Geography of masting synchrony creates more famines than feasts

Jakub Szymkowiak*[1,2], Jessie Foest[1], Marcin K. Dyderski[3], Szymon Jastrzębowski[4], Maciej Barczyk[1], Andrew Hacket-Pain[5], Michał Bogdziewicz*[1]

[1]Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland.
[2]Population Ecology Research Unit, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland.
[3]Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, Kórnik, 62-035, Poland.
[4]Department of Silviculture and Forest Tree Genetics, Forest Research Institute, Braci Leśnej 3, Sękocin Stary, 05-090, Raszyn, Poland.
[5]Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom.

*corresponding authors: jakub.szymkowiak@amu.edu.pl, michalbogdziewicz@gmail.com

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Abstract

Interannually highly variable and synchronized production of large seed crops by perennial plants, called masting, drives resource pulses and famines with cascading effects on food webs. While the spatial scale of masting synchrony is well documented, it remains unclear how synchrony differs between years of seed abundance and failure, and how such dynamics extend across species and space. These gaps are important to resolve, as they determine the magnitude and spatial extent of masting effects on food webs. Using a 36-year dataset from 431 sites spanning seven dominant tree species in temperate Europe, we provide evidence that seed failures are more spatially synchronized than mast peaks, indicating that regional coherence in seed production is structured primarily by reproductive failure. Among-species synchrony was localized, suggesting that temperate forests are unlikely to impose region-wide starvation–satiation cycles on mobile seed consumers: a contrast with highly synchronous tropical dipterocarp systems. From an applied perspective, failure years affect seed availability over broad regions, limiting sourcing options for afforestation and restoration, and underscoring the value of spatially explicit masting forecasting. Because mast peaks and failures differ fundamentally in their food web consequences, our findings highlight the need to better understand and anticipate the ecological impacts of synchronized seed scarcity.

Significance statement

Our study shows that synchronous seed failures, rather than peaks in seed production, dominate regional masting synchrony across temperate tree species. Since reproductive failures are more strongly synchronized over space than mast peaks, the ecological consequences of seed scarcity, such as food web bottlenecks and altered animal movements, may be more extensive and predictable than previously recognized. In contrast, among-species synchrony is limited in spatial extent, implying that generalist seed consumers are unlikely to experience coordinated starvation–satiation cycles across species. These findings highlight the need to reassess the ecological importance of synchronized seed failures and the buffering role of forest diversity in moderating masting-driven resource fluctuations.

Introduction

When ecological processes fluctuate together across locations, i.e., exhibit spatial synchrony, they shape regional ecosystem dynamics by amplifying resource pulses and shortages (Ostfeld & Keesing, 2000; Earn *et al.*, 2000; Bjørnstad *et al.*, 2002). A major example is mast seeding, a reproductive strategy common in perennial plants that involves occasional, synchronized episodes of large seed production separated by frequent years of scarcity (Journé *et al.*, 2023; Qiu *et al.*, 2023; Kondrat *et al.*, 2025). These spatially correlated fluctuations generate cascading effects across ecological levels through resource pulses and famines (LaMontagne *et al.*, 2020; Ostfeld & Keesing, 2000; Clark *et al.*, 2019). For plants, high-seeding years alter allocation patterns, reducing growth and defense investment, while increasing pollination success and seed predation escape (Kelly *et al.*, 2001; Lauder *et al.*, 2019; Zwolak *et al.*, 2022; Hacket-Pain *et al.*, 2025). For consumers, mast peaks trigger resource pulses that drive outbreaks of rodents, insects, and other seed consumers (Schmidt & Ostfeld, 2003; Gamelon *et al.*, 2017), increase rodent-borne disease risk in humans (Jones *et al.*, 1998; Bregnard *et al.*, 2021), and elevate allergenic pollen levels (Tseng *et al.*, 2020). In contrast, mast failures lead to widespread food scarcity, causing rodent crashes (Zwolak *et al.*, 2018), reproductive failure in insects, birds, and mammals (Ruf *et al.*, 2006; Fidler *et al.*, 2008; Bonal *et al.*, 2010; Cachelou *et al.*, 2022), shifts in animal movement such as emigration of seed predators (Zuckerberg *et al.*, 2020), immigration of birds (Szymkowiak & Thomson, 2019; Maag *et al.*, 2024), and elevated human-wildlife conflict as animals search beyond forests for food (Bautista *et al.*, 2023; Tattoni *et al.*, 2025). The magnitude of these ecological effects depends on masting synchrony, including whether masting synchronizes across species, whether peaks or failures synchronize more strongly, and how far such coherence extends (Woodman *et al.*, 2025; Bogdziewicz *et al.*, 2025).

