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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Abstract

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

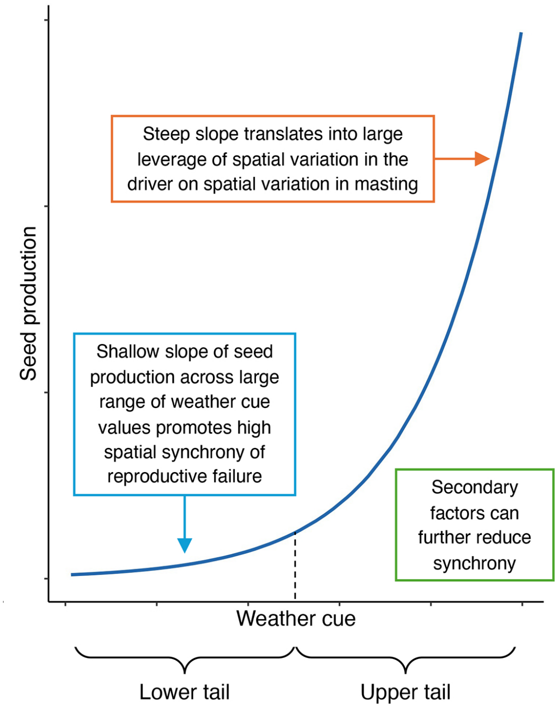
keywords: Moran effect | mast seeding | geography of synchrony | pulsed resources | plant reproduction | seed production | spatial synchrony | tail-dependent synchrony

Introduction

Spatial synchrony, the tendency of ecological phenomena to manifest correlated fluctuations across diverse locations, impacts regional ecosystem functioning, leading to both large-scale outbreaks and shortages (Ostfeld & Keesing, 2000; Earn *et al.*, 2000; Liebhold *et al.*, 2004; Bjørnstad *et al.*, 2002). One ecological phenomenon exhibiting diverse ecosystem consequences and considerable spatial synchrony is mast seeding, a common reproductive strategy in perennial plants (Koenig & Knops, 2000; Kelly & Sork, 2002; LaMontagne *et al.*, 2020; Journé *et al.*, 2023). In masting plants, seed production varies markedly between years, characterized by frequent reproductive failures interspersed with peaks many times greater than the long-term average (Kelly, 1994). This year-to-year variation is synchronized among individuals and can extend to subcontinental scales, thereby triggering extensive disruptions in food webs (Ostfeld & Keesing, 2000; Bogdziewicz *et al.*, 2016; Clark *et al.*, 2019). On the one hand, mast peaks generate a resource pulse resulting in outbreaks of rodents, insects, and other seed consumers that spread up the food web (Schmidt & Ostfeld, 2003), spikes in rodent-borne human diseases (Jones *et al.*, 1998; Bregnard *et al.*, 2021), and elevated concentrations of allergenic pollen (Tseng *et al.*, 2020). Conversely, years devoid of seed production lead to famines, causing rodent population crashes (Zwolak *et al.*, 2018), poor or skipped reproduction in birds and mammals (Ruf *et al.*, 2006; Fidler *et al.*, 2008; Cachelou *et al.*, 2022), the emigration of seedeating wildlife (Zuckerberg *et al.*, 2020), immigration of birds attracted to habitats where rodents are scarce (Szymkowiak & Thomson, 2019; Maag *et al.*, 2024), or increased human-wildlife conflicts as consumers seek food outside of forests (Kozakai *et al.*, 2011; Bautista *et al.*, 2023). The consequences of pulsed resources from mast peaks and famines resulting from years of seed scarcity are magnified by the spatial scale of their synchrony (Yang *et al.*, 2008; Bogdziewicz *et al.*, 2016; Clark *et al.*, 2019). Novel theory indicates that this spatial synchrony may exhibit tail-dependency, being stronger in either mast peaks or troughs (seed scarcity) (Walter *et al.*, 2022), with significant and distinct ecosystem implications, but this has never been explored.

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

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



Glossary:

Upper/lower tail:
values in time series separated into two groups, based on, for example, their median value.

Upper/lower tail synchrony:
Correlation between time series in upper/lower part of their distribution.

Tail-dependent environmental effects:
correlation between response and environmental variables, segmented into upper and lower portions of the environmental driver distribution.

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.

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

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

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

In this study, we analyzed data from 99 populations of the major European species, European beech (*Fagus sylvatica*), sampled across the species' range, to investigate the presence of tail-dependence in regional masting synchrony. The regional synchronization of beech masting is attributed to the Moran effect (Vacchiano *et al.*, 2017; Bogdziewicz *et al.*, 2021a, 2023a; Journé *et al.*, 2024). Past research investigated mechanisms leading to large-scale synchrony in overall masting pattern (Vacchiano *et al.*, 2017; Bogdziewicz *et al.*, 2023a), but a clear understanding of the relative importance of peaks and troughs synchrony remains unexplored. The forest-forming nature and extensive range of European beech (Leuschner & Ellenberg, 2017) amplify the consequences of potential tail-dependence in beech masting synchrony. Beech's seed production is responsive to consecutive summer temperatures, with sequential cold and hot summers cueing high flowering initiation (Piovesan & Adams, 2001; Journé *et al.*, 2023). Here we used ΔT (difference between summer temperatures in one and two years before seed fall) as the weather cue. First, we estimated the shape of the relationship between weather cue and beech masting, expecting a non-linear response where the relationship is steeper in the upper tail. This implies that seed production will have a weaker association with the weather cue until large cue values are reached. According to the tail-dependence theory (Ghosh *et al.*, 2020, 2021; Walter *et al.*, 2022), such upper tail-dependence in the weather-masting association should result in higher synchrony of masting peaks compared to synchrony of seed scarcity. Alternatively, the synchrony of seed scarcity may surpass the synchrony of peaks if non-linear association of masting and weather cue results in little seed production occurs across relatively large temperature ranges in the lower tails. This allows seed scarcity to synchronize as long as temperature variations remain within that range (Fig. 1).

