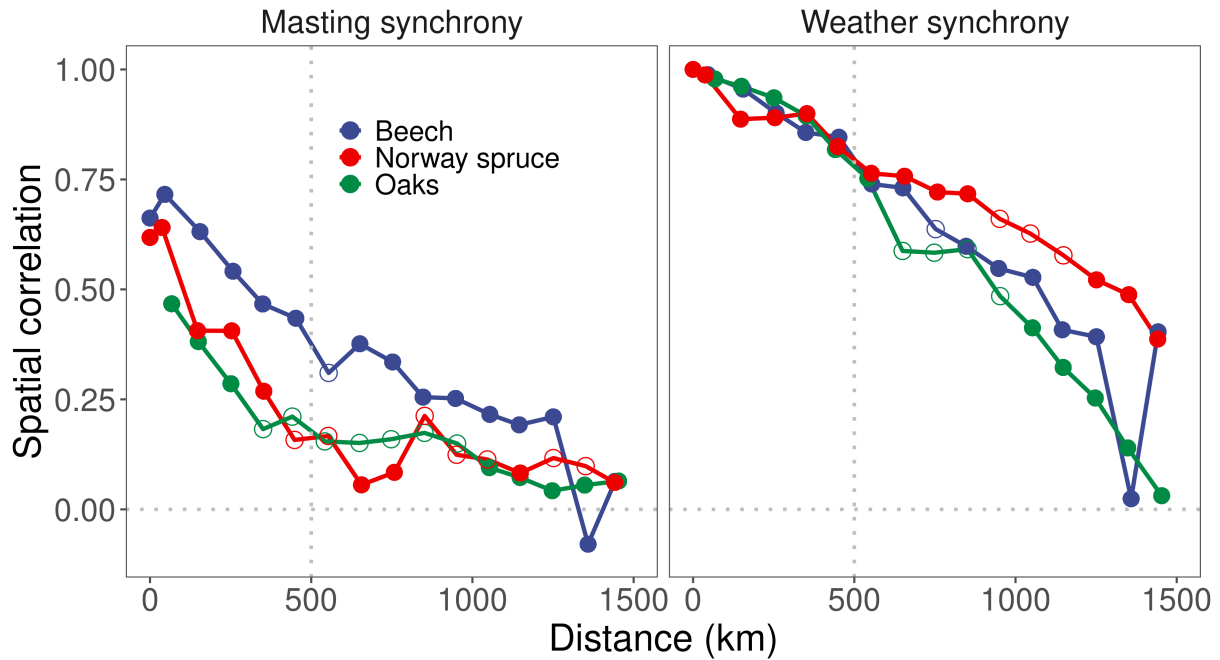


Figure 3: Spatial correlation in seed production and weather. Lines are Mantel correlograms for each species. Full circles indicate significant Mantel correlations. The vertical line highlights the difference in seed production (or lack of it in case of weather) synchrony at 500 km. The weather synchrony is summer (June-July) mean max temperature in beech, mean July temperature in Norway spruce, and mean April temperature for oaks. The time series are from the period 1954-2020 (beech) or 1954-2019 (oaks and spruce), sample size provided in Table S1. Mantel correlograms were cut at 1500 km due to a limited sample size above that distance.

203 Moving window correlations indicated differences in spatiotemporal conservation of seed
 204 production - weather relationships among species. In accordance with our predictions, seasonal
 205 peaks in relationships between seed production and seasonal weather cues were conserved in
 206 beech (Fig. 4). Despite $>10^\circ$ latitudinal difference in locations among beech populations
 207 that translated into $>10^\circ$ C difference in mean annual temperatures (Fig. S3), the strongest
 208 relationships between seed production and seasonal weather cues occurred in the June-July
 209 period at the majority of sites. The stability was especially clear for the negative correlation
 210 with June-July temperature in year T-2. In contrast, seasonal peaks in relationships between
 211 seed production and seasonal weather cues were less conserved in oaks and Norway spruce
 212 (Fig. 4). Consistent timing of cue was generally absent in oaks, with populations responding
 213 to winter, spring, and summer temperatures, depending on the location (Fig. 4). In Norway
 214 spruce, several populations responded consistently to temperatures in June-July (year T-1),
 215 although for a number of populations the strongest signal occurred in spring or autumn (Fig. 4).
 216 Within species, the variation in climate among sites did not correlate with the timing of in seed
 217 production - weather relationships (Table S3).