On a proximate level, variation in seed production is commonly driven by weather cues that influence flowering and seed maturation (Kelly *et al.*, 2013; Koenig *et al.*, 2015; Journé *et al.*, 2024). Consequently, the regional synchronization of masting arises from the Moran effect, i.e., spatially correlated fluctuations in environmental drivers of reproduction (Koenig & Knops, 2013; Ascoli *et al.*, 2017; LaMontagne *et al.*, 2020; Wion *et al.*, 2020; Bogdziewicz *et al.*, 2021; Reuman *et al.*, 2023). Masting plants often respond non-linearly to weather cues, with low reproduction across a wide gradient of weather conditions and strong responses when cue values reach favorable levels (Kelly *et al.*, 2013; Fernández-Martínez *et al.*, ????). For example, in European temperate oaks (*Quercus robur* and *Q. petraea*), seed production is suppressed below 12°C spring temperatures but rises sharply above that threshold (Schermer *et al.*, 2020). Similarly, European beech (*Fagus sylvatica*) exhibits a non-linear response to its previous summer temperature cue, with weak responses at low temperatures that increase disproportionately under warmer conditions (Szymkowiak *et al.*, 2024b). Because individuals and populations respond collectively to shared weather cues, spatial synchrony in masting reflects the extent of regional weather synchrony (Bogdziewicz *et al.*, 2023). The nature of weather–seed production relationships shapes synchrony patterns, affecting among-species synchrony (Szymkowiak *et al.*, 2024a; LaMontagne *et al.*, 2024), synchrony of peaks and failures (Szymkowiak *et al.*, 2024b), and the spatial extent of masting coherence (Koenig & Knops, 2013; Bogdziewicz *et al.*, 2023).

Co-occurring species may respond to overlapping weather cues, resulting in among-species synchrony within communities (Koenig *et al.*, 2016; Szymkowiak *et al.*, 2024a). In North American forests, such cross-species synchrony averaged 0.29 (mean Spearman cross-correlation) but varied widely, from strong asynchrony (–0.72) to near-perfect alignment (0.89) (LaMontagne *et al.*, 2024). The extent of community-wide coordination has implications both for plant fitness and broader ecosystem dynamics. For plants, high among-species synchrony can enhance predator satiation by limiting the availability of alternative seed sources for generalist consumers (Curran & Leighton, 2000; Szymkowiak *et al.*, 2024a). On the other hand, asynchrony can limit competition among seedlings (Shibata *et al.*, 2002). For ecosystems, high community-level synchrony concentrates seed availability into fewer years, potentially amplifying the strength of resource pulses (Yang *et al.*, 2008). Conversely, low synchrony, particularly in species-rich communities, can distribute seed input more evenly over time, buffering food webs against extreme booms and busts (Clark *et al.*, 2019). However, the spatial scale of among-species synchrony in temperate forests remains poorly understood due to limited broad-scale data, leaving it unclear whether it is local or regional in scope.

Synchrony in ecological processes can be tail-dependent, meaning it differs between high and low values of the ecological variable, such as between mast peaks and failures. This recently developed concept has revealed that either population crashes or booms often synchronize more strongly than the other, depending on the shape of species–environment relationships (Ghosh *et al.*, 2020). Tail-dependent synchrony has been described across terrestrial and aquatic systems, with key consequences for population dynamics and conservation (Ghosh *et al.*, 2020, 2021; Walter *et al.*, 2022; Ghosh *et al.*, 2025). In mast seeding, tail dependence would result in either seed abundance or seed scarcity synchronizing more strongly across space. This was recently demonstrated in European beech, where synchrony in years of seed scarcity extended up to 1800 km, nearly twice as far as the synchrony of mast peaks (Szymkowiak *et al.*, 2024b). Synchrony was higher in the lower tail because reproduction remained uniformly low across a broad range of less favorable climatic conditions (Szymkowiak *et al.*, 2024b). Such asymmetry alters the geography of seed availability, influencing the spatial scale and direction of masting effects on ecological interactions. Yet, the synchrony of extremes has not been systematically investigated only for European beech. The generality of such tail-dependence would indicate an asymmetry in the ecological consequences of masting, with regional-scale seed scarcity exerting stronger and more coherent impacts on food webs than resource pulses.