Materials and Methods

Materials

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

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

Analysis

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

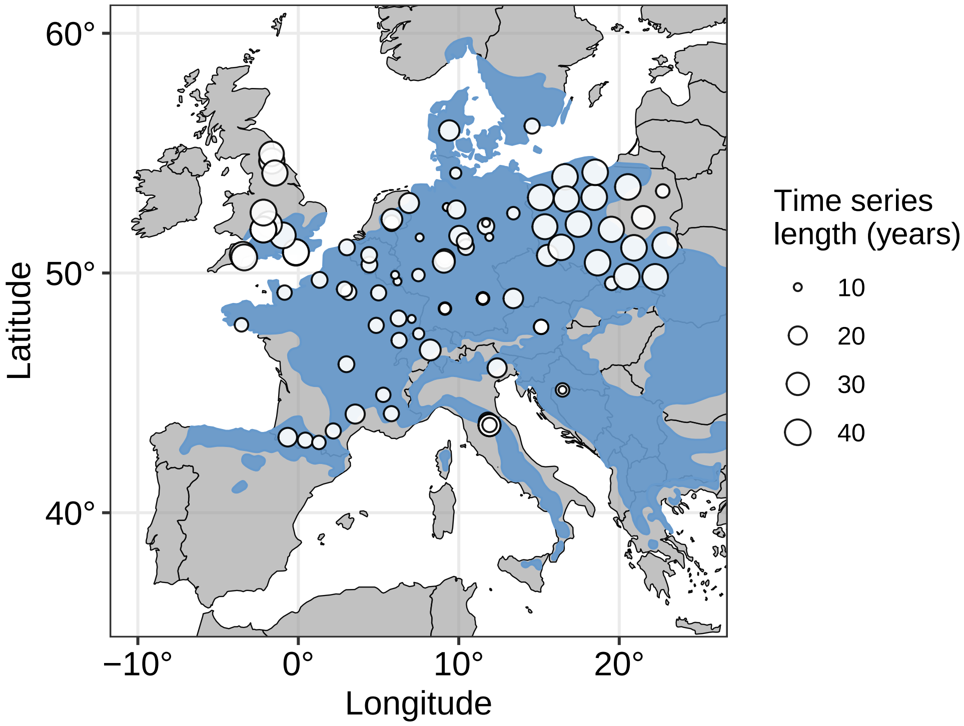


Figure 2: Locations of the 99 time series of annual seed production of European beech used in the study. Point size is scaled to the number of years (N) masting was monitored at the focal location, and the blue shading highlights the European beech natural range. An animation showing the spatiotemporal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

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

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

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

Tail-dependence in regional masting synchrony

Categorization of masting and weather into tails Our framework follows that of Walter *et al.* (2022). First, we divided masting and weather data into tails. Masting lower tail includes annual values of seed production ≤ 0.2, while upper those > 0.2, for seed production scaled within each site to values between 0 and 1 (see above). That categorization reflects the distribution of annual values of seed production (Fig. S1), and provides 1347 observations in the lower, and 890 in the upper masting tail. The weather cue was divided into roughly two equal parts, using ΔT = 0 as the threshold. This follows from the nature of the masting-cue association, as high seeding occurs once temperatures in summer T1 are larger than in T2, resulting in positive ΔT values (Kelly *et al.*, 2013; Vacchiano *et al.*, 2017). The thresholds are fairly arbitrary in the sense that neither masting nor weather is a categorical variable. Nonetheless, categorization was tailored to the nature of the data, is biologically justified, and allows the tail-dependence to be analyzed (Ghosh *et al.*, 2021; Walter *et al.*, 2022). Tail separation of masting data is required to estimate the synchrony of mast peaks and seed scarcity. In turn, tail separation of the weather cue is required to estimate the tail-dependent weather effects on masting (Fig. 1).

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

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

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

Drivers of tail-dependent masting synchrony We used the multiple regression quadratic assignment procedure with double-semipartialing (MRQAP) to investigate what drives the spatial synchrony of mast seeding within the lower and upper tail. The MRQAP is a modeling framework allowing investigation of the relationship between a dependent matrix and independent matrices while considering the non-independence of network data by using permutation techniques to test the significance of effect sizes (Dekker *et al.*, 2007). We built two MRQAP models in which masting synchrony within each tail, as measured by partial Spearman correlations, were the response matrices. In both models, the explanatory matrices were the synchrony (partial Spearman correlations) of the weather cue (ΔT) and between-site similarity in the masting-weather cue relationship in the focal tail. For the latter, we fitted site-level beta regression models with seed production (scaled to fall in a set (0, 1)) as a response and ΔT as a predictor, separately for the lower and upper tail of the weather data series. From these models, we extracted slopes for ΔT, providing a measure of the strength of the masting-weather cue relationship at a given site and in a given tail. We then calculated between-site pairwise similarities of those relationships, by first calculating the Euclidean distances between the slopes for all pairs of sites and then converting them into similarity indices by the formula (1 - [distance/maximum distance] (Bogdziewicz *et al.*, 2021a). Further explanatory matrices were between-site similarities in mean annual temperature and mean annual precipitation, as well as between-site spatial distance. To facilitate effects comparison, all matrices were linearly scaled between 0 and 1. In both MRQAP models, we tested for statistical significance using t-statistics and 1000 permutations. The models were fitted using *asnipe* ver. 1.1.16 R package (Farine, 2013).

