

Tail-dependence of masting synchrony results in continent-wide seed scarcity

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Author Contributions Statement

MB and JSz conceived the study, JSz, MB, VJ, JF, AHP designed the study. JSz performed the analysis, MB led the writing of the manuscript. All authors contributed critically to the interpretation of the analysis and drafts, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data accessibility statement

The data and R code used in this study have been deposited in the Open Science Framework (OSF): https://osf.io/vny4b/?view_only=5e233556ebed48e79fa89ef3ec002544. The full MASTREE+ dataset is available in Hacket-Pain *et al.* (2022).

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38 Abstract

39 Spatial synchrony may be tail-dependent, meaning it is stronger for peaks rather than troughs,
40 or vice versa. High interannual variation in seed production in perennial plants, called masting,
41 can be synchronized at subcontinental scales, triggering extensive resource pulses or famines.
42 We used data from 99 populations of European beech (*Fagus sylvatica*) to examine whether
43 masting synchrony differs between mast peaks and years of seed scarcity. Our results revealed
44 that seed scarcity occurs simultaneously across the majority of the species range, extending to
45 populations separated by distances up to 1800 km. Mast peaks were spatially synchronized
46 at distances up to 1000 km and synchrony was geographically concentrated in northeastern
47 Europe. Extensive synchrony in the masting lower tail means that famines caused by beech seed
48 scarcity are amplified by their extensive spatial synchrony, with diverse consequences for food
49 web functioning and climate change biology.

50 *keywords:* Moran effect | mast seeding | geography of synchrony | pulsed resources | plant
51 reproduction | seed production | spatial synchrony | tail-dependent synchrony

52

53 Introduction

54 Spatial synchrony, the tendency of ecological phenomena to manifest correlated fluctuations
55 across diverse locations, impacts regional ecosystem functioning, leading to both large-scale
56 outbreaks and shortages (Ostfeld & Keesing, 2000; Earn *et al.*, 2000; Liebhold *et al.*, 2004;
57 Bjørnstad *et al.*, 2002). One ecological phenomenon exhibiting diverse ecosystem consequences
58 and considerable spatial synchrony is mast seeding, a common reproductive strategy in perennial
59 plants (Koenig & Knops, 2000; Kelly & Sork, 2002; LaMontagne *et al.*, 2020; Journé *et al.*,
60 2023). In masting plants, seed production varies markedly between years, characterized by
61 frequent reproductive failures interspersed with peaks many times greater than the long-term
62 average (Kelly, 1994). This year-to-year variation is synchronized among individuals and can
63 extend to subcontinental scales, thereby triggering extensive disruptions in food webs (Ostfeld
64 & Keesing, 2000; Bogdziewicz *et al.*, 2016; Clark *et al.*, 2019). On the one hand, mast peaks
65 generate a resource pulse resulting in outbreaks of rodents, insects, and other seed consumers
66 that spread up the food web (Schmidt & Ostfeld, 2003), spikes in rodent-borne human diseases
67 (Jones *et al.*, 1998; Bregnard *et al.*, 2021), and elevated concentrations of allergenic pollen
68 (Tseng *et al.*, 2020). Conversely, years devoid of seed production lead to famines, causing
69 rodent population crashes (Zwolak *et al.*, 2018), poor or skipped reproduction in birds and
70 mammals (Ruf *et al.*, 2006; Fidler *et al.*, 2008; Cachelou *et al.*, 2022), the emigration of seed-

71 eating wildlife (Zuckerberg *et al.*, 2020), immigration of birds attracted to habitats where rodents
72 are scarce (Szymkowiak & Thomson, 2019; Maag *et al.*, 2024), or increased human-wildlife
73 conflicts as consumers seek food outside of forests (Kozakai *et al.*, 2011; Bautista *et al.*, 2023).
74 The consequences of pulsed resources from mast peaks and famines resulting from years of seed
75 scarcity are magnified by the spatial scale of their synchrony (Yang *et al.*, 2008; Bogdziewicz
76 *et al.*, 2016; Clark *et al.*, 2019). Novel theory indicates that this spatial synchrony may exhibit
77 tail-dependency, being stronger in either mast peaks or troughs (seed scarcity) (Walter *et al.*,
78 2022), with significant and distinct ecosystem implications, but this has never been explored.

79 A recently introduced framework for investigating tail-dependence in spatial synchrony
80 helps to uncover novel patterns and enhance our understanding of the processes underlying
81 ecological synchrony (Ghosh *et al.*, 2020, 2021; Walter *et al.*, 2022). This framework explores
82 the tendency for the strength of the relationship between two variables to vary across the upper
83 and lower portions of their distribution (high and low tails, see Fig. 1), thereby influencing the
84 synchrony of peaks and troughs (Ghosh *et al.*, 2020, 2021; Walter *et al.*, 2022). In essence, a
85 strong association between an environmental driver and ecological response in either tail should
86 result in higher ecological synchrony within that tail (Ghosh *et al.*, 2020, 2021; Walter *et al.*,
87 2022). For instance, fluctuations in plankton (*Ceratium*) biomass exhibit greater synchrony
88 when scarce (lower tail) or abundant (upper tail), depending on whether the local relationship
89 with temperature is stronger in the lower or upper tail, respectively (Ghosh *et al.*, 2020). In the
90 case of giant kelp (*Macrocystis pyrifera*), exposure to intense waves leads to declines in kelp
91 canopy (Walter *et al.*, 2022). The relationship is non-linear, with low impact on kelp biomass
92 when waves are calm, resulting in increased synchrony of kelp population crashes in areas
93 where waves are intense (Walter *et al.*, 2022). The tail-dependent nature of regional synchrony
94 shapes the resilience of regional populations, as regions marked by asynchronous crashes might
95 exhibit greater resilience to disturbance (Walter *et al.*, 2022). Such non-linear relationships
96 between ecological and environmental variables are widespread and were anticipated to be a key
97 mechanism contributing to the emergence of tail-dependence in synchrony (Ghosh *et al.*, 2020,
98 2021; Walter *et al.*, 2022).

99 In masting plants, a major mechanism governing the annual allocation of resources to seed
100 production involves non-linear responses of seed production to weather variations, known as
101 weather cues (Kelly *et al.*, 2013; Pearse *et al.*, 2016). Consequently, the regional synchronization
102 of masting arises from the Moran effect, i.e. spatially correlated fluctuations in environmental
103 drivers of masting (Koenig & Knops, 2013; Ascoli *et al.*, 2017; LaMontagne *et al.*, 2020; Wion
104 *et al.*, 2020; Bogdziewicz *et al.*, 2021a; Reuman *et al.*, 2023). The mechanisms underlying
105 weather cues are species-specific, with a common cue being the impact of summer temperature
106 on the stimulation of flower initiation, which is a primary determinant of subsequent seed
107 production (Satake & Kelly, 2021; Samarth *et al.*, 2021; Journé *et al.*, 2024). Thus, substantial
108 flowering effort, and subsequent large seed production, are triggered when the weather aligns with
109 species-specific criteria (Piovesan & Adams, 2001; Schaubert *et al.*, 2002; Fernández-Martínez