We used a uniquely extensive dataset on seed production from 431 sites across Poland, spanning 36 years (1987–2022) and covering seven dominant forest-forming species: *Fagus sylvatica*, *Quercus robur*, *Q. petraea*, *Pinus sylvestris*, *Abies alba*, *Picea abies*, and *Larix decidua*. This large-scale, long-term monitoring enables us to quantify both within- and among-species synchrony in masting, assess how synchrony decays with distance, and map its spatial structure. We partitioned synchrony into upper and lower tails, allowing comparison of the spatial scale and strength of synchrony in mast peaks and failures. We predicted that tail-dependence in masting synchrony will be general, due to the common non-linear relationships between seed production and weather cues in masting trees (Fernández-Martínez *et al.*, ????; Szymkowiak *et al.*, 2024b; Bogdziewicz *et al.*, 2025). Consequently, synchrony in failures should be more spatially extensive across all species. The among-species masting synchrony will be locally relatively high (Szymkowiak *et al.*, 2024a; LaMontagne *et al.*, 2024), but it should quickly decay with distance, as interspecific variation in cues and their phenology will be amplified with increasing distance among populations (Bogdziewicz *et al.*, 2023). We also predicted that among-species synchrony in masting upper tail (peaks) will be lower than lower-tail (failure) synchrony, for the same reason, i.e., the species-specific nature of cues will lead to more spatially heterogeneous masting peaks. Alternatively, to the extent that masting in temperate species is commonly linked to spring and summer temperatures, including our model species (Ascoli *et al.*, 2017; Vacchiano *et al.*, 2017; Bogdziewicz *et al.*, 2017), interspecific masting failure synchrony could be relatively high.

Such spatially extensive analysis, covering multiple species, has not been conducted so far, as it requires monitoring of multiple species across multiple sites; data that are logistically demanding to collect and slow to accumulate (Clark *et al.*, 2021). Thus, our results offer the first spatially explicit quantification of tail-dependent synchrony in both intra- and interspecific masting, with direct implications for understanding the dynamics of seed supply in temperate forests.

Results

Regional masting synchrony. The extent of regional masting synchrony differed among the studied species, with the highest synchrony in European beech (mean pairwise Spearman rank correlation across all sites and 95% CI: 0.393, 0.390–0.396, n = 27966), followed by oaks (0.280, 0.279–0.282, n = 73536), fir (0.261, 0.254–0.267, n = 4278), and spruce (0.263, 0.256–0.271, n = 3081) (Fig. 1A). Synchrony was noticeably lower in the remaining two conifers: pine (0.163, 0.161–0.164, n = 72010), and larch (0.178, 0.174–0.182, n = 9453) (Fig. 1A). Note that data for oaks was merged as separate records were only available after 2008.

Failures dominate: tail-dependence in regional masting synchrony is general. Following predictions, in all species, the synchrony of masting failures (lower tail) was higher than synchrony in mast peaks (upper tail) (Fig. 1). On average (i.e., across all distances), the synchrony in the lower tail was 1.7-fold higher than upper tail synchrony in beech (n = 27,808), 2.6-fold higher in oaks (n = 72,393), 2.9-fold higher in spruce (n = 3,076), 8.6-fold higher in fir (n = 4,277), 9.4-fold higher in larch (n = 9,430), and 12.1-fold higher in pine (n = 70,937).