Results

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

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

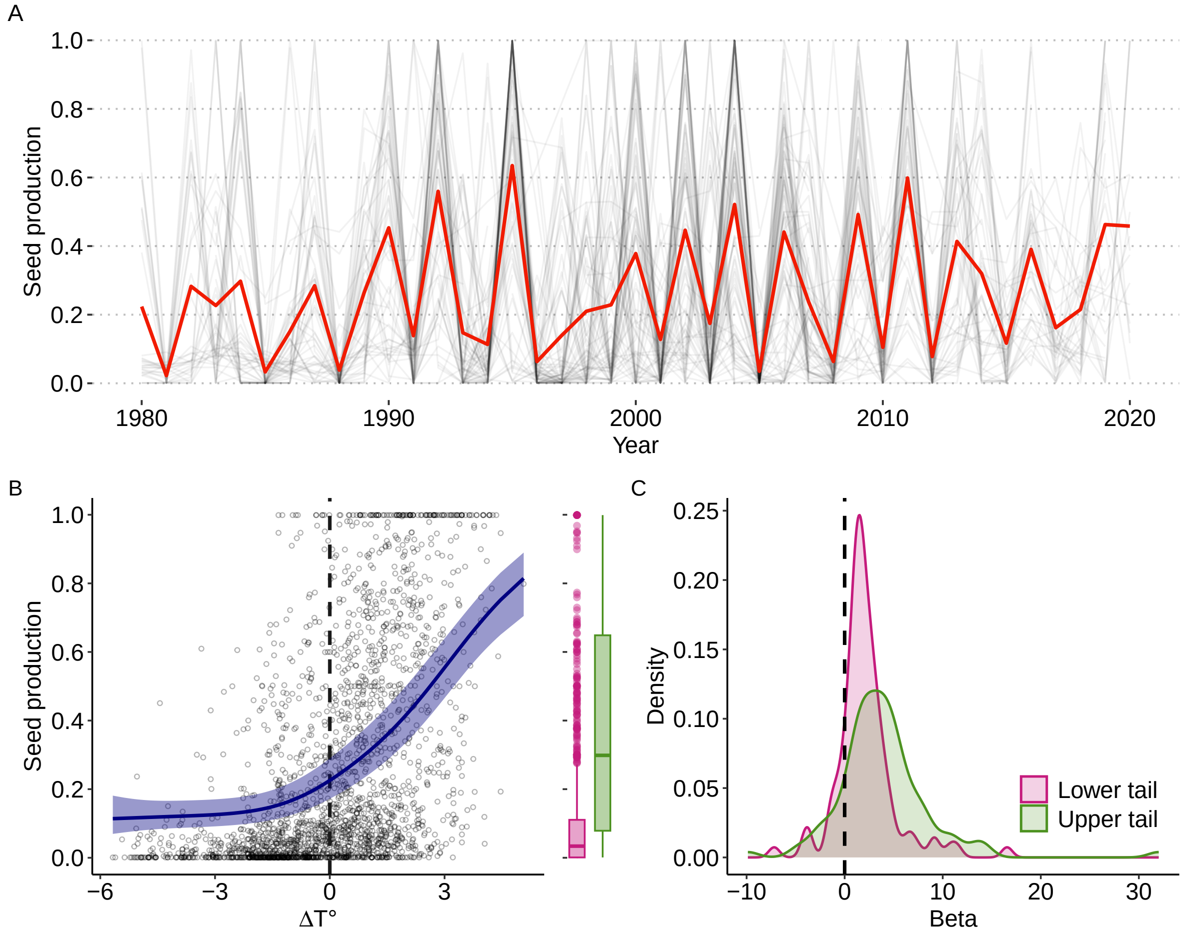


Figure 3: (A) Temporal dynamics of European beech *Fagus sylvatica*) seed production, with grey lines showing population-level data series, and the red line showing the yearly mean across all 99 sites. (B) Relationship between beech seed production and weather cue (ΔT, i.e. the difference between June-July 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.

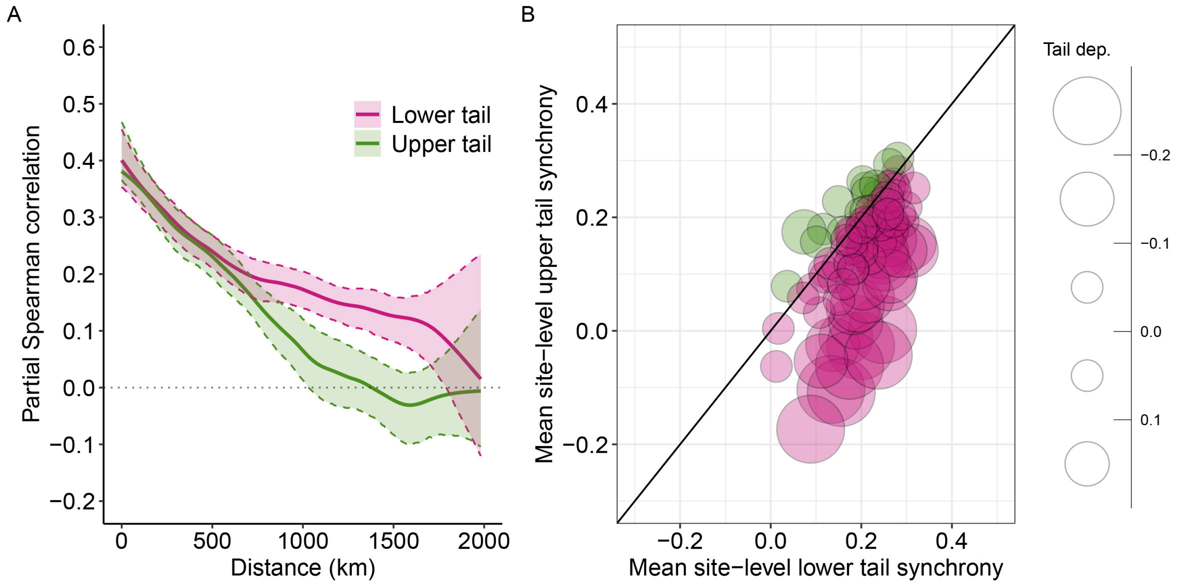


Figure 4: Tail dependence in beech masting synchrony. A) distance decay of beech masting synchrony in the upper and lower tail. The lower tail is seed production below 0.2, while the upper is above, for annual values scaled within each site to between 0 and 1. That categorization follows from the shape 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.