218 In the final step of our analysis, we re-run the MRQAP models using temporally-adjusted
 219 weather synchrony matrices. The goal of that analysis was to test whether adjusting for among-
 220 site temporal differences in cues can help explain the interspecific differences in regional syn-
 221 chrony among species. The temporal adjusting improved model fit for all species, with clear
 222 interspecific differences. In beech, temporal adjusting of the cue had a small impact on the
 223 proportion of the variance in regional masting synchrony explained by weather synchrony (by a
 224 factor of 1.25; Table 1). The improvement was clearly higher in spruce (by a factor of 1.9), and

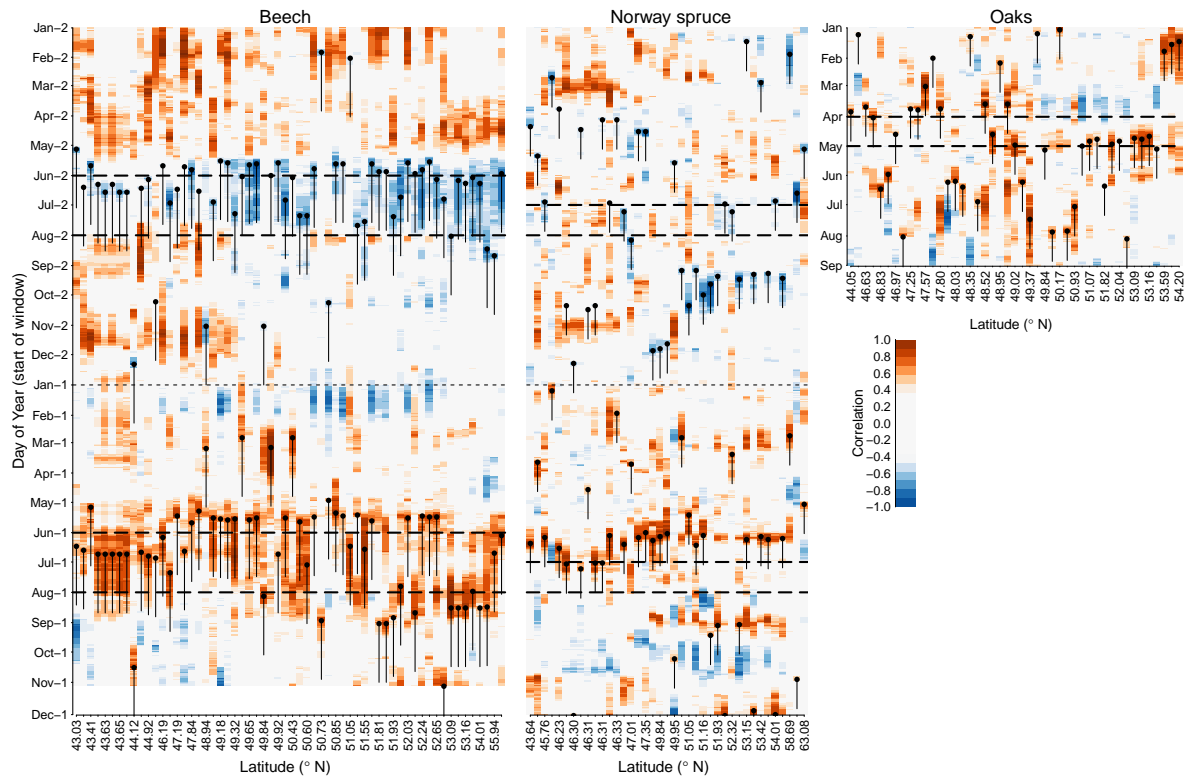


Figure 4: Spatiotemporal variation in seed production – weather cues correlations. Correlations are reported as the start DOY for the seasonal cues (y-axis) either T -2 and T-1 (beech and Norway spruce) or T (oaks) years before seed production, and the site location ordered by latitude (x-axis). The band highlighted by horizontal dashed lines in the figures indicates the 60- (beech, June-July) or 30- (Norway spruce; June, oak; April) day window of fixed weather cues. The strongest correlations as indicated by sliding windows are highlighted with vertical lines (vertical line length matches the length of the time window).

225 improved dramatically, i.e. by a factor of ten, in oaks (Table 1). Once the synchrony of weather
 226 was adjusted temporally, its spatial decay reassembled the spatial decay of masting synchrony,
 227 which was strikingly clear in oaks (Fig. 5, Fig. S2).

228 Discussion

229 Spatiotemporal conservation of the seed production - weather relationships explains interspecific
 230 variation in the extent of regional synchrony of mast seeding. Regional synchrony of masting
 231 in beech was about 1.5 higher compared to other studied species. At the same time, beech
 232 was characterized by remarkably conservative timing of weather cues. Despite large spatial and
 233 climatic distances among studied populations, the strongest correlation between seed production
 234 and temperature in beech populations consistently occurred in the same summer months. In
 235 turn, regional synchrony of masting was limited in oaks and Norway spruce. Oaks and spruce
 236 lack conservative timing in seed production - weather relationships across populations. Our
 237 study offers three major and novel results. First, large variation in the timing of weather cues
 238 exists in masting trees and offers solutions to long-standing questions in the discipline. Second,
 239 species vary in the extent to which their weather cueing is conserved in time and space, with
 240 consequences that may reach beyond those described here, including an interspecific variation
 241 of masting vulnerability to climate change. Third, the spatiotemporal stability of weather cueing