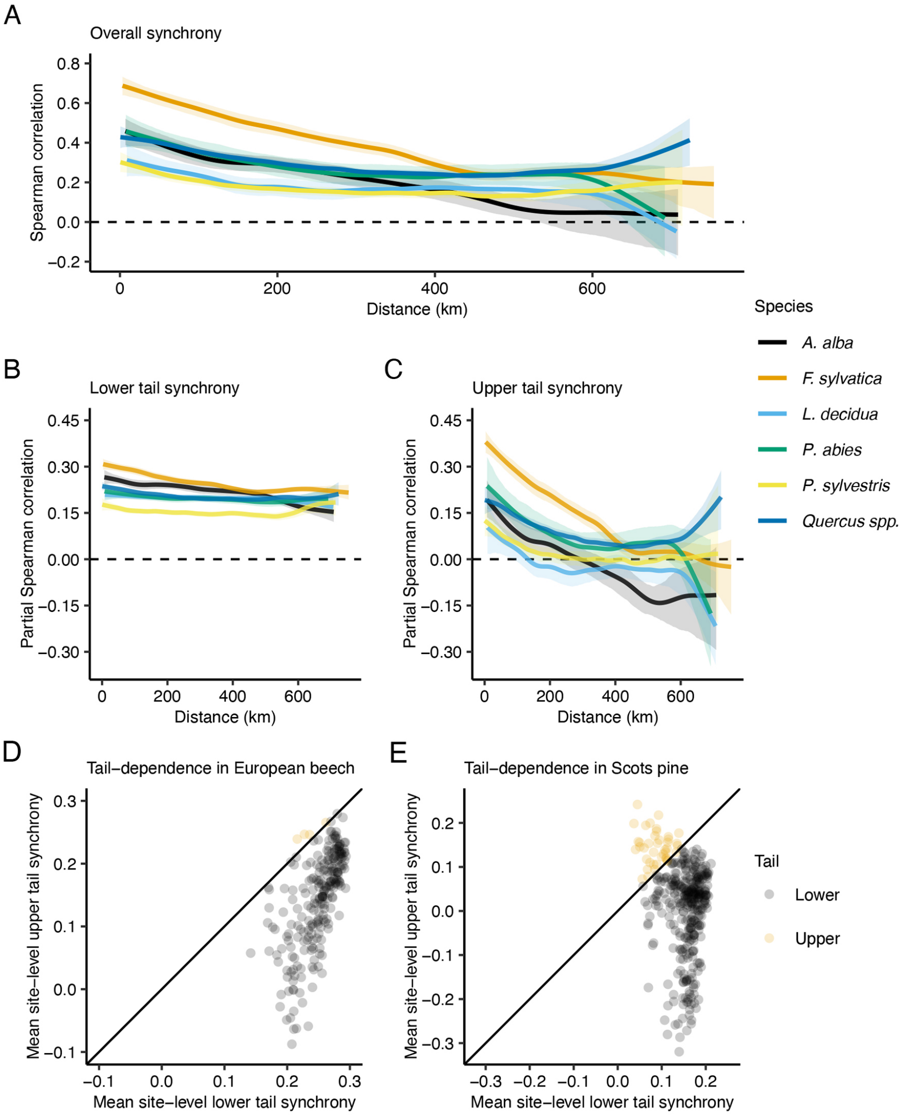

Figure 1: **Distance decay and tail-dependence in masting synchrony in the species studied.** Distance-decay in A) overall, B) lower tail, and C) upper tail synchrony. The lower tail is seed production below 0.25, while the upper is above 0.25, for annual values scaled within each species-site to between 0 and 1. This 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, which follows from categorization into tails and estimation based on partial Spearman correlation. Ribbons indicate 95% confidence intervals. D) and E) Relationship between site-level mean synchrony of seed production in the upper and lower tail in European beech (D) and Scots pine (E), with points size 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. Analogous figures to D) and E) for other studied species are provided in Fig. S1. The synchrony is based on annual (1987-2022) observations of seed production across 431 sites, but the specific number of sites per species varies due to range differences (see Methods, Data). Note that data for oaks was merged as separate records were only available after 2008.

Looking at the tail-dependence across space, the upper-tail synchrony declined with distance relatively quickly, e.g., synchrony reached 0 at 450 km in beech, 200 km in fir, or about 100 km in larch (Fig. 1C). In contrast, the synchrony in the lower tail was characterized by a lack of (e.g., pine, larch) or very shallow distance-decay (e.g. beech, fir) at the scale observable in our study, and remained relatively stable across the distances of up to 700 km in all species (Fig. 1B).

Mapping these patterns revealed a consistent picture in which mast failures' synchrony was extending evenly over the entire studied region, again for all studied species (Fig. 2 shows beech, while other species are presented in Fig. S2 and S3). In contrast, the synchrony of mast peaks was spatially heterogeneous, resulting in substantial variation in the spatial extent and intensity of pulsed resources (Fig. 2). For example, the three failure years visualized for European beech at Fig. 2 show extensive seed shortage across the vast majority of 237 monitored sites. Conversely, the three peak years show seed pulses scattered over the region (year 1993), or concentrated in the North (year 2004), or South (year 2020). Importantly, this does not mean that region-wide mast years are absent, but that they occur less frequently and with smaller synchrony than region-wide seed failures.

Interspecific masting synchrony is largely local. Among-species masting synchrony was moderate within sites, and it quickly decayed with distance. Considering all species pairs together, the mean interspecific synchrony at the local level (within-site) was 0.14 (n = 1628) (Fig. 3), being highest between species pairs such as pine and spruce (0.30, n = 70), pine and larch (0.29, n = 119), and spruce and larch (0.27, n = 35), while lowest within pairs of beech and larch (0.01, n = 109), beech and pine (0.06, n = 191), and fir and pine (0.08, n = 60) (Fig. S4).

Looking at these patterns in space, interspecific masting synchrony reached or was close to 0 at distances lower than 50 km in the majority (66.67%) of species pairs (i.e. 95% CI overlapped with 0; Fig. 4). In some pairs, including fir-beech, fir-oaks, fir-pine, beech-spruce, pine-larch, and pine-spruce, the synchrony remained higher than 0 at distances over 200 km, but was still negligible compared to within-species synchrony.