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

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

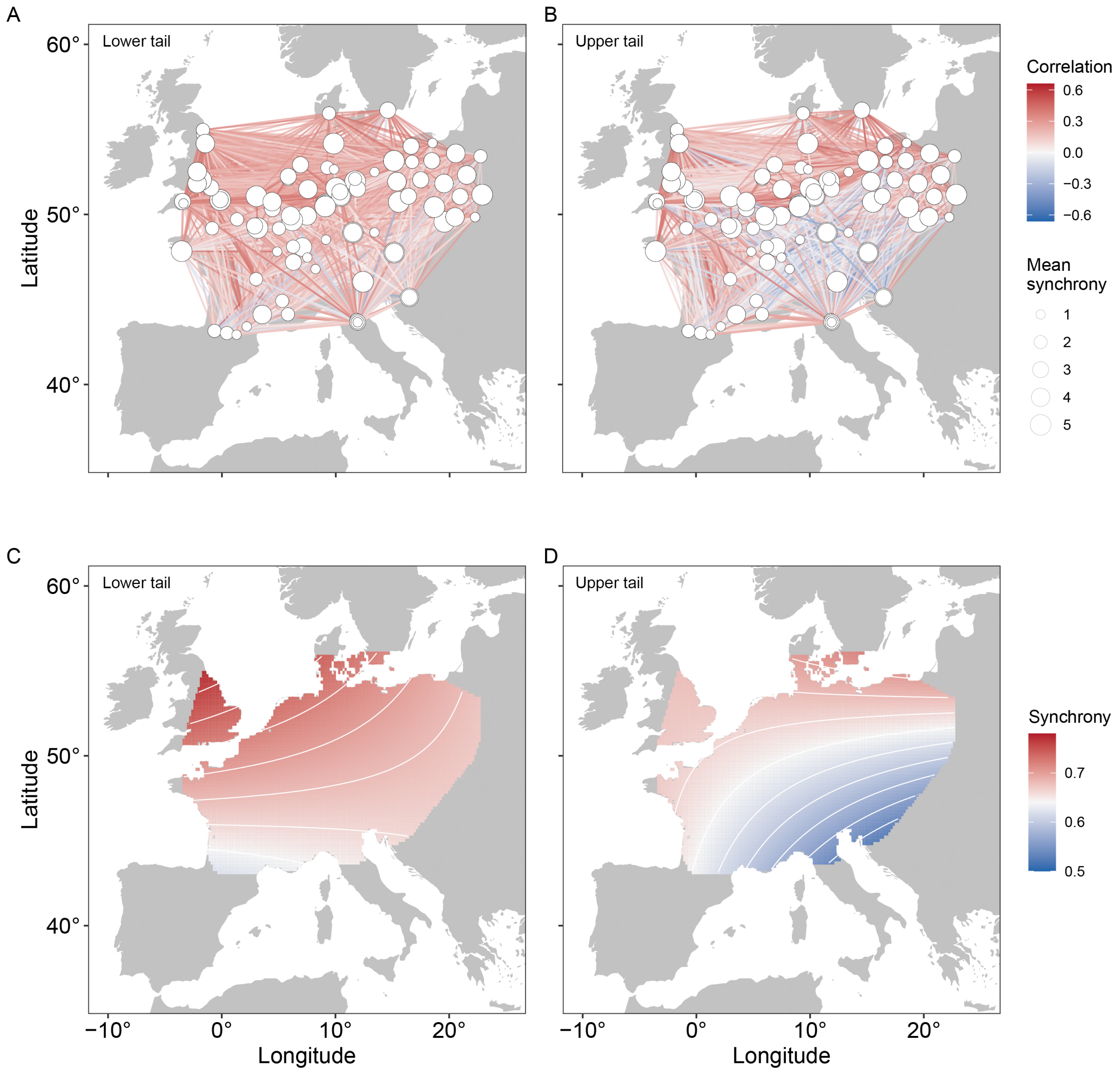


Figure 5: Networks of masting synchrony in A), C) lower and B), D) upper tail. At A) and B) points are sites and lines show their pairwise synchrony in masting. Point sizes are scaled according to site-level mean synchrony of seed production within a given tail. C) and D) show synchrony as estimated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

masting synchrony in both tails (Table 1). Moreover, in both tails, the spatial distance between 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

Discussion

Analyzing tail-dependent, regional beech masting synchrony revealed that seed scarcity can occur simultaneously across the vast majority of the species range. Moreover, the synchrony of seed scarcity extends 1.8 times further (approximately 1800 km) than the already extensive synchrony of mast peaks (approximately 1000 km). Contrary to the predictions of the tail-dependence theory (Ghosh *et al.*, 2020, 2021; Walter *et al.*, 2022), the upper-tail association between weather cues and masting did not result in stronger synchrony of masting peaks. Upper-tail masting synchrony was not higher than lower tail at any distance and started to decline more rapidly. This result appears to stem from the nature of the relationship between beech masting and its weather cue. The relationship translates into a minor increase in seed production across a relatively broad range of cue values, promoting spatial synchrony of seed scarcity by buffering against fluctuations within that cue range. In turn, for large values of the cue, the relatively small among-site variation in temperature results in a large variation in seed production investment across sites. Additionally, while it is sufficient for one factor to veto seed production (Pesendorfer *et al.*, 2016; Abe *et al.*, 2016; Bogdziewicz *et al.*, 2018), various other factors determine the size of a mast peak (Ascoli *et al.*, 2017, 2021; Journé *et al.*, 2023). The identification of tail-dependency in masting synchrony presented here provides new insights into the consequences of masting association with weather variation, with diverse consequences for food web functioning, masting forecasting, and climate change biology.

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

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

The regional synchrony of seed scarcity surpassing the synchrony of mast peaks holds significant implications for food webs, forest and wildlife management, and seed production forecasting. A key fitness benefit of masting lies in predator satiation (Kelly, 1994; Pearse *et al.*, 2016). The synchronized, substantial year-to-year variation in seed production starves seed consumers in low-seeding years, facilitating the satiation of these consumer populations in mast years (Zwolak *et al.*, 2022). High regional synchrony of seed scarcity can enhance the starvation of highly mobile seed consumers, such as large mammals or birds (Curran & Leighton, 2000; Bogdziewicz *et al.*, 2022). This finding is especially relevant for southeastern Europe, where synchronous seed scarcity will aid satiation despite desynchronized mast peaks. Forecasting years of high and low seed production emerges as an important tool for aiding management and conservation efforts in ecosystems dominated by masting species (Pearse *et al.*, 2021; Journé *et al.*, 2023). The higher spatial synchrony of seed scarcity means that spatial extrapolation of failure forecasts is more feasible compared to mast peaks. In restoration projects, the extensive spatial scale of seeding failure implies that acquiring material for replanting may be restricted in some years, as poor seeding can extend over the majority of the species range. Finally, in some species, including European beech, tree and leaf growth is reduced in years of high seed production, leading to synchronized fluctuations in carbon sequestration (Hacket-Pain *et al.*, 2018; Vergotti *et al.*, 2019; Mund *et al.*, 2020). Dividing masting synchrony into tails indicates less extensive synchrony of peaks, and consequently a more geographically restricted role for masting as a driver of synchrony in forest growth and carbon sequestration variability.