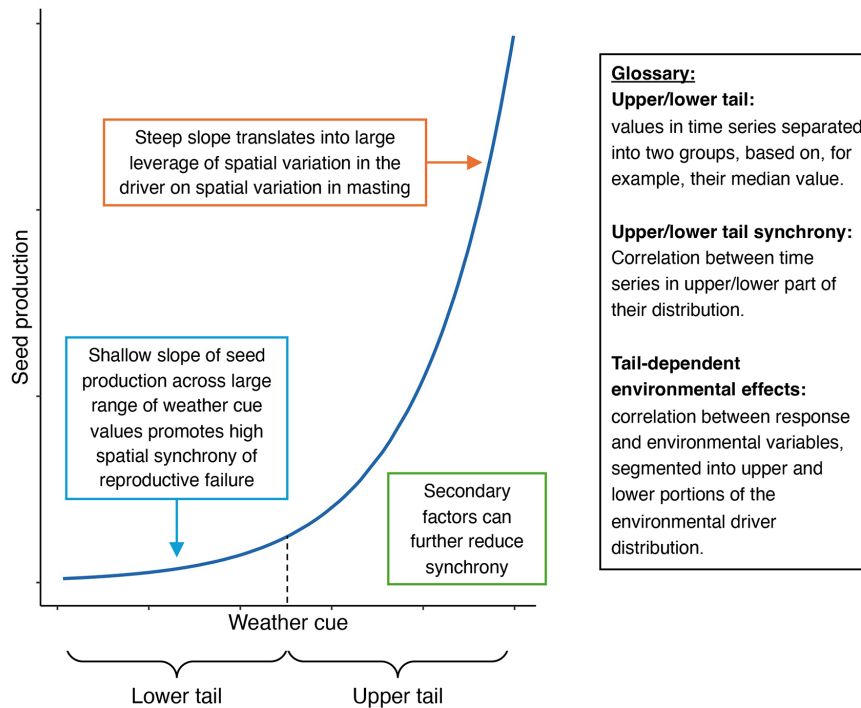


Figure 1: A graphical representation of the hypothetical association of seed production and weather cue and its consequence for spatial synchrony of mast seeding. In masting plants, seed production commonly increases only weakly at low values of the weather cue. Thus, in the lower tail of the environmental driver, the change in seed production per unit of weather cue is relatively small, promoting high spatial synchrony. In turn, the relationship between masting and weather cues in the upper tail is characterized by a steeper slope. Thus, relatively small spatial variations in weather translate into larger spatial variation in seed production (lower synchrony in the masting upper tail). In addition, in the lower tail, a single factor is sufficient to largely block seeding (i.e. low values of the weather cue), but multiple factors interact to determine the size of the final seed crop once high cue values trigger heavy reproduction (cue alignment). Secondary cues such as weather conditions during spring, which determine pollination success, shape the final seed production and create additional spatial variation.

110 *et al.*, 2017; Nussbaumer *et al.*, 2018). If individuals and populations collectively respond to
 111 the same cue across different populations, the spatial scale of masting synchrony aligns with the
 112 broad-scale synchronization of weather patterns (Koenig & Knops, 2013; LaMontagne *et al.*,
 113 2020; Wion *et al.*, 2020; Bogdziewicz *et al.*, 2023a).

114 Tail-dependence in masting synchrony may arise from the often exponential or logistic
 115 relationships between seed production and weather cues (Fernández-Martínez *et al.*, 2017). For
 116 instance, the logistic shape of the relationship between seed production and spring temperature
 117 in temperate oaks (*Quercus robur* and *Q. petraea*) results in consistently low seed production for
 118 temperatures below 12 C°, followed by a sharp increase above it (Schermer *et al.*, 2020). Similar
 119 non-linear responses have been observed in New Zealand flora (Kelly *et al.*, 2013), Mediterranean
 120 oaks (Koenig *et al.*, 2015), pines (Parmenter *et al.*, 2018), and American hardwoods (Smith *et al.*,
 121 2021). Logistic, log-linear, or sigmoidal responses to weather, leading to tail-dependence in the
 122 relationship between masting and weather, can consequently drive tail-dependence in masting
 123 synchrony.

124 On one hand, a strong association between masting and weather in the upper tail should

125 result in stronger synchrony in mast peaks (Walter *et al.*, 2022). Alternatively, synchrony in
126 seed scarcity may outweigh synchrony in masting peaks, owing to the differing influence of
127 weather cues on seed production at low versus high values. (Fig. 1). For low values of the
128 weather cue, a non-linear relationship results in little or no seed production across a relatively
129 broad range of weather cue, promoting spatial synchrony in seed scarcity by buffering against
130 fluctuations within that weather cue range (Fig. 1). In turn, the relationship between masting and
131 weather cues in the upper tail is characterized by a steeper slope (Kelly *et al.*, 2013; Fernández-
132 Martínez *et al.*, 2017; Schermer *et al.*, 2020). Due to that hypersensitivity, relatively small
133 spatial variations in weather translate into large spatial variation in seed production, lowering
134 synchrony in the masting upper tail. Another mechanism favoring the dominance of synchrony
135 in seed scarcity over peaks is that, while a single factor, such as the absence of a weather cue, is
136 sufficient to largely inhibit seeding, large mast peaks are contingent upon a sequence of events
137 occurring subsequently, termed cue alignment (Pesendorfer *et al.*, 2016; Ascoli *et al.*, 2021;
138 Yukich-Clendon *et al.*, 2023). In European beech (*Fagus sylvatica*), for example, once flowers
139 are initiated, spring weather conditions can either enhance (in dry conditions) or impede (in
140 wet conditions) pollination (Ascoli *et al.*, 2017; Journé *et al.*, 2023). Even after successful
141 pollination, summer drought and heatwaves can still reduce the eventual seed crop (Nussbaumer
142 *et al.*, 2020). As a substantial mast peak requires the sequential occurrence of all these cues
143 (Ascoli *et al.*, 2021), spatial synchrony diminishes in the upper tail.

144 In this study, we analyzed data from 99 populations of the major European species, European
145 beech (*Fagus sylvatica*), sampled across the species' range, to investigate the presence of tail-
146 dependence in regional masting synchrony. The regional synchronization of beech masting
147 is attributed to the Moran effect (Vacchiano *et al.*, 2017; Bogdziewicz *et al.*, 2021a, 2023a;
148 Journé *et al.*, 2024). Past research investigated mechanisms leading to large-scale synchrony
149 in overall masting pattern (Vacchiano *et al.*, 2017; Bogdziewicz *et al.*, 2023a), but a clear
150 understanding of the relative importance of peaks and troughs synchrony remains unexplored.
151 The forest-forming nature and extensive range of European beech (Leuschner & Ellenberg, 2017)
152 amplify the consequences of potential tail-dependence in beech masting synchrony. Beech's
153 seed production is responsive to consecutive summer temperatures, with sequential cold and hot
154 summers cueing high flowering initiation (Piovesan & Adams, 2001; Journé *et al.*, 2023). Here
155 we used ΔT (difference between summer temperatures in one and two years before seed fall)
156 as the weather cue. First, we estimated the shape of the relationship between weather cue and
157 beech masting, expecting a non-linear response where the relationship is steeper in the upper
158 tail. This implies that seed production will have a weaker association with the weather cue until
159 large cue values are reached. According to the tail-dependence theory (Ghosh *et al.*, 2020, 2021;
160 Walter *et al.*, 2022), such upper tail-dependence in the weather-masting association should result
161 in higher synchrony of masting peaks compared to synchrony of seed scarcity. Alternatively,
162 the synchrony of seed scarcity may surpass the synchrony of peaks if a non-linear association
163 of masting and weather cue results in little seed production occurring across relatively large

164 temperature ranges in the lower tails. This allows seed scarcity to synchronize as long as
165 temperature variations remain within that range (Fig. 1).