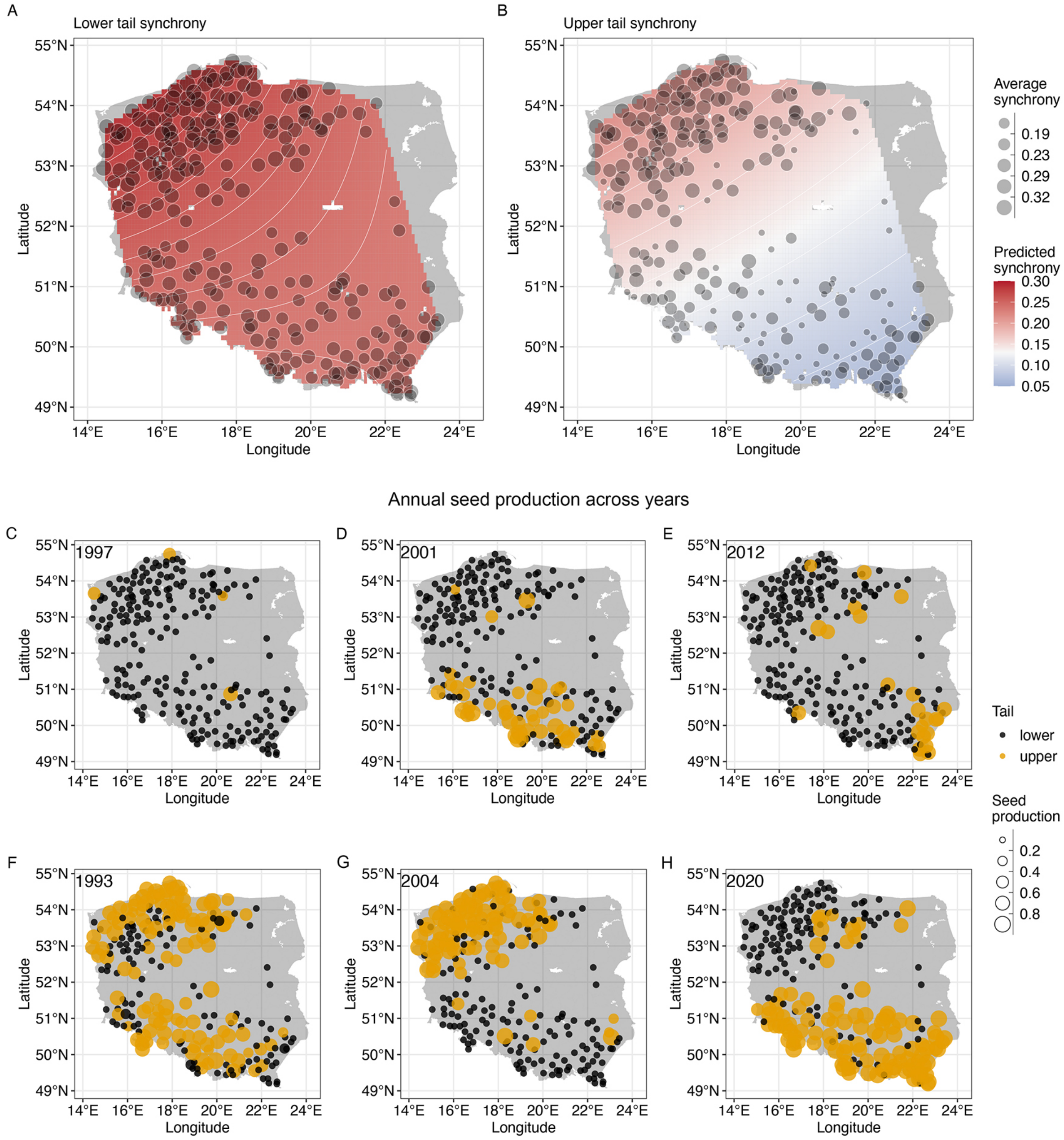

Figure 2: **Maps of masting synchrony** in A) lower tail and B) upper tail of seed production in European beech. At A) and B) points show sites scaled according to site-level mean synchrony of seed production within a given tail. The background color of A) and B) shows the geography of synchrony as estimated with a GLMM model, see Table S1 for the model summary. The three panels in the middle row (C, D, E) show three exemplary years dominated by low-tail seed production (1997, 2001, 2012) in European beech, while the bottom row shows three years dominated by peaks (1993, 2004, 2020). Point size is scaled to site-level annual seed production during plotted years, colored according to whether the site-year falls into the lower or upper tail. Maps for other species are provided in the Supplement (Fig. S2 and S3).