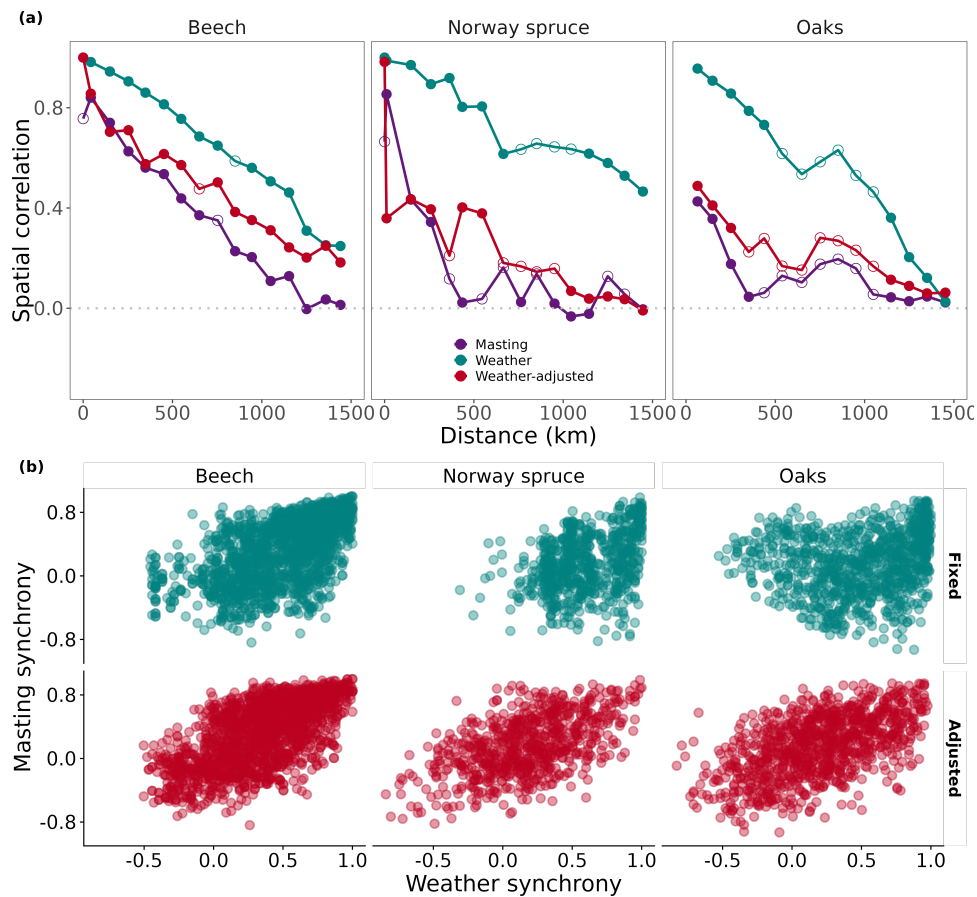


Figure 5: Relationship between weather synchrony and masting (seed production) synchrony in beech, Norway spruce, and oaks. Points show pairwise synchrony between populations, with weather synchrony calculated in either fixed time windows or temporally-adjusted time windows as revealed by moving windows analysis (Fig. 4). That analysis was run on a dataset limited to time series with 10 years of overlapping, continuous data records (see Methods). An alternative version of this Figure, with Mantel correlograms, is shown in Fig. S2.

242 is a major mechanism determining the regional synchrony of masting.

243 A key question is whether a factor exists that would allow predicting which species have
 244 stable spatiotemporal weather cueing. At least two, mutually non-exclusive, hypotheses can be
 245 formulated. First, plant phenology, such as the timing of leaf out or flowering, is determined
 246 by two major cues: temperature and photoperiod (Flynn & Wolkovich, 2018; Fu *et al.*, 2019).
 247 Species differ in their sensitivity to these cues (Körner & Basler, 2010; Flynn & Wolkovich,
 248 2018). For example, beech is highly photoperiod sensitive (Vitasse & Basler, 2013), while
 249 Norway spruce and oaks are less so (Zohner & Renner, 2015); experimental short-day conditions
 250 delayed budburst in beech for 41 days, while had no impact on budburst in Norway spruce
 251 (Zohner & Renner, 2015). In another experiment, common oak leaf-out phenology showed
 252 low sensitivity to photoperiod, compared to high sensitivity in beech (Laube *et al.*, 2014;
 253 Zohner *et al.*, 2016). Experiments in the mast-seeding grass *Chionochloa rigida* indicated that
 254 promotion of flowering by high temperatures occurred only on long days (>14 h) (Mark, 1965).
 255 Thus, the timing of masting cues in some species may be linked to certain photoperiod lengths,
 256 limiting the regional variation in cue timing. In that context, studies exploring the phenology of
 257 hormone secretion that are responsible for floral initiation and its dependency on photoperiod
 258 appear an important avenue for future research (Satake & Kelly, 2021).

259 The weather cues' effects on seed production could be also spatiotemporally consistent

Table 1: Proportion of variance in regional masting synchrony explained by the MRQAP models that included weather synchrony matrix as explanatory variables. In the uncorrected model, the weather synchrony matrix includes temperatures from the same time window across sites (e.g. June-July temperature in beech, see Methods). In the corrected model, we used the seasonal peaks in relationships between seed production and weather cues, identified for each site-species with moving windows correlations. That analysis was run on a dataset limited to time series with 10 years of overlapping, continuous data records (see Methods).