166 **Materials and Methods**

167 **Materials**

168 **Study system** European beech (*Fagus sylvatica* L.) is a major forest-forming species in tem-
169 perate Europe. Beech is a model masting species, with seed production characterized by large
170 interannual variation and synchrony of seed production (Nilsson & Wastljung, 1987; Ascoli
171 *et al.*, 2017; Mund *et al.*, 2020). Beech masting allows seeds to escape predation and increases
172 pollination efficiency (Nilsson & Wastljung, 1987; Bogdziewicz *et al.*, 2020). Subsequent cold
173 (two years before seed fall) and hot (one year before seed fall) temperatures in June and July
174 trigger large seed production in European beech (Piovesan & Adams, 2001; Vacchiano *et al.*,
175 2017; Journé *et al.*, 2024).

176 **Seed production and environmental data** Annual observations of seed production of Eu-
177 ropean beech were extracted from MASTREE+, an open-access database of annual records of
178 population-level reproductive effort Hackett-Pain *et al.* (2022). For our analysis, we restricted
179 the European beech time series to the continuous observations of seed production that covered
180 at least 10 years, observed after 1980. We choose 1980 as a cutoff as data before that date is
181 restricted spatially. We excluded pollen-based and ordinal records. This resulted in 99 time
182 series available for the analysis (median time series length, 29 years; maximum length, 41 years).
183 The number of years per time series is given in Fig. 2. We extracted daily weather data for each
184 site from the corresponding 0.1° grid cell of the E-OBS dataset (Cornes *et al.*, 2018).

185 **Analysis**

186 **Masting and weather cue relationship** Our analysis started by estimating the relationship
187 between European beech seed production and the weather cue. Generally, beech seed production
188 is triggered by subsequent cold (two years before seedfall, T2) and hot (one year before seedfall,
189 T1) summers, specifically mean maximum temperature in June and July (Vacchiano *et al.*, 2017).
190 The timing of that cue is conservative across the whole species range, as it is anchored to the
191 summer solstice (Journé *et al.*, 2024). These two parameters (temperature in T1 and T2) can be
192 collapsed into one by taking their difference (ΔT , i.e. the difference between mean maximum
193 June-July temperatures in T1 and T2) (Kelly *et al.*, 2013). Thus, we used ΔT in our analysis as
194 it allows the estimation of masting-cue relationships in the tails with just one parameter. Model
195 fit, as judged with AIC, indicated a similar fit of ΔT model and T1 \times T2 model (Table S1). The
196 relationship between masting and ΔT was estimated with a generalized additive mixed model

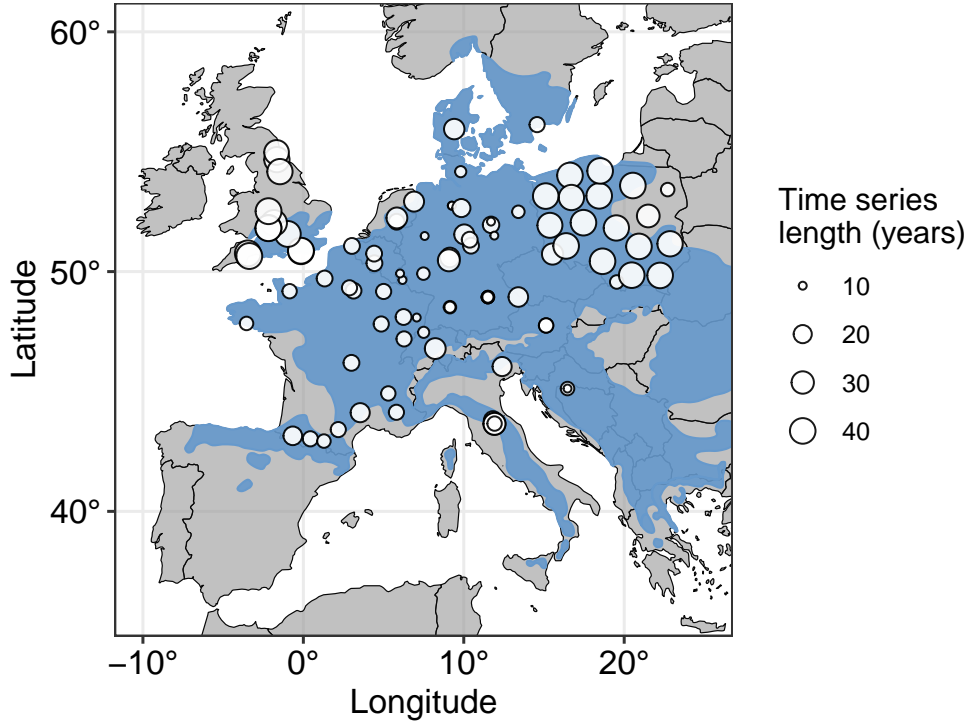


Figure 2: Locations of the 99 time series of annual seed production of European beech used in the study. Point size is scaled to the number of years (N) masting was monitored at the focal location, and the blue shading highlights the European beech natural range. An animation showing the spatiotemporal variation of seed production across the continent is supplemented as Video S1.

197 (GAMM) in which annual, per-site seed production was included as a response, site ID as a
 198 random intercept, and ΔT as a predictor. To accommodate among-site variation in methods of
 199 seed production monitoring, we scaled seed production for each site to fall in a set (0, 1) and
 200 fitted the GAMM with a beta family error term and logit-link (Journé *et al.*, 2023; Journé *et al.*,
 201 2024). To scale the seed production values, we used the following equation:

$$y_i = \frac{min - max}{(max_y - min_y) \times (y_i - min_y)} + min \quad (1)$$

202 where y_i is seed production value of series y in year i , min_y and max_y are, respectively,
 203 minimal and maximal seed production values of series y , while min and max are minimal and
 204 maximal values to which seed production values of series y are scaled. GAMM model was fitted
 205 using *R* ver. 4.2.3 and *mgcv* ver. 1.8-42 package (R Core Team, 2023; Wood, 2011).

206 Tail-dependence in regional masting synchrony

207 **Categorization of masting and weather into tails** Our framework follows that of Walter *et al.*
 208 (2022). First, we divided masting and weather data into tails. Masting lower tail includes annual
 209 values of seed production ≤ 0.2 , while upper those > 0.2 , for seed production scaled within each
 210 site to values between 0 and 1 (see above). That categorization reflects the distribution of annual

211 values of seed production (Fig. S1), and provides 1347 observations in the lower, and 890 in
212 the upper masting tail. The weather cue was divided into roughly two equal parts, using $\Delta T =$
213 0 as the threshold. This follows from the nature of the masting-cue association, as high seeding
214 occurs once temperatures in summer T1 are larger than in T2, resulting in positive ΔT values
215 (Kelly *et al.*, 2013; Vacchiano *et al.*, 2017). The thresholds are fairly arbitrary in the sense that
216 neither masting nor weather is a categorical variable. Nonetheless, categorization was tailored
217 to the nature of the data, is biologically justified, and allows the tail-dependence to be analyzed
218 (Ghosh *et al.*, 2021; Walter *et al.*, 2022). Tail separation of masting data is required to estimate
219 the synchrony of mast peaks and seed scarcity. In turn, tail separation of the weather cue is
220 required to estimate the tail-dependent weather effects on masting (Fig. 1).

221 **Within-tails masting synchrony** We estimated the regional synchrony in masting tails using
222 a partial Spearman correlation, defined as the portion of the standard Spearman rank correlation
223 arising due to the range of values in the two variables being bounded by tails thresholds (Walter
224 *et al.*, 2022). Pairwise correlations were calculated separately for the lower (≤ 0.2) and upper ($>$
225 0.2) tail of the seed production time series. In cases when the annual value of seed production for
226 the two sites falls into opposite tails, that value was included when calculating partial Spearman
227 correlation in both tails. Thus, if one site experienced a mast peak and the other a year of
228 seed scarcity in the same year, synchrony was reduced in both tails. We calculated pairwise
229 correlations between all pairs of sites, excluding pairs with less than 10 years of overlap. Note
230 that normalization of the masting data does not affect the correlations calculated via Spearman
231 correlation, as these are calculated on ranked data.