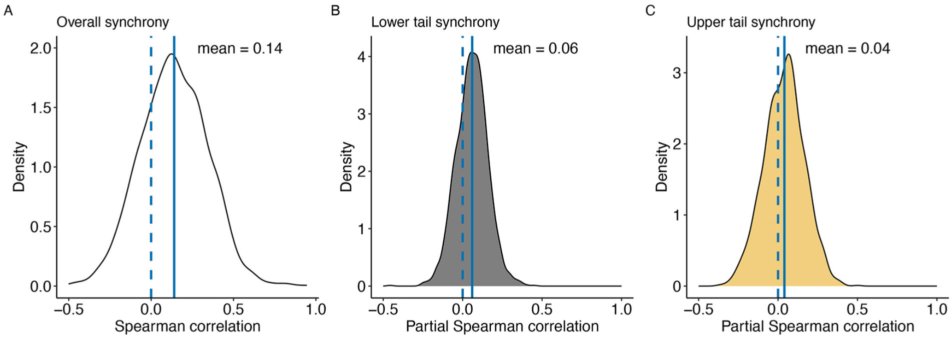

Figure 3: **Local among-species masting synchrony.** Density plots of within-site A) overall, B) lower tail, and C) upper tail synchrony. Plots are based on synchrony (Spearman or, in the case of lower and upper tails, partial Spearman correlation) between all possible pairs of studied species. The vertical solid line indicates the mean value, while the dashed line indicates zero. The synchrony is based on annual (1987-2022) observations of seed production across 431 sites, but the specific number of sites per species varies due to range differences (see Methods). Density plots for individual pairs of species are provided in Fig. S4.

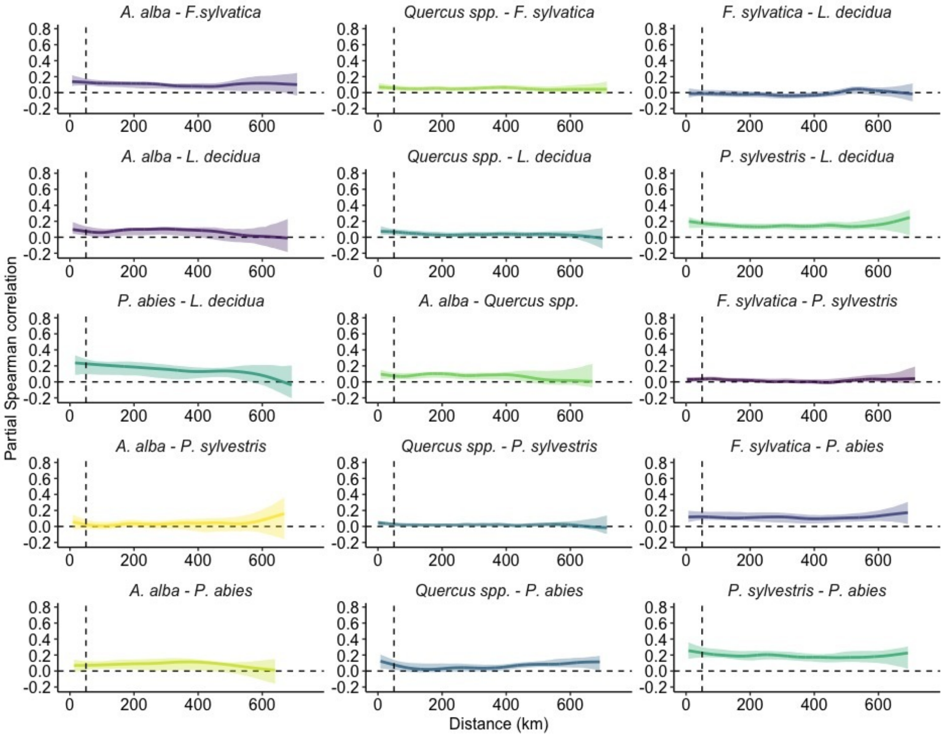

Figure 4: **Regional among-species masting synchrony** for each species pair, based on Spearman correlation estimated using non-parametric spatial covariance functions. Note that y-axes on the graphs are adjusted to be comparable with Fig. 1A. The vertical dashed line highlights 50km. Ribbons show 95% confidence intervals. The synchrony is based on annual (1987-2022) observations of seed production across 431 sites, but the specific number of sites per species varies due to range differences (see Methods). Regional among-species synchrony separated into tails is provided in Fig. S5.

Low interspecific synchrony of mast peaks and failures Separating interspecific masting synchrony into tails shows that neither mast peaks nor failures are synchronized extensively. Locally, the mean interspecific synchrony in the lower tail was 0.06 (n = 1628), while in the upper tail it equaled 0.04 (n = 1628) (Fig. 3B, C). Regionally, in the vast majority of species pairs, the among-species synchrony of mast failures and peaks was near 0, or was overlapping with 0, at all distances (Fig. S5).