Species	Uncorrected model	Temporally-corrected model	R2 improvement
Beech	32%	40%	1.25
Oaks	3%	31%	10.33
Norway spruce	20%	38%	1.9

among populations in species in which one factor dominates the determination of seed production (Bogdziewicz *et al.*, 2019; Koenig *et al.*, 2020). In beech, that major factor could be flowering extent determined by temperatures during secretion of flowering hormones (Vacchiano *et al.*, 2017; Satake *et al.*, 2019). In other species, multiple factors can have similarly important effects on seed production, including winter temperatures that determine resource levels (Wu *et al.*, 2019; Harvey *et al.*, 2020), spring temperatures that determine pollination efficiency (Koenig *et al.*, 2015; Schermer *et al.*, 2019), and summer temperatures that determine seed abortion (Pérez-Ramos *et al.*, 2010; Girard *et al.*, 2012). Such species can lack a consistent dominant weather cue across the entire range; the dominant, population-specific weather cue will be determined by local conditions. Past studies suggested that for oaks, spring-temperature effects on pollination are more important in moist habitats, while drought-driven acorn abortion is more important in arid habitats (Bogdziewicz *et al.*, 2017; Nussbaumer *et al.*, 2021). Thus, two mechanisms may be at work: stable phenology of the same weather cue (e.g. beech) and varying dominance of different weather cues depending on local conditions (e.g. oaks).

Our study recognizes that limiting weather cues to species-specific time windows is oversimplistic, especially in the category of species to which oaks and Norway spruce fell in our study. The important role of weather variation in driving seed production in masting plants is widely recognized (Pearse *et al.*, 2016). Early studies in that subject were characterized by the wide search for correlates, with mechanisms often assigned post-hoc, resulting in incremental progress (Crone & Rapp, 2014). However, recent years brought important progress in the understanding of the mechanistic links between weather variation and seed production (Pesendorfer *et al.*, 2016; Samarth *et al.*, 2021). Oaks are a notable example. Effects of spring temperatures on acorn production arise through variation in weather-driven synchrony of flowering among trees that determines pollination efficiency (Schermer *et al.*, 2020; Pearse *et al.*, 2015; Koenig *et al.*, 2015). Yet, even in this well-studied species, the driver of the flowering synchrony is still disputed (Bogdziewicz *et al.*, 2020b; Koenig *et al.*, 2015). According to the photoperiod-sensitivity hypothesis, the period when the temperature is important can be months before flowering occurs (Bogdziewicz *et al.*, 2020b), while the temperature during flowering is important according to the micro-climatic hypothesis (Koenig *et al.*, 2015). As the flowering period can move by itself several weeks among years (Zohner *et al.*, 2018), it is perhaps unsurprising that anchoring the weather cue to a specific calendar period is overly coarse. In fact, our results imply that the seeding-weather relationships can be even more complicated. Seed production in some oak populations was not primarily driven by spring temperatures, as predicted by the phenological synchrony hypothesis (Koenig *et al.*, 2015), but by winter or summer temperatures. The variation

294 in the timing of the signal lacked a clear climatic pattern. Perhaps site characteristics, such as
295 soil conditions, density, or stand age, that affect reproductive investment (Journé *et al.*, 2022;
296 Pesendorfer *et al.*, 2020; Qiu *et al.*, 2022), would help to structure the variation in the timing
297 of strongest weather cues among populations. **The mechanisms described here provide a sub-**
298 **stantial improvement in our understanding of proximate mechanisms driving regional masting**
299 **synchrony, but substantial variation remains unexplained.** We now know that spatiotemporal
300 variation in weather cueing exists, and its extent is species-specific and ecologically important,
301 which opens new venues for future research.

302 The spatiotemporal variation in weather cueing we uncovered is likely to be important in
303 the global change ecology of tree reproduction. In European beech, global warming led to
304 a breakdown in interannual variation and synchrony of masting that translated into dramatic
305 increases in seed predation and pollination failure (Bogdziewicz *et al.*, 2020a). In these pop-
306 ulations, warming increased the frequency of summer weather cues. In consequence, trees'
307 responses to the weather cue weakened, and interannual variation and synchrony of seed pro-
308 duction declined (Bogdziewicz *et al.*, 2021b). From that perspective, the conservation of cues
309 may prove to be a major determinant of the species-specific masting responses to warming. On
310 one hand, the conservative cueing phenology in European beech prevented the species from
311 shifting the temperature-sensitive period to earlier in the year, which might otherwise have
312 enabled the species to compensate for the change in cueing frequency associated with warming
313 (Bogdziewicz *et al.*, 2021b). Other species that are similarly conservative in the weather cueing
314 may also be as vulnerable to warming-caused masting breakdown as beech. On the other hand,
315 unconservative species such as oaks could potentially shift the sensitive periods to compensate
316 for the eventual change in cueing frequency (Schermer *et al.*, 2020). Exploring that hypothesis
317 will require multidecadal-long series of reproduction monitoring that are increasingly available.