232 We calculated distance-decay of within-tail seed production synchrony using non-parametric
233 spatial covariance functions (Bjørnstad & Falck, 2021). We used the matrices of partial Spear-
234 man correlations within the lower and upper tails as the response (synchrony variables), explained
235 by the matrices of pairwise geographical distances between sites. To calculate 95% confidence
236 bands for each function, we used standard bootstrapping procedure (Bjørnstad & Falck, 2021).

237 We used network analysis to visualize the biogeography of tail-dependent masting synchrony.
238 We built spatially-explicit networks of masting synchrony, whereby sites were nodes, while edges
239 were the pairwise synchrony of seed production within the lower and upper tail (scaled between
240 0 and 1). To test for spatial patterns in tail-dependent masting synchrony, we fitted generalized
241 linear mixed models (GLMM) with between-site synchrony (network edges) in either lower
242 or upper tail as a response, while including sites' latitude, longitude, and their interaction as
243 predictors. The models were fitted with beta error structure (logit link) and included site ID as a
244 random intercept. The models were fitted using *glmmTMB* ver. 1.1.5 R package, while networks
245 were delineated using *igraph* ver. 1.4.1 R package (Brooks *et al.*, 2017; Csardi & Nepusz, 2006).

246 **Drivers of tail-dependent masting synchrony** We used the multiple regression quadratic as-
247 signment procedure with double-semipartialing (MRQAP) to investigate what drives the spatial

248 synchrony of mast seeding within the lower and upper tail. The MRQAP is a modeling framework
249 allowing investigation of the relationship between a dependent matrix and independent matrices
250 while considering the non-independence of network data by using permutation techniques to
251 test the significance of effect sizes (Dekker *et al.*, 2007). We built two MRQAP models in which
252 masting synchrony within each tail, as measured by partial Spearman correlations, were the re-
253 sponse matrices. In both models, the explanatory matrices were the synchrony (partial Spearman
254 correlations) of the weather cue (ΔT) and between-site similarity in the masting-weather cue
255 relationship in the focal tail. For the latter, we fitted site-level beta regression models with seed
256 production (scaled to fall in a set (0, 1)) as a response and ΔT as a predictor, separately for the
257 lower and upper tail of the weather data series. From these models, we extracted slopes for ΔT ,
258 providing a measure of the strength of the masting-weather cue relationship at a given site and in
259 a given tail. We then calculated between-site pairwise similarities of those relationships, by first
260 calculating the Euclidean distances between the slopes for all pairs of sites and then converting
261 them into similarity indices by the formula $(1 - [\text{distance}/\text{maximum distance}])$ (Bogdziewicz
262 *et al.*, 2021a). Further explanatory matrices were between-site similarities in mean annual tem-
263 perature and mean annual precipitation, as well as between-site spatial distance. To facilitate
264 effects comparison, all matrices were linearly scaled between 0 and 1. In both MRQAP models,
265 we tested for statistical significance using t-statistics and 1000 permutations. The models were
266 fitted using *asnipe* ver. 1.1.16 R package (Farine, 2013).

267 Results

268 **Beech masting and weather.** The relationship between beech seed production and summer
269 temperatures was sigmoidal (Fig. 3). We used ΔT (difference in June-July mean maximum
270 temperatures between one and two years before seed fall) as the weather cue because it captures
271 the effects of the past two summers in one parameter (see Methods). Seed production was
272 consistently low for ΔT values below 0 and started to sharply increase above that threshold.
273 Median seed production for ΔT values above 0 was 10-fold larger compared to below (Fig. 3b).
274 Separating weather into lower and upper tails confirmed tail-dependence in the masting-weather
275 cue relationship. Slopes of the relationship between masting and ΔT are higher in the ΔT upper
276 (mean = 3.88, logit scale, $n = 99$) tail compared to the lower (mean = 2.12, $n = 99$) tail (Fig. 3c).

277 **Tail-dependence in regional masting synchrony.** Regional beech masting synchrony was
278 high in both tails. Nonetheless, synchrony was higher in lower tails (little or no seed production)
279 compared to upper tails, despite the upper-tail association of masting and weather (Fig. 4). The
280 mean absolute value of masting synchrony was higher in the lower tail compared to the upper
281 tail at the majority (81 out of 99) of sites (Fig. 4B). Looking at these patterns in space, upper
282 and lower tail masting synchrony were largely similar for distances up to 600 km. Tails started
283 to diverge afterwards, with upper tail-synchrony 95% CI overlapping zero at ~ 1000 km. In