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

One aspect of regional masting synchrony not addressed in our analysis is its potential variability over time, which may be influenced by climate oscillations. The North Atlantic Oscillation (NAO) is the leading climatic driver in Europe, exerting influence over spatial weather patterns (Ascoli *et al.*, 2021). Consequently, the extent of regional masting synchrony may fluctuate in response to shifts in the NAO phase (Ascoli *et al.*, 2017). Similarly, the positioning of the jet stream over Europe plays an important role in shaping continental weather patterns, thereby impacting forest productivity (Dorado-Liñán *et al.*, 2022). The dynamic weather dipoles created by the jet stream's positioning can thus alter the geographical distribution of masting events. By averaging across temporal conditions, as done in our analysis, these effects are overlooked. For instance, the geographical patterns of masting synchrony described in this study are likely to exhibit temporal dynamics, representing an interesting avenue for future research.

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

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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 availability statement

The data 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).

References

Abe, T., Tachiki, Y., Kon, H., Nagasaka, A., Onodera, K., Minamino, K. *et al.* (2016). Parameterisation and validation of a resource budget model for masting using spatiotemporal flowering data of individual trees. *Ecology Letters*, 19, 1129–1139.

Ascoli, D., Hacket-Pain, A., Pearse, I.S., Vacchiano, G., Corti, S. & Davini, P. (2021). Modes of climate variability bridge proximate and evolutionary mechanisms of masting. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200380.

Ascoli, D., Vacchiano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J. *et al.* (2017). Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications 2017 8:1*, 8, 1–9.

Bautista, C., Oeser, J., Kuemmerle, T. & Selva, N. (2023). Resource pulses and human–wildlife conflicts: linking satellite indicators and ground data on forest productivity to predict brown bear damages. *Remote Sensing in Ecology and Conservation*, 9, 90–103.

Bjørnstad, O. & Falck, W. (2021). Nonparametric spatial covariance functions: estimation and testing. *Ecology Letters*, 8, 53–70.

Bjørnstad, O.N., Peltonen, M., Liebhold, A.M. & Baltensweiler, W. (2002). Waves of larch budmoth outbreaks in the european alps. *Science*, 298, 1020–1023.

Bogdziewicz, M., Hacket-Pain, A., Ascoli, D. & Szymkowiak, J. (2021a). Environmental variation drives continental-scale synchrony of european beech reproduction. *Ecology*, 102, e03384.

Bogdziewicz, M., Hacket-Pain, A., Kelly, D., Thomas, P.A., Lageard, J. & Tanentzap, A.J. (2021b). Climate warming causes mast seeding to break down by reducing sensitivity to weather cues. *Global Change Biology*, 27, 1952–1961.

Bogdziewicz, M., Journé, V., Hacket-Pain, A. & Szymkowiak, J. (2023a). Mechanisms driving interspecific variation in regional synchrony of trees reproduction. *Ecology Letters*, 26, 754–764.

Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P., Foest, J., Lageard, J. *et al.* (2023b). Reproductive collapse in european beech results from declining pollination efficiency in large trees. *Global Change Biology*, 29, 4595–4604.

Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A. & Hacket-Pain, A. (2020). Climate warming disrupts mast seeding and its fitness benefits in european beech. *Nature Plants*, 6, 88–94.

Bogdziewicz, M., Kuijper, D., Zwolak, R., Churski, M., drzejewska, B.J., Wysocka-Fijorek, E. *et al.* (2022). Emerging infectious disease triggered a trophic cascade and enhanced recruitment of a masting tree. *Proceedings of the Royal Society B: Biological Sciences*, 289.

Bogdziewicz, M., Steele, M.A., Marino, S. & Crone, E.E. (2018). Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytologist*, 219, 98–108.

Bogdziewicz, M., Zwolak, R. & Crone, E.E. (2016). How do vertebrates respond to mast seeding? *Oikos*, 125, 300–307.

Bregnard, C., Rais, O. & Voordouw, M.J. (2021). Masting by beech trees predicts the risk of lyme disease. *Parasites and Vectors*, 14, 1–22.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. *et al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Cachelou, J., Saint-Andrieux, C., Baubet, E., Nivois, E., Richard, E., Gaillard, J.M. *et al.* (2022). Does mast seeding shape mating time in wild boar? a comparative study. *Biology Letters*, 18.

Clark, J.S., Nuñez, C.L. & Tomasek, B. (2019). Foodwebs based on unreliable foundations: spatiotemporal masting merged with consumer movement, storage, and diet. *Ecological Monographs*, 89, e01381.

Cornes, R.C., van der Schrier, G., van den Besselaar, E.J. & Jones, P.D. (2018). An ensemble version of the e-obs temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123, 9391–9409.

Craig, P.M. & Allan, R.P. (2022). The role of teleconnection patterns in the variability and trends of growing season indices across europe. *International Journal of Climatology*, 42, 1072–1091.

Crone, E.E., Miller, E. & Sala, A. (2009). How do plants know when other plants are flowering? resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters*, 12, 1119–1126.

Crone, E.E. & Rapp, J.M. (2014). Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences*, 1322, 21–34.

Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal*, Complex Systems, 1695.

Curran, L.M. & Leighton, M. (2000). Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting dipterocarpaceae. *Ecological Monographs*, 70, 101–128.

Dekker, D., Krackhardt, D. & Snijders, T.A. (2007). Sensitivity of mrqap tests to collinearity and autocorrelation conditions. *Psychometrika*, 72, 563–581.

Dorado-Liñán, I., Ayarzagüena, B., Babst, F., Xu, G., Gil, L., Battipaglia, G. *et al.* (2022). Jet stream position explains regional anomalies in european beech forest productivity and tree growth. *Nature Communications*, 13.

Earn, D.J., Levin, S.A. & Rohani, P. (2000). Coherence and conservation. *Science*, 290, 1360–1364.

Farine, D.R. (2013). Animal social network inference and permutations for ecologists in r using asnipe. *Methods in Ecology and Evolution*, 4, 1187–1194.