318 In summary, we found that the spatiotemporal stability of the seed production - weather
319 relationships is responsible for interspecific variation in the regional synchrony of mast seeding.
320 With that discovery in hand, we may now search for species traits that determine what makes
321 a species spatiotemporally stable or not in weather cueing. The ecological consequences of the
322 interspecific variation in regional synchrony of masting are diverse and potentially great. For
323 example, reforestation strategies widely planned to mitigate climate change (Walker *et al.*, 2022)
324 require a large seed supply that is difficult to meet, especially in masting species (Kettle *et al.*,
325 2010; Whittet *et al.*, 2016; Jalonen *et al.*, 2018). Species characterized by large-scale regional
326 synchrony will share nil seed production years over entire subcontinents, which requires planning
327 to stabilize the supply of seeds to nurseries (Kettle *et al.*, 2010). The good news here is that highly
328 synchronized beech reproduction consistently depends on clearly defined weather cues even in
329 distant populations. Therefore, masting forecasts that are based on weather variation might
330 be relatively easy to develop in such species (Pearse *et al.*, 2021; Chiavetta & Marzini, 2021).
331 However, in the case of species like oaks or spruce, weather-based forecasting will require the
332 identification of the population-specific weather drivers, a task that currently requires expensive
333 long-term monitoring of seed production.

334 **Acknowledgements**

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338 **Competing interests**

340 The authors declare no competing interests.

341

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534 **Supplementary material**

Table S1: Summary of dataset used in the study. *N for subset of data limited to timeseries with 10 years of continuous data overlap.

Species	N time-series	N time-series*
Beech	148	60
Oaks	53	45
Norway spruce	89	39

Table S2: Multiple Regression Quadratic Assignment Procedure (MRQAP) models summaries that regressed the matrices of masting synchrony against matrices of distance among sites and matrices of weather synchrony.

	Beech	Norway spruce	Oaks
Intercept	4.82e01; p < 0.001	2.91e-01; p < 0.001	1.14e-01; p = 0.18
Distance	-3.08e-07; p < 0.001	-1.59e-07; p < 0.001	-2.18e-08; p = 0.74
Weather synchrony	1.41e-01; p < 0.001	7.99e-02; p = 0.037	2.07e-01; p = 0.002

Table S3: Results of generalized additive models that regressed series-specific start of optimal time window (i.e., for which seed production-weather relationship peaks) against series-level long-term mean temperature and precipitation.

	Beech	Norway spruce	Oaks
Long-term mean temperature	6.257; p = 0.068	4.51; p = 0.315	1.00; p = 0.765
Long-term mean precipitation	2.268; p = 0.132	1.00; p = 0.559	1.00; p = 0.957

Table S4: Proportion of variance in regional masting synchrony explained by the MRQAP models that included weather synchrony matrix as explanatory variables. In the uncorrected model, the weather synchrony matrix includes temperatures from the same time window across sites (i.e. April temperatures). In the corrected model, we used the seasonal peaks in relationships between seed production and weather cues, identified for each site-species with moving windows correlations.