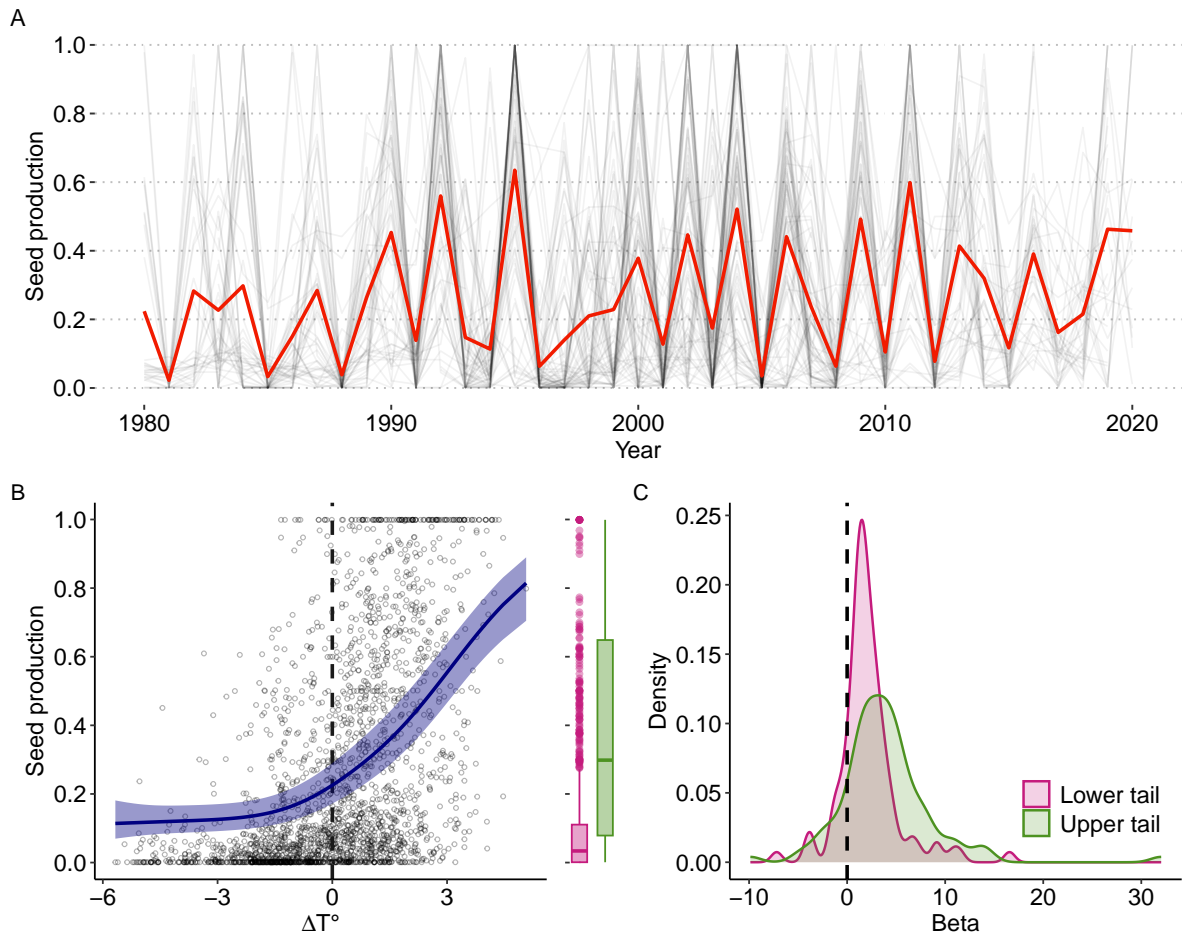


Figure 3: (A) Temporal dynamics of European beech *Fagus sylvatica*) seed production, with grey lines showing population-level data series, and the red line showing the yearly mean across all 99 sites. (B) Relationship between beech seed production and weather cue (ΔT , i.e. the difference between June-July mean maximum temperatures one and two years before seed fall). The solid line shows the model fit and shading associated 95% confidence intervals. The vertical dashed line shows the threshold used to define lower and upper tails in the ΔT . Box plots show the seed production for ΔT values in the lower (pink) and upper (green) tails. (C) Distribution of population-level slopes (logit scale) from beta regression models examining masting vs ΔT relationships within the upper and lower tail of ΔT . Seed production is scaled within each site to values between 0 and 1.

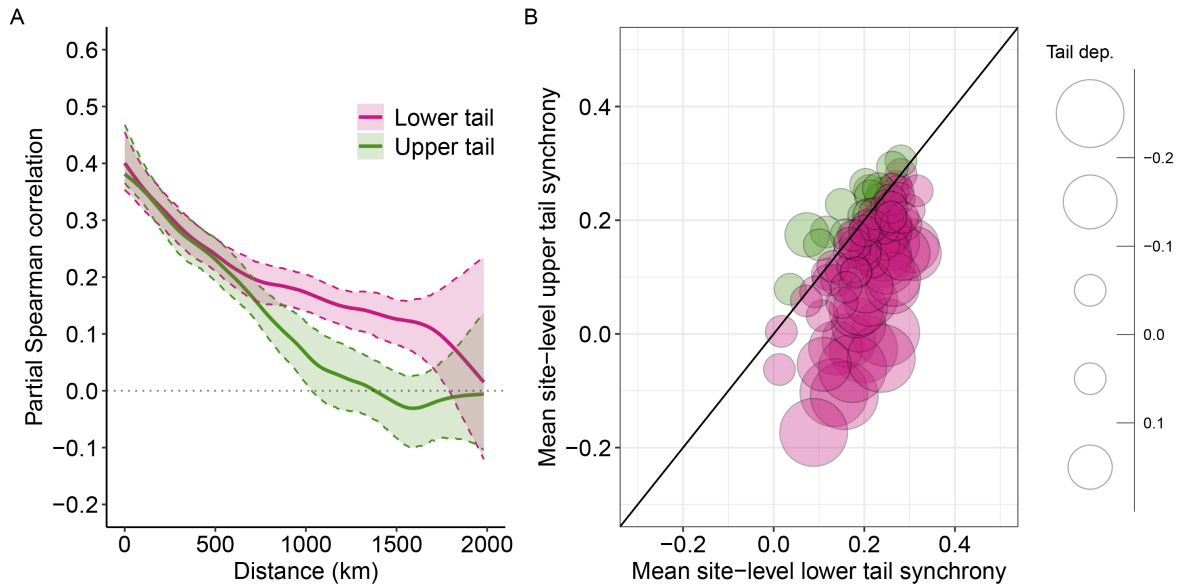


Figure 4: Tail dependence in beech masting synchrony. A) distance decay of beech masting synchrony in the upper and lower tail. The lower tail is seed production below 0.2, while the upper is above, for annual values scaled within each site to between 0 and 1. That categorization follows from the shape of the distribution of the annual values (see Methods). Note that the values of synchrony in tails are slightly lower compared to overall regional synchrony (Fig. S2), which follows from categorization into tails and estimation based on partial Spearman correlation. B) Relationship between site-level mean synchrony of seed production in the upper and lower tail, with points scaled according to tail dependence strength (difference between mean synchrony in the upper and lower tail), and color-coded according to whether the mean falls into stronger upper- or lower-tail synchrony. Distribution and spatial synchrony of ΔT is provided in Fig. S3.

284 contrast, synchrony in the lower tail extends 1.8-fold further, with 95% CI overlapping 0 at 1800
 285 km (Fig. 4a). Mapping tail-dependence of masting synchrony over Europe revealed that mast
 286 peaks synchrony is lower in the southeast of the continent, but that pattern is largely absent in
 287 the lower tails (Fig. 5, Table S2).

288 **Drivers of tail-dependent regional masting synchrony.** We used the multiple regression
 289 quadratic assignment procedure (MRQAP) (Dekker *et al.*, 2007) to investigate the role of weather
 290 synchrony and the tail-dependent masting-cue relationship in driving the spatial synchrony of
 291 mast seeding (Bogdziewicz *et al.*, 2021a, 2023a). First, in agreement with masting synchrony
 292 being driven by the Moran effect, among-site masting synchrony was positively associated with
 293 among-site weather synchrony in both tails (Table 1). Interestingly, the effect size of weather
 294 synchrony on masting synchrony was almost 3-fold larger in the upper tails ($\beta = 0.42$) than in
 295 the lower tails ($\beta = 0.17$), which agrees with the notion that variation in weather synchrony has a
 296 larger leverage on masting synchrony in the upper tail (Fig. 1). Masting synchrony in the lower
 297 tails was associated with the masting-cue association in the lower tails, but that effect was not
 298 significant in the upper tail (Table 1). In other words, the synchrony of seed scarcity between
 299 sites was higher if these sites shared a similar response to the weather cue in that tail. Sites
 300 that shared more similar mean annual precipitation and mean annual temperature had higher