Discussion

Using a uniquely comprehensive dataset spanning 36 years and major forest-forming tree species across more than 700 km of temperate Europe, we provide the first spatially explicit analysis of regional masting synchrony that integrates both intra- and interspecific patterns and accounts for tail-dependent dynamics (Ghosh *et al.*, 2020; Walter *et al.*, 2022). Following theory (Szymkowiak *et al.*, 2024b), mast peaks are consistently less synchronized than mast failures: failures extend over broad regions and dominate the overall signal of regional coherence. In species such as pine, larch, and spruce, mast peaks are not synchronized beyond 200 km, revealing that whole-distribution metrics of synchrony used so far to quantify it (Koenig & Knops, 1998; Vacchiano *et al.*, 2017; LaMontagne *et al.*, 2020; Bogdziewicz *et al.*, 2021), obscure important asymmetries in reproductive synchrony. Furthermore, among-species synchrony, though often relatively high within sites (LaMontagne *et al.*, 2024), rarely persists beyond tens of kilometers. These findings challenge the prevailing assumption that mast peaks and failures are equally extensive in space. Thus, the largest-scale ecological impacts of masting may arise not from seed abundance but from its synchronized absence.

Tail dependence in masting is general in temperate Europe: in all studied species, mast failures exhibit 1.7 - 12.1-fold higher regional synchrony than mast peaks and show little or no distance decay at distances up to 700 km. This indicates a consistent spatial asymmetry in reproductive dynamics, as seed scarcity synchronizes more strongly and over broader areas than seed abundance. Research so far has largely focused on the effects of pulsed resources generated by mast peaks, leading to extensive documentation of consumer outbreaks, trophic cascades, and associated shifts in species interactions (Ostfeld & Keesing, 2000; Bogdziewicz *et al.*, 2025).

The ecological consequences of synchronized seed failure have been comparatively overlooked (Bogdziewicz *et al.*, 2016), although theory emphasizes that famine events are not merely the inverse of resource pulses (Sears *et al.*, 2004). Famine and resource pulses differ in several fundamental ways. Whereas responses to pulsed resources are often graded or show diminishing returns, responses to famine are shaped by nonlinear thresholds (Holt, 2008). Organisms may tolerate low resource availability to a point, beyond which survival or reproduction collapses abruptly (Holt, 2008). Moreover, famine propagates cascading constraints in food webs, not amplification, and restricts trophic energy flow (Sears *et al.*, 2004). Furthermore, famine triggers behavioral shifts, including movement to new habitats, skipping reproduction, or altered foraging strategies (Clark *et al.*, 2019; Maag *et al.*, 2024; Widick *et al.*, 2025). Finally, recovery from famine is delayed, often limited by demographic bottlenecks or resource depletion, making the legacy of scarcity more persistent than that of abundance (Holt, 2008). Our findings highlight an underexplored dimension of masting dynamics and suggest that greater attention should be directed toward the ecological consequences of synchronized seed failure, which may play a more extensive role in shaping food web dynamics than so far recognized.

The quantification of the distance decay in among-species masting synchrony, including in masting peaks and failures, shows that it is largely localized. This spatially constrained synchrony implies that high tree species diversity interacts with the limited coherence of masting across species, potentially stabilizing seed supply within forests. Synchrony between pairs like beech and spruce or fir is likely less important for processes such as mammal population dynamics (Sachser *et al.*, 2021). In contrast, low synchrony among large-seeded oaks and beech, below 0.1 at all distances, may help stabilize food webs. The low level of interspecific synchrony may also decrease competition between seedlings of shade-tolerant and light-demanding tree species, diversifying temporal regeneration niches. The extent of this buffering effect requires further investigation. For example, both beech and oaks are individually recognized to significantly influence the population dynamics of seed consumers and their predators, yet such insights typically stem from studies focusing on single tree species (Clotfelter *et al.*, 2007; Saitoh *et al.*, 2007; Touzot *et al.*, 2020). Our results suggest that it would be worthwhile to systematically explore how the food web effects generated by masting vary across forests ranging from single-species dominance to diverse co-occurrence. Such research could investigate whether diverse forests exhibit more stable consumer populations and fewer extreme demographic fluctuations.