Species	Uncorrected model	Temporally-corrected model
Q. robur	12%	15%
Q. petraea	3%	32%

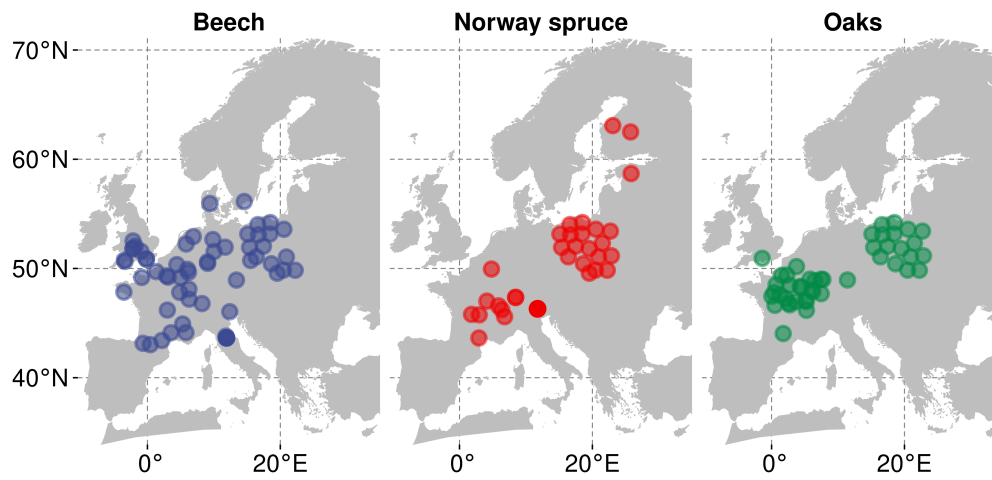


Figure S1: Sites location for beech, Norway spruce and oaks from MASTREE+ limited to sites with 10 years of overlapping, continuous data records used for moving window correlation analysis.

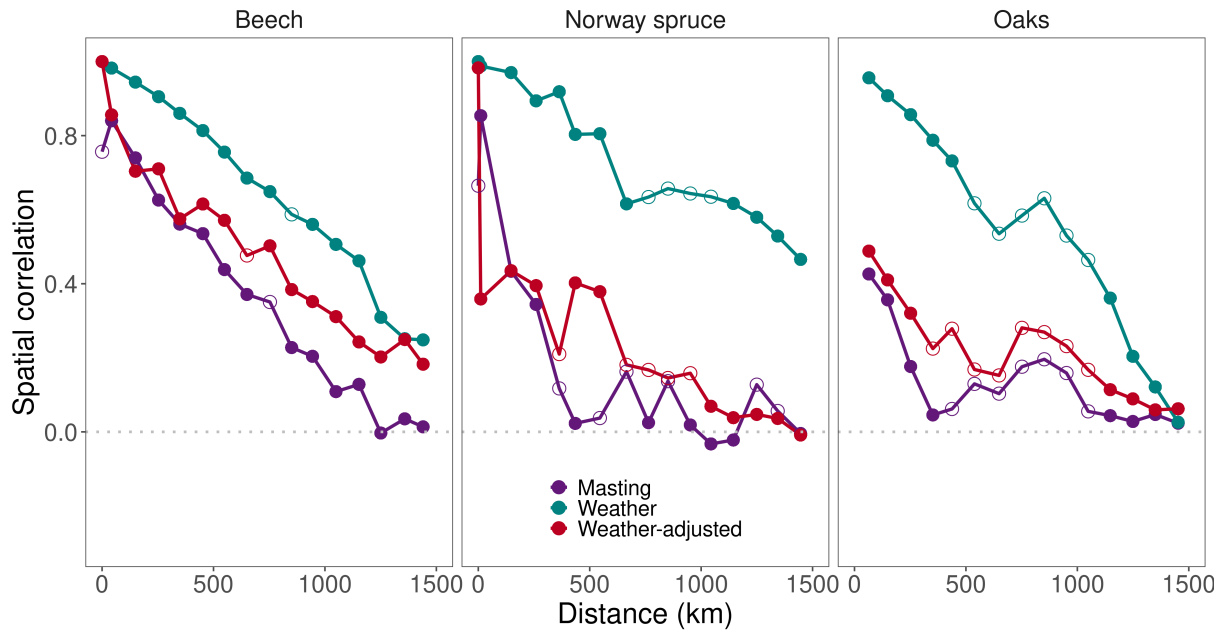


Figure S2: Spatial correlation in masting, weather, and temporally-adjusted weather patterns. **The temporally-adjusted weather patterns show spatial synchrony of weather cues that appear actually used by trees as revealed by our moving windows analysis** (Fig. 4). Lines are Mantel correlograms for each species. Full circles indicate significant Mantel correlations. That analysis was run on a dataset limited to time series with 10 years of overlapping, continuous data records (see Methods).