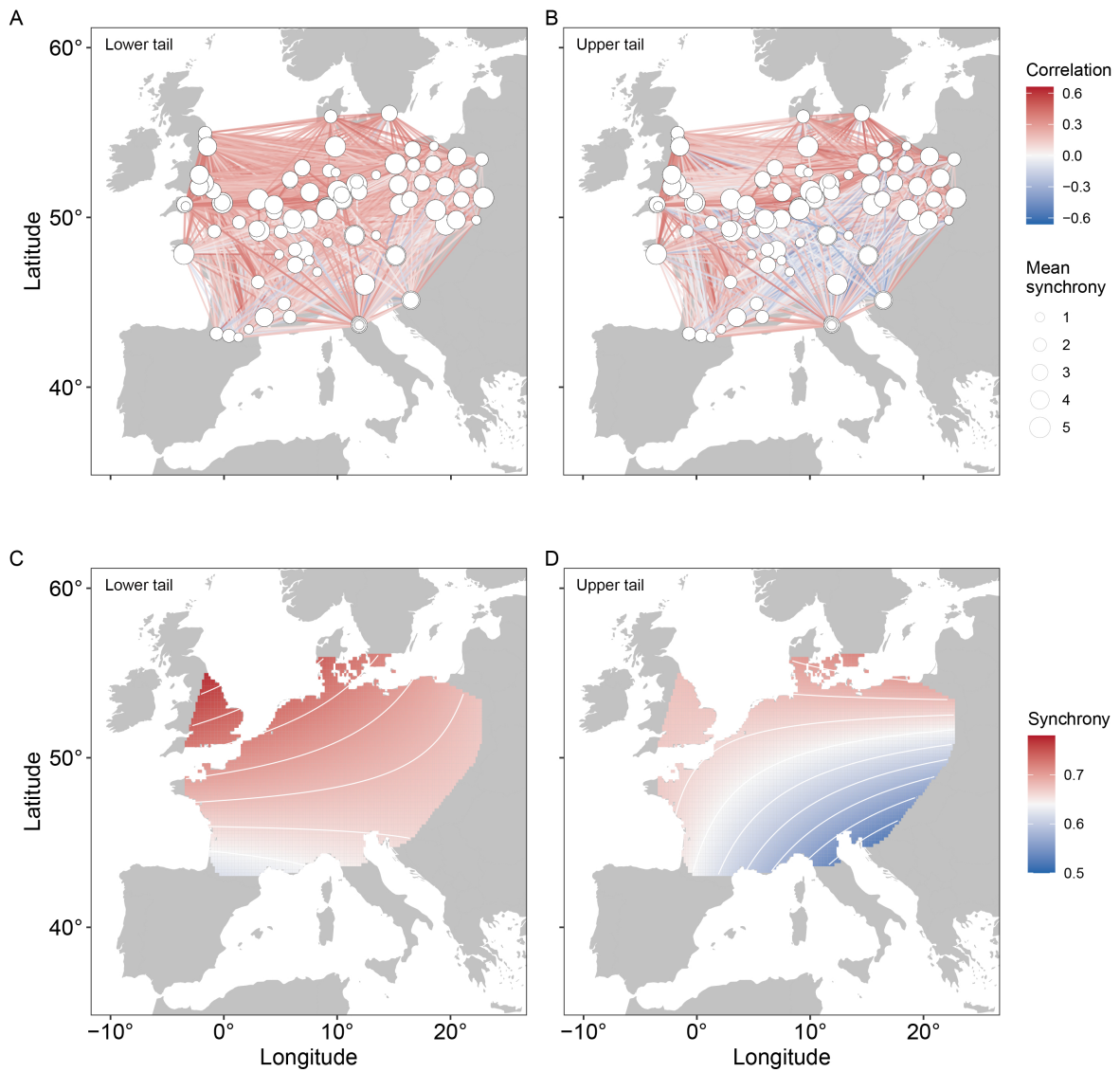


Figure 5: Networks of masting synchrony in A), C) lower and B), D) upper tail. At A) and B) points are sites and lines show their pairwise synchrony in masting. Point sizes are scaled according to site-level mean synchrony of seed production within a given tail. C) and D) show synchrony as estimated with a GLMM model, see Table S2 for the model summary.

301 masting synchrony in both tails (Table 1). Moreover, in both tails, the spatial distance between
 302 sites negatively correlated with their synchrony.

Table 1: Multiple Regression Quadratic Assignment Procedure (MRQAP) models summaries that regressed the matrices of masting synchrony in the lower and upper tails against matrices of similarities in a masting-weather cue relationship in the focal tail, weather synchrony, similarity in climate (MAT: mean annual temperature, MAP: mean annual precipitation), and spatial distance. The weather cue used is ΔT (the difference between June-July mean maximum temperatures in one and two years before seed fall (see Methods). Key definitions of tail-dependence are provided in Fig. 1.

Predictor	slope	p-value
A) Lower tail synchrony ($R^2 = 0.21$)		
Intercept	0.33	<0.001
Masting-weather cue similarity	0.10	0.004
Weather synchrony	0.17	<0.001
Mean annual temperature similarity	0.09	<0.001
Mean annual precipitation similarity	0.07	<0.001
Spatial distance	-0.18	<0.001
B) Upper tail synchrony ($R^2 = 0.38$)		
Intercept	0.21	<0.001
Masting-weather cue similarity	0.06	0.189
Weather synchrony	0.42	<0.001
Mean annual temperature similarity	0.14	<0.001
Mean annual precipitation similarity	0.04	0.037
Spatial distance	-0.18	<0.001

303 Discussion

304 Analyzing tail-dependent, regional beech masting synchrony revealed that seed scarcity can
 305 occur simultaneously across the vast majority of the species range. Moreover, the synchrony
 306 of seed scarcity extends 1.8 times further (approximately 1800 km) than the already extensive
 307 synchrony of mast peaks (approximately 1000 km). Contrary to the predictions of the tail-
 308 dependence theory (Ghosh *et al.*, 2020, 2021; Walter *et al.*, 2022), the upper-tail association
 309 between weather cues and masting did not result in stronger synchrony of masting peaks. Upper-
 310 tail masting synchrony was not higher than lower tail at any distance and started to decline more
 311 rapidly. This result appears to stem from the nature of the relationship between beech masting
 312 and its weather cue. The relationship translates into a minor increase in seed production across
 313 a relatively broad range of cue values, promoting spatial synchrony of seed scarcity by buffering
 314 against fluctuations within that cue range. In turn, for large values of the cue, the relatively small
 315 among-site variation in temperature results in a large variation in seed production investment

316 across sites. Additionally, while it is sufficient for one factor to veto seed production (Pesendorfer
317 *et al.*, 2016; Abe *et al.*, 2016; Bogdziewicz *et al.*, 2018), various other factors determine the
318 size of a mast peak (Ascoli *et al.*, 2017, 2021; Journé *et al.*, 2023). The identification of tail-
319 dependency in masting synchrony presented here provides new insights into the consequences of
320 masting association with weather variation, with diverse consequences for food web functioning,
321 masting forecasting, and climate change biology.

322 Synchrony in seed scarcity is higher compared to synchrony of mast peaks, despite the upper-
323 tail association between masting and weather. We attribute that to the specific nature of the
324 relationship between masting and weather. In the case of environmentally-induced synchrony
325 in plankton, aphids, and kelp, a weak correlation with abundance across a specific range of
326 the focal environmental driver results in abundance fluctuations due to other local drivers. In
327 consequence, regional synchrony decreases in the focal tail (Ghosh *et al.*, 2020, 2021; Walter
328 *et al.*, 2022). In the context of masting, including in European beech, when the weather cue
329 values are low, seeding is inhibited or low rather than influenced by other environmental drivers.
330 Second, while the absence of the weather cue largely blocks seeding across distant sites, large
331 mast peaks require the simultaneous occurrence of several events (Ascoli *et al.*, 2017; Journé
332 *et al.*, 2023). These events involve weather conditions throughout the stages of flower and fruit
333 maturation (Pearse *et al.*, 2016). Mast peaks of similar magnitude require more events to align
334 through time and space, potentially diminishing synchrony. This notion is supported by the
335 MRQAP models, which found that similarity in the response of masting to the weather cue in
336 the upper tail was not a strong predictor of between-site masting synchrony.

337 The synchrony of mast peaks exhibits a biogeographical pattern, which is absent in the
338 regional synchrony of seed scarcity. A past study on European beech revealed that the regional
339 synchrony of masting decreases from northwest to southeast Europe (Bogdziewicz *et al.*, 2021a).
340 This biogeographical division mirrors the regional synchrony of temperature, following from
341 the higher complexity of topography in southeastern Europe and the prevalence of a unique
342 mode of climate variability in the northwest (the North Atlantic Oscillation) when compared
343 to the southeast of Europe (East Atlantic pattern, Scandinavian pattern and East Atlantic/West
344 Russia pattern) (Folland *et al.*, 2009; Zuckerberg *et al.*, 2020; Craig & Allan, 2022). Lack of
345 that geographical pattern in the synchrony of seed scarcity supports the notion that synchrony in
346 lower tails is partially buffered against temperature fluctuations compared to the more sensitive
347 synchrony of mast peaks. By segregating masting synchrony into tails, our results demonstrate
348 that mast failures are widespread, and synchronized across the species distribution. In turn,
349 while mast peaks exhibit synchrony across northern Europe, peaks in southeastern Europe are
350 desynchronized from the rest of central and northern Europe.