Fernández-Martínez, M., Bogdziewicz, M., Espelta, J.M. & Peñuelas, J. (2017). Nature beyond linearity: Meteorological variability and jensen's inequality can explain mast seeding behavior. *Frontiers in Ecology and Evolution*, 5.

Fidler, A.E., Lawrence, S.B. & McNatty, K.P. (2008). An hypothesis to explain the linkage between kakapo (strigops habroptilus) breeding and the mast fruiting of their food trees. *Wildlife Research*, 35, 1–7.

Fleurot, E., Lobry, J.R., Boulanger, V., Debias, F., Mermet-Bouvier, C., Caignard, T. *et al.* (2023). Oak masting drivers vary between populations depending on their climatic environments. *Current Biology*, 33, 1117–1124.E4.

Foest, J.J., Bogdziewicz, M., Pesendorfer, M.B., Ascoli, D., Cutini, A., Nussbaumer, A. *et al.* (2024). Widespread breakdown in masting in european beech due to rising summer temperatures. *Global Change Biology*, 30.

Folland, C.K., Knight, J., Linderholm, H.W., Fereday, D., Ineson, S. & Hurrel, J.W. (2009). The summer north atlantic oscillation: Past, present, and future. *Journal of Climate*, 22, 1082–1103.

Ghosh, S., Cottingham, K.L. & Reuman, D.C. (2021). Species relationships in the extremes and their influence on community stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376.

Ghosh, S., Sheppard, L.W., Reid, P.C. & Reuman, D. (2020). A new approach to interspecific synchrony in population ecology using tail association. *Ecology and Evolution*, 10, 12764–12776.

Hacket-Pain, A., Foest, J.J., Pearse, I.S., LaMontagne, J.M., Koenig, W.D., Vacchiano, G. *et al.* (2022). Mastree+: Time-series of plant reproductive effort from six continents. *Global Change Biology*, 28, 3066–3082.

Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M. *et al.* (2018). Climatically controlled reproduction drives interannual growth variability in a temperate tree species. *Ecology Letters*, 21, 1833–1844.

Han, Q. & Kabeya, D. (2017). Recent developments in understanding mast seeding in relation to dynamics of carbon and nitrogen resources in temperate trees. *Ecological Research 2017 32:6*, 32, 771–778.

Jones, C.G., Ostfeld, R.S., Richard, M.P., Schauber, E.M. & Wolff, J.O. (1998). Chain reactions linking acorns to gypsy moth outbreaks and lyme disease risk. *Science*, 279, 1023–1026.

Journé, V., Hacket-Pain, A. & Bogdziewicz, M. (2023). Evolution of masting in plants is linked to investment in low tissue mortality. *Nature Communications*, 14, 7998.

Journé, V., Hacket-Pain, A., Oberklammer, I., Pesendorfer, M.B. & Bogdziewicz, M. (2023). Forecasting seed production in perennial plants: identifying challenges and charting a path forward. *New Phytologist*, 239, 466–476.

Journé, V., Szymkowiak, J., Foest, J., Hacket-Pain, A., Kelly, D. & Bogdziewicz, M. (2024). Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants*.

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology Evolution*, 9, 465–470.

Kelly, D., Geldenhuis, A., James, A., Holland, E.P., Plank, M.J., Brockie, R.E. *et al.* (2013). Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters*, 16, 90–98.

Kelly, D. & Sork, V.L. (2002). Mast seeding in perennial plants: Why, how, where? *Annual Review of Ecology and Systematics*, 33, 427–447.

Koenig, W.D., Knops, J.M., Carmen, W.J. & Pearse, I.S. (2015). What drives masting? the phenological synchrony hypothesis. *Ecology*, 96, 184–192.

Koenig, W.D. & Knops, J.M.H. (2000). Patterns of annual seed production by northern hemisphere trees: A global perspective. *American Naturalist*, 155, 59–69.

Koenig, W.D. & Knops, J.M.H. (2013). Large-scale spatial synchrony and cross-synchrony in acorn production by two california oaks. *Ecology*, 94, 83–93.

Kozakai, C., Yamazaki, K., Nemoto, Y., Nakajima, A., Koike, S., Abe, S. *et al.* (2011). Effect of mast production on home range use of japanese black bears. *Journal of Wildlife Management*, 75, 867–875.

LaMontagne, J.M., Pearse, I.S., Greene, D.F. & Koenig, W.D. (2020). Mast seeding patterns are asynchronous at a continental scale. *Nature Plants*, 6, 460–465.

Leuschner, C. & Ellenberg, H. (2017). Beech and mixed beech forests. *Ecology ofCentral European Forests: Vegetation Ecology of Central Europe*, 1, 351–441).

Liebhold, A., Sork, V., Peltonen, M., Koenig, W., Bjørnstad, O.N., Westfall, R. *et al.* (2004). Within-population spatial synchrony in mast seeding of north american oaks. *Oikos*, 104, 156–164.

Maag, N., Korner-Nievergelt, F., Szymkowiak, J., Hałas, N., Maziarz, M., Neubauer, G. *et al.* (2024). Wood warbler population dynamics in response to mast seeding regimes in europe. *Ecology*.

Mund, M., Herbst, M., Knohl, A., Matthäus, B., Schumacher, J., Schall, P. *et al.* (2020). It is not just a ‘trade-off’: indications for sink- and source-limitation to vegetative and regenerative growth in an old-growth beech forest. *New Phytologist*, 226, 111–125.

Nilsson, S.G. & Wastljung, U. (1987). Seed predation and cross-pollination in mast-seeding beech (fagus sylvatica) patches. *Ecology*, 68, 260–265.

Nussbaumer, A., Meusburger, K., Schmitt, M., Waldner, P., Gehrig, R., Haeni, M. *et al.* (2020). Extreme summer heat and drought lead to early fruit abortion in european beech. *Scientific Reports 2020 10:1*, 10, 1–11.

Nussbaumer, A., Waldner, P., Apuhtin, V., Aytar, F., Benham, S., Bussotti, F. *et al.* (2018). Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in europe. *Forest Ecology and Management*, 429, 336–350.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology Evolution*, 15, 232–237.