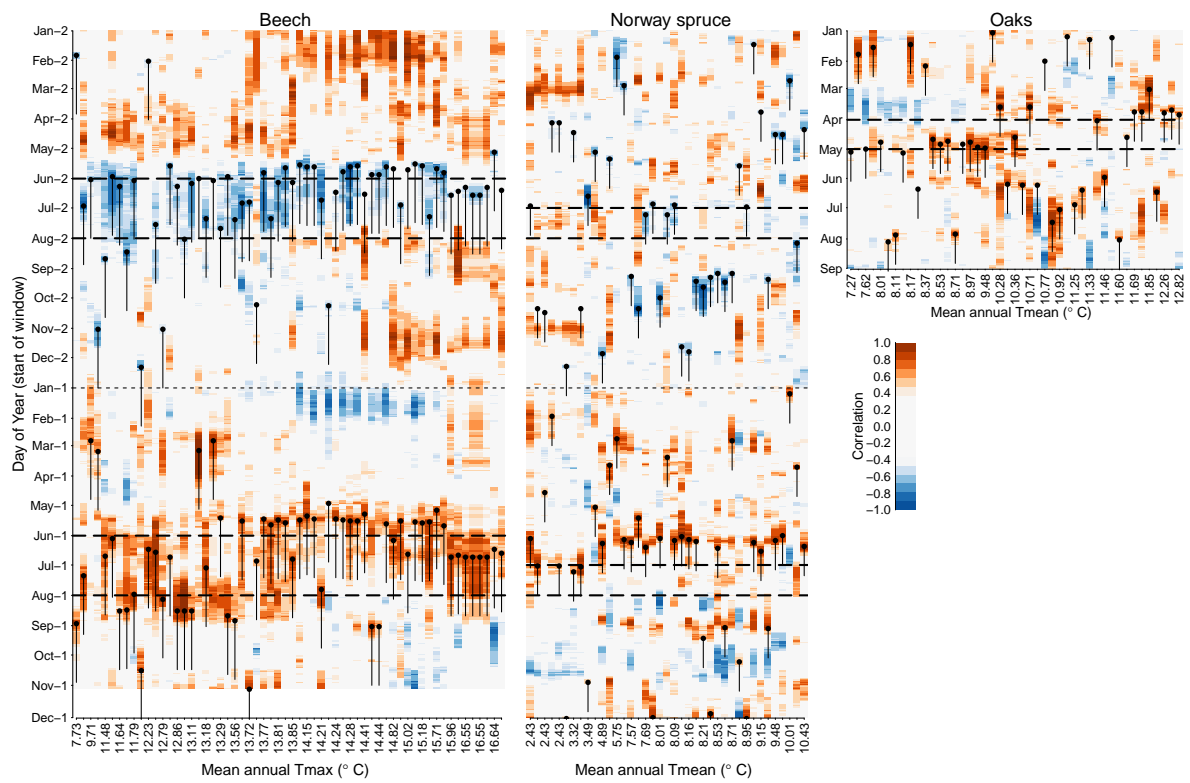


Figure S3: Spatiotemporal variation in seed production – weather cues correlations. Correlations are reported as the start DOY for the seasonal cues (y -axis) either T -2 and T-1 (beech, Norway spruce) or T (oaks) years before seed production, and the site location ordered by latitude (x -axis). The dashed lines in the figures indicate the 60- (beech, June-July) or 30- (Norway spruce; June, oaks; April) day window of fixed weather cues. The strongest correlations as indicated by sliding windows are highlighted with vertical lines.