351 The regional synchrony of seed scarcity surpassing the synchrony of mast peaks holds
352 significant implications for food webs, forest and wildlife management, and seed production
353 forecasting. A key fitness benefit of masting lies in predator satiation (Kelly, 1994; Pearse *et al.*,
354 2016). The synchronized, substantial year-to-year variation in seed production starves seed

355 consumers in low-seeding years, facilitating the satiation of these consumer populations in mast
356 years (Zwolak *et al.*, 2022). High regional synchrony of seed scarcity can enhance the starvation
357 of highly mobile seed consumers, such as large mammals or birds (Curran & Leighton, 2000;
358 Bogdziewicz *et al.*, 2022). This finding is especially relevant for southeastern Europe, where
359 synchronous seed scarcity will aid satiation despite desynchronized mast peaks. Forecasting
360 years of high and low seed production emerges as an important tool for aiding management and
361 conservation efforts in ecosystems dominated by masting species (Pearse *et al.*, 2021; Journé
362 *et al.*, 2023). The higher spatial synchrony of seed scarcity means that spatial extrapolation of
363 failure forecasts is more feasible compared to mast peaks. In restoration projects, the extensive
364 spatial scale of seeding failure implies that acquiring material for replanting may be restricted
365 in some years, as poor seeding can extend over the majority of the species range. Finally, in
366 some species, including European beech, tree and leaf growth is reduced in years of high seed
367 production, leading to synchronized fluctuations in carbon sequestration (Hackett-Pain *et al.*,
368 2018; Vergotti *et al.*, 2019; Mund *et al.*, 2020). Dividing masting synchrony into tails indicates
369 less extensive synchrony of peaks, and consequently a more geographically restricted role for
370 masting as a driver of synchrony in forest growth and carbon sequestration variability.

371 Interannual variation in seed production is driven by two major physiological mechanisms:
372 non-linear responses of seed production to weather variation, or weather cues, and endogenous
373 resource dynamics (Satake & Iwasa, 2000; Crone & Rapp, 2014; Pearse *et al.*, 2016). Years
374 with little or no seed production happen either when weather cue was absent, or following high-
375 seeding years when resources are depleted after high reproductive effort (Crone *et al.*, 2009;
376 Han & Kabeya, 2017). Thus, high regional synchrony in seed scarcity could also be a direct
377 consequence of the synchrony of mast peaks, to the extent that synchronized resource depletion
378 prevents seeding across extensive scales. Two outcomes of our analysis do not support such a
379 hypothesis. First, at distances above 600 km, synchrony in seed scarcity is higher than synchrony
380 in mast peaks. Second, in southeastern Europe mast peaks showed lower synchronization than
381 elsewhere in Europe, but synchrony of years of seed scarcity showed little difference between
382 southeastern Europe and the rest of the continent. Thus, while resource-related processes appear
383 important as synchronizing factors at local scales (Crone *et al.*, 2009; Abe *et al.*, 2016), they do
384 not drive synchrony of seed scarcity at regional scales.

385 One aspect of regional masting synchrony not addressed in our analysis is its potential
386 variability over time, which may be influenced by climate oscillations. The North Atlantic
387 Oscillation (NAO) is the leading climatic driver in Europe, exerting influence over spatial weather
388 patterns (Ascoli *et al.*, 2021). Consequently, the extent of regional masting synchrony may
389 fluctuate in response to shifts in the NAO phase (Ascoli *et al.*, 2017). Similarly, the positioning
390 of the jet stream over Europe plays an important role in shaping continental weather patterns,
391 thereby impacting forest productivity (Dorado-Liñán *et al.*, 2022). The dynamic weather dipoles
392 created by the jet stream's positioning can thus alter the geographical distribution of masting
393 events. By averaging across temporal conditions, as done in our analysis, these effects are

394 overlooked. For instance, the geographical patterns of masting synchrony described in this
395 study are likely to exhibit temporal dynamics, representing an interesting avenue for future
396 research.

397 In summary, our findings reveal tail-dependence in mast seeding synchrony, stemming from
398 the nature of the relationship between seed production and weather variation. The next step is
399 to investigate whether the described tail dependence in European beech applies to other masting
400 plants. While the logistic or sigmoidal shape of seed production response to weather conditions
401 is common, it is not universal (Fernández-Martínez *et al.*, 2017; Wion *et al.*, 2020). We predict
402 that in cases where the response of masting to weather is linear, tail dependency in synchrony will
403 either not manifest (Walter *et al.*, 2022), or be weaker and follow only from the secondary cue
404 effect (cue alignment; Fig. 3). Additionally, some species exhibit population-specific weather
405 cues (Bogdziewicz *et al.*, 2023a; Fleurot *et al.*, 2023). For example, the main determinants of
406 sessile oaks (*Quercus petraea*) seed production vary along climatic gradients (Fleurot *et al.*,
407 2023). Exploring how such cue variation affects the regional synchrony of mast peaks versus
408 the synchrony of seed scarcity would provide valuable insights. Furthermore, our results
409 suggest that the synchrony of seed scarcity may absorb larger changes in temperature regimes
410 associated with climate change. In European beech, climate warming disrupts the interannual
411 variation and synchrony of mast seeding, leading to elevated losses to seed predators and lower
412 pollination success (Bogdziewicz *et al.*, 2023b; Foest *et al.*, 2024). Higher temperatures result
413 in an increased frequency of hot summers, which weaken the tree's responsiveness to the cue
414 (Bogdziewicz *et al.*, 2021b). To the extent that this disruption affects the relationship between
415 masting and weather in the upper tail, the synchrony of mast peaks may be more adversely
416 affected than the synchrony of seed scarcity. Applying a tail-dependence framework to masting
417 ecology opens up new research avenues that will contribute to an enhanced understanding of
418 masting biology and how tail dependence manifests across and influences ecological systems.

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427 **Author Contributions Statement**

428 MB and JSz conceived the study, JSz, MB, VJ, JF, AHP designed the study. JSz performed
429 the analysis, MB led the writing of the manuscript. All authors contributed critically to the
430

431 interpretation of the analysis and drafts, and gave final approval for publication.

432

433 **Declaration of interests**

434 No competing interests to declare.

435

436 **Data availability statement**

437 The data used in this study have been deposited in the Open Science Framework (OSF):
438 https://osf.io/vny4b/?view_only=5e233556ebed48e79fa89ef3ec002544. The full
439 MASTREE+ dataset is available in Hacket-Pain *et al.* (2022).

440

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665 **Supporting Information**

666 Szymkowiak et al. Tail-dependence of masting synchrony results in continent-wide seed scarcity

Table S1: AIC-based comparison of generalized linear mixed models testing the relationships between European beech masting and weather cues. We used mean maximum temperatures, T1 is one year while T2 is two years before seedfall. ΔT is the difference between the June-July mean maximum temperature in T1 and T2.

Model	AIC	ΔAIC	d.f.
June-July temp (T1) \times June-July temp (T2)	-3941.0	0	6
June-July temp (T1) + June-July temp (T2)	-3937.2	3.8	5
ΔT	-3937.0	4.0	4
June-July temp (T2)	-3511.9	429.1	4
June-July temp (T1)	-3475.6	465.4	4

Table S2: Spatial patterns in tail-dependent masting synchrony. Effect sizes were estimated using generalized linear mixed models with beta error structure (logit link) that included between-site synchrony in either lower or upper tail as a response, and sites' geographical coordinates as predictors.