Parmenter, R.R., Zlotin, R.I., Moore, D.I. & Myers, O.B. (2018). Environmental and endogenous drivers of tree mast production and synchrony in piñon–juniper–oak woodlands of new mexico. *Ecosphere*, 9, e02360.

Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212, 546–562.

Pearse, I.S., Wion, A.P., Gonzalez, A.D. & Pesendorfer, M.B. (2021). Understanding mast seeding for conservation and land management. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 34657466.

Pesendorfer, M.B., Koenig, W.D., Pearse, I.S., Knops, J.M. & Funk, K.A. (2016). Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (quercus lobata). *Journal of Ecology*, 104, 637–645.

Piovesan, G. & Adams, J.M. (2001). Masting behaviour in beech: Linking reproduction and climatic variation. *Canadian Journal of Botany*, 79, 1039–1047.

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reuman, D.C., Castorani, M.C.N., Cavanaugh, K.C., Sheppard, L.W., Walter, J.A. & Bell, T.W. (2023). How environmental drivers of spatial synchrony interact. *Ecography*, 2023, e06795.

Ruf, T., Fietz, J., Schlund, W., & Bieber, C. (2006). High survival in poor years: life history tactics adopted to mast seeding in edible dormouse. *Ecology*, 87, 372–381.

Samarth, Lee, R., Kelly, D., Turnbull, M.H., Macknight, R.C., Poole, A.M. *et al.* (2021). Molecular control of the floral transition in the mast seeding plant celmisia lyallii (asteraceae). *Molecular Ecology*, 30, 1846–1863.

Satake, A. & Iwasa, Y. (2000). Pollen coupling of forest trees: Forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology*, 203, 63–84.

Satake, A. & Kelly, D. (2021). Studying the genetic basis of masting. *Philosophical Transactions of the Royal Society B*, 376, 20210116.

Schauber, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B. *et al.* (2002). Masting by eighteen new zealand plant species: The role of temperature as a synchronizing cue. *Ecology*, 83, 1214–1225.

Schermer, E., Bel-Venner, M.C., Gaillard, J.M., Dray, S., Boulanger, V., Roncé, I.L. *et al.* (2020). Flower phenology as a disruptor of the fruiting dynamics in temperate oak species. *New Phytologist*, 225, 1181–1192.

Schmidt, K.A. & Ostfeld, R.S. (2003). Songbird populations in fluctuating environments: Predator responses to pulsed resources. *Ecology*, 84, 406–415.

Smith, S.J., McCarthy, B.C., Hutchinson, T.F. & Snell, R.S. (2021). Both weather and resources influence masting in chestnut oak (quercus montana willd.) and black oak (q. velutina lam.). *Plant Ecology*.

Szymkowiak, J. & Thomson, R.L. (2019). Nest predator avoidance during habitat selection of a songbird varies with mast peaks and troughs. *Behavioral Ecology and Sociobiology*, 73, 91.

Tseng, Y.T., Kawashima, S., Kobayashi, S., Takeuchi, S. & Nakamura, K. (2020). Forecasting the seasonal pollen index by using a hidden markov model combining meteorological and biological factors. *Science of the Total Environment*, 698, 134246.

Vacchiano, G., Hacket-Pain, A., Turco, M., Motta, R., Maringer, J., Conedera, M. *et al.* (2017). Spatial patterns and broad-scale weather cues of beech mast seeding in europe. *New Phytologist*, 215, 595–608.

Vergotti, M.J., Fernández-Martínez, M., Kefauver, S.C., Janssens, I.A. & Peñuelas, J. (2019). Weather and trade-offs between growth and reproduction regulate fruit production in european forests. *Agricultural and Forest Meteorology*, 279, 107711.

Walter, J.A., Castorani, M.C., Bell, T.W., Sheppard, L., Cavanaugh, K.C. & Reuman, D.C. (2022). Tail-dependent spatial synchrony arises from nonlinear driver–response relationships. *Ecology Letters*, 25, 1189–1201.

Wion, A.P., Weisberg, P.J., Pearse, I.S. & Redmond, M.D. (2020). Aridity drives spatiotemporal patterns of masting across the latitudinal range of a dryland conifer. *Ecography*, 43, 569–580.

Wood, S. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, 73, 3–36.

Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008). What can we learn from resource pulses. *Ecology*, 89, 621–634.

Yukich-Clendon, O.M.M., Carpenter, J.K., Kelly, D., Timoti, P., Burns, B.R., Boswijk, G. *et al.* (2023). Global change explains reduced seeding in a widespread new zealand tree: indigenous tūhoe knowledge informs mechanistic analysis. *Frontiers in Forests and Global Change*, 6, 1172326.

Zuckerberg, B., Strong, C., LaMontagne, J.M., George, S.S., Betancourt, J.L. & Koenig, W.D. (2020). Climate dipoles as continental drivers of plant and animal populations. *Trends in Ecology Evolution*, 35, 440–453.

Zwolak, R., Celebias, P. & Bogdziewicz, M. (2022). Global patterns in the predator satiation effect of masting: A meta-analysis. *Proceedings of the National Academy of Sciences of the United States of America*, 119, e2105655119.

Zwolak, R., Witczuk, J., Bogdziewicz, M., Rychlik, L. & Pagacz, S. (2018). Simultaneous population fluctuations of rodents in montane forests and alpine meadows suggest indirect effects of tree masting. *Journal of Mammalogy*, 99, 586–595.

Supporting Information

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) × 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

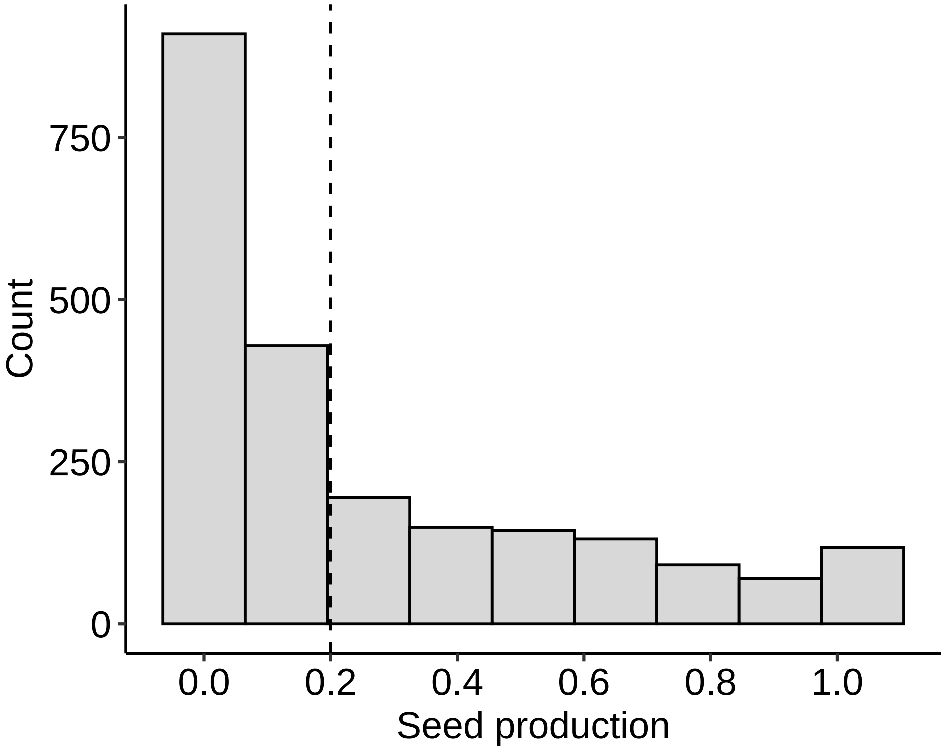

Figure S1: Distribution of annual seed production values used in the analysis, scaled within each site to values between 0 and 1. The vertical dashed line shows the categorization of masting into lower (left) and upper (right) tails.

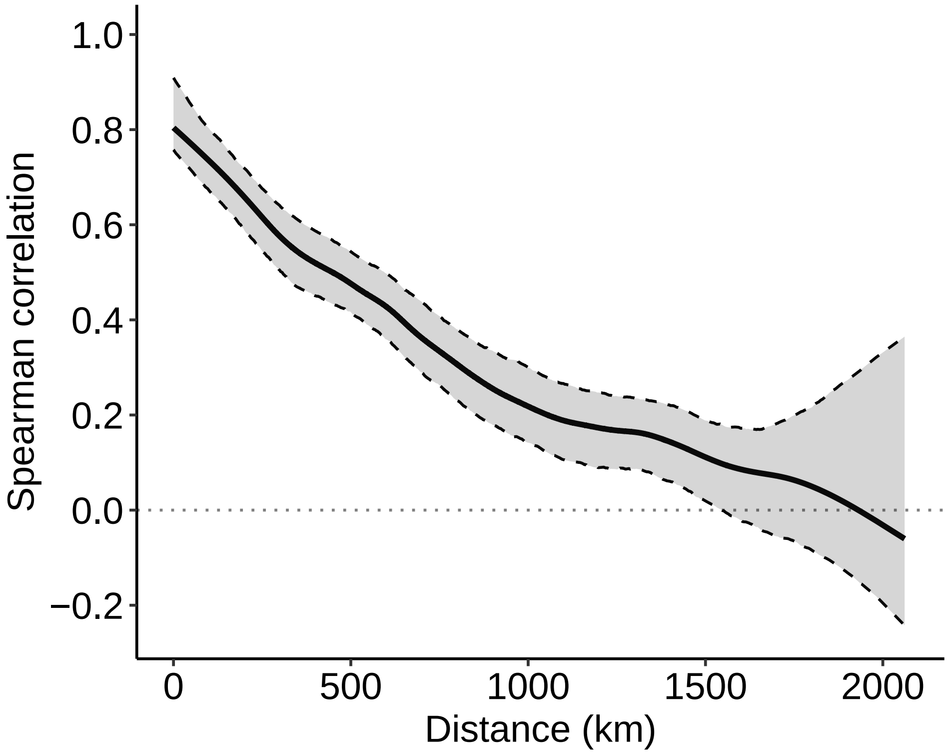

Figure S2: Distance decay of beech masting synchrony, as measured by pairwise Spearman correlation, if seed production series were not split into tails. The data used is visualized in Fig 2.

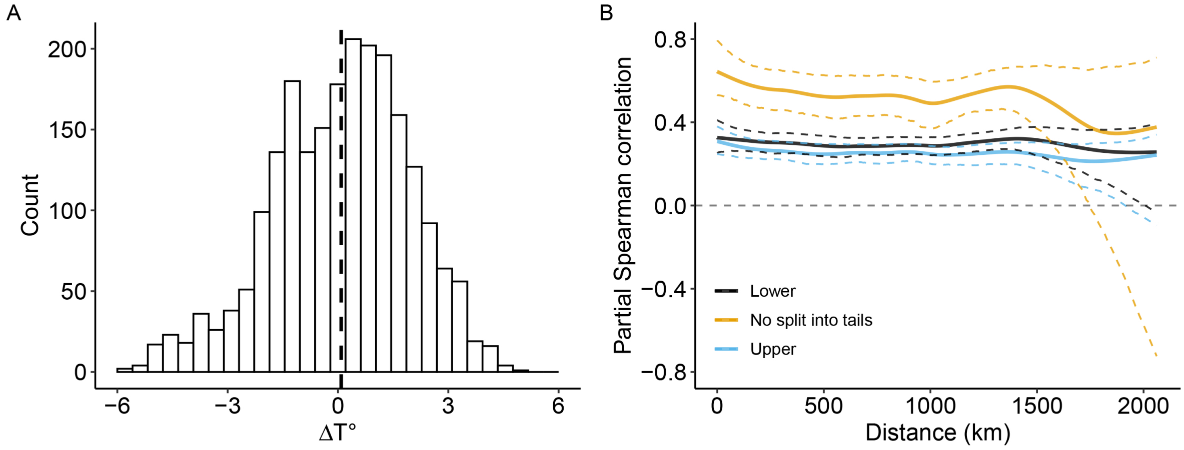

Figure S3: (A) Distribution of ΔT values observed during the studied period. Vertical dashed line indicades mean ΔT value of 0.09. (B) Distance decay of spatial synchrony in ΔT, as measured by pairwise Spearman correlation, in the lower and upper tail, as well as if the ΔT time series were not split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