Predictor	β	SE	z-value	p-value
A) Lower tail synchrony				
Intercept	-2.006	0.479	-4.19	<0.001
Latitude	0.058	0.009	6.08	<0.001
Longitude	0.107	0.047	2.290	0.022
Latitude*Longitude	-0.002	0.001	-2.51	0.012
B) Upper tail synchrony				
Intercept	-0.142	0.688	-0.21	0.836
Latitude	0.016	0.014	1.19	0.235
Longitude	-0.198	0.066	-2.97	0.003
Latitude*Longitude	0.004	0.001	2.84	0.005

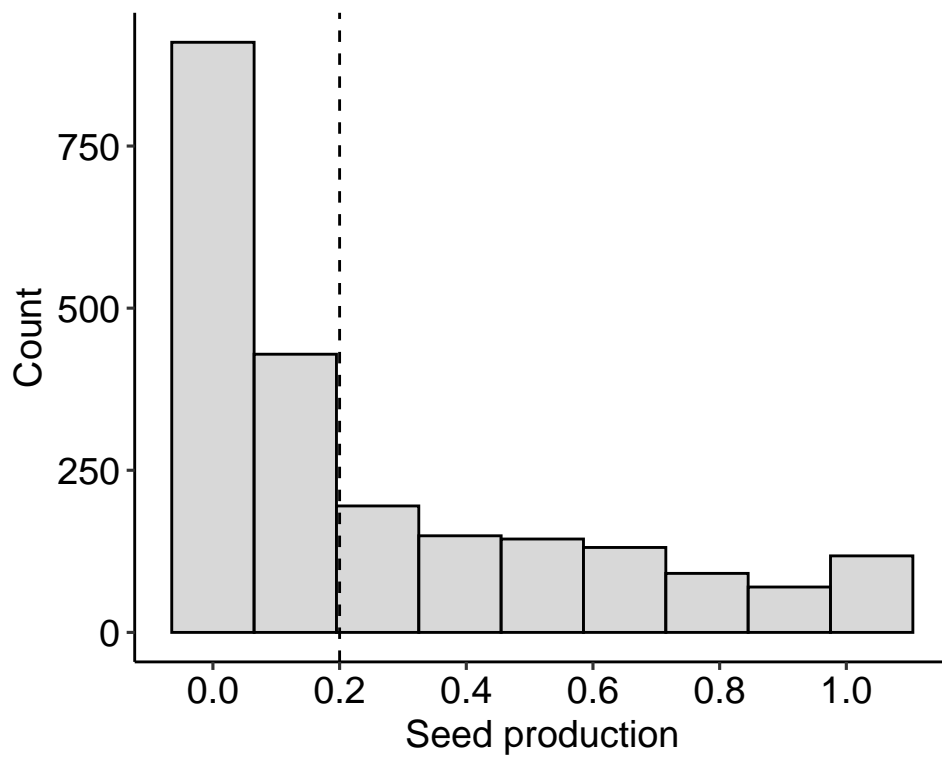


Figure S1: Distribution of annual seed production values used in the analysis, scaled within each site to values between 0 and 1. The vertical dashed line shows the categorization of masting into lower (left) and upper (right) tails.

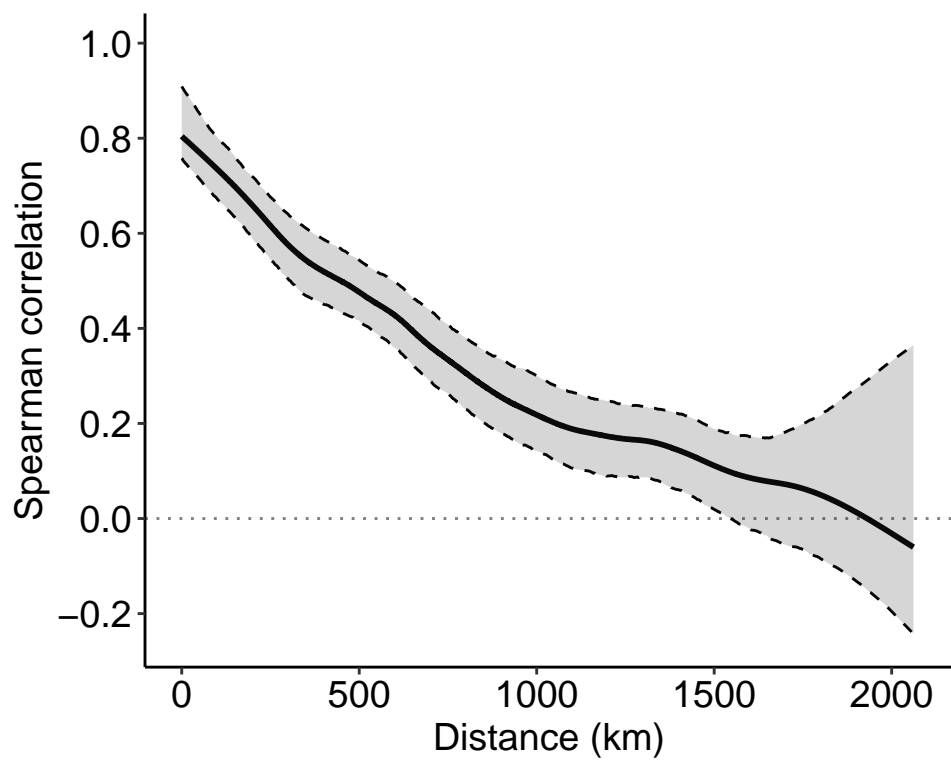


Figure S2: Distance decay of beech masting synchrony, as measured by pairwise Spearman correlation, if seed production series were not split into tails. The data used is visualized in Fig 2.

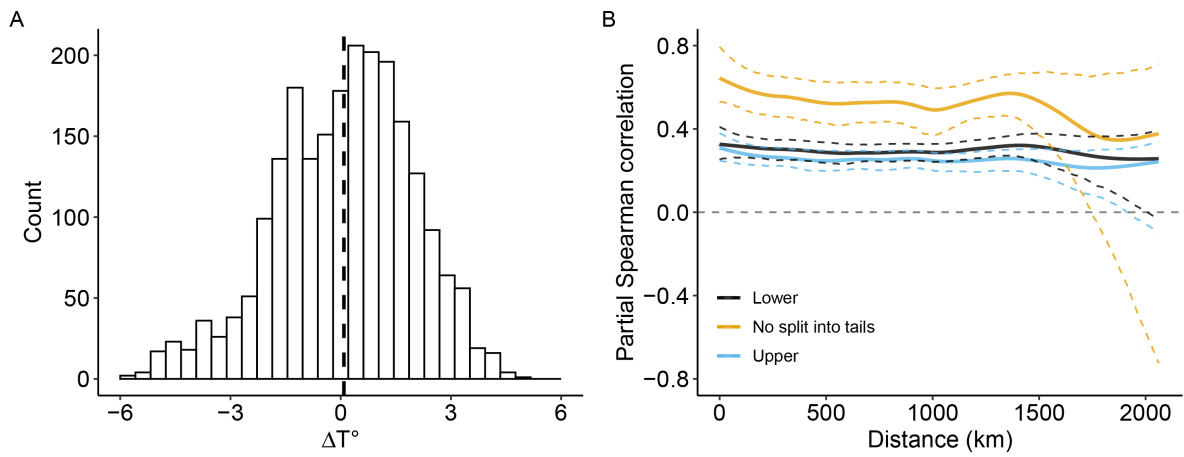


Figure S3: (A) Distribution of ΔT values observed during the studied period. Vertical dashed line indicates mean ΔT value of 0.09. (B) Distance decay of spatial synchrony in ΔT , as measured by pairwise Spearman correlation, in the lower and upper tail, as well as if the ΔT time series were not split into tails.