We argue that the patterns of masting synchrony and their variation among species arise from fundamental differences in the relationships between seed production and weather cues, including in the timing of cue responsiveness across populations. The generality of tail dependence in masting synchrony reflects a general feature of masting species: the non-linear response of seed production to weather drivers (Kelly *et al.*, 2013; Bogdziewicz *et al.*, 2024). Seed output is commonly inhibited or remains low across a broad range of suboptimal cue values, generating relatively uniform low reproduction across sites during a broad range of unfavorable years (Szymkowiak *et al.*, 2024b). This buffering effect promotes high synchrony in the lower tail. In contrast, seed production increases sharply once cues exceed species-specific critical values, so small spatial differences in favorable weather lead to large variation in reproductive effort, reducing synchrony during mast peaks (Szymkowiak *et al.*, 2024b). Beyond these nonlinear responses, variation in the spatial scale of synchrony among species is shaped by the degree to which the timing of weather cue sensitivity is conserved across populations (Bogdziewicz *et al.*, 2023). European beech exhibits the most extensive regional synchrony because its cue window is anchored to the summer solstice, synchronizing temperature sensitivity across large distances (Journé *et al.*, 2024). In contrast, in species where cue timing shifts with local phenology, akin to flowering or leafing time, synchrony deteriorates with distance more strongly (Bogdziewicz *et al.*, 2023). Finally, we argue that locally, intraspecific synchrony is often high due to shared weather cues (e.g., summer warmth in beech, spruce, pine; c.f. Ascoli *et al.* (2017)), which generate a degree of interspecific synchrony (Szymkowiak *et al.*, 2024a). Because the functional relationships between cues and reproduction differ between species (Fernández-Martínez *et al.*, ????), interspecific synchrony is lower than intraspecific and declines more steeply with distance. These cue mismatches, when compounded with differences in cue timing, can explain the low regional interspecific synchrony. Testing these hypotheses will require substantial effort, but it offers a promising direction for research.

One caveat of our study is that it relies on seed harvest data, which may include noise introduced by seed demand. This likely contributes to the somewhat lower synchrony estimates we report compared to previous studies. For example, synchrony in beech masting reaches ~0.8 at low distances and ~0.6 at 300 km in the MASTREE+ analysis by Szymkowiak *et al.* (2024b), while corresponding values in our study are ~0.7 and ~0.4. Similarly, our mean local-level intraspecific synchrony is about half of that observed in a recent study of North American oaks (LaMontagne *et al.*, 2024). These comparisons suggest that the synchrony in seed production may be higher than our estimates imply. However, patterns such as general tail dependence, the contrast between coherent synchrony in failures and more heterogeneous synchrony in peaks, and the limited spatial scale of interspecific synchrony compared to intraspecific synchrony, are unlikely to be affected by this bias. Importantly, the taxonomic and spatial breadth of our dataset remains unmatched in ecological monitoring. Synchrony estimation requires both long-term time series and broad regional coverage, and only a few species, such as European beech or white spruce, have sufficient coverage to support analyses at this scale (LaMontagne *et al.*, 2020; Journé *et al.*, 2024). For other species, data exist but are too fragmented in time or space to permit similar analysis. Even the well-known California oak survey, a cornerstone of research on masting synchrony, spans 10 sites (Koenig & Knops, 2013; Koenig *et al.*, 2017). Thus, no other dataset currently offers the same analytical scope as the one used here.

Our study provides a general demonstration of tail-dependent synchrony in masting across multiple species, showing that regional-scale coherence is primarily structured by synchronized reproductive failure rather than seed abundance. The spatial extent and consistency of failures suggest that ecological impacts of seed scarcity, such as trophic bottlenecks, skipped reproduction, and altered animal movement, may be more predictable and widespread than previously appreciated. In contrast, the among-species synchrony was moderate and local, as in North American forests (LaMontagne *et al.*, 2024), and regionally low. Thus, mobile, generalist seed consumers are unlikely to experience coordinated starvation–satiation cycles across temperate forests. This contrasts with tropical systems such as Southeast Asian dipterocarps, where community-wide synchrony appears necessary to aid overwhelming generalist seed predators (Curran & Webb, 2000; Curran & Leighton, 2000) — highlighting a potential divergence in the structure and function of masting between tropical and temperate regions. Our findings also carry applied implications. In failure years, the geographic extent of seed scarcity means that seed collection for restoration or forestry cannot be remedied by shifting locations, highlighting the need for reliable masting forecasts (Journé *et al.*, 2023; Wion *et al.*, 2025; Oberklammer *et al.*, 2025). Our results suggest that forecasting failures across space may be more tractable than forecasting mast peaks, as failure synchrony is more spatially stable. Notably, failures are already more predictable in time (Journé *et al.*, 2023), and our findings support their extrapolation across large regions. In contrast, spatial forecasts of mast peaks should be treated with caution. Finally, since seed production in mast years is highly sensitive to extreme values of weather cues, masting peaks may be more vulnerable to disruption under climate warming (Szymkowiak *et al.*, 2024b), while failure synchrony is likely more robust. The generality of tail dependence revealed here points to an important next step: testing how climate change alters synchrony in the tails, and thus reshapes the geography of both resource pulses and shortages.

Materials and Methods

Data

Masting data Information on seed production was obtained from the Polish State Forests and is based on annual harvest rates by the local forest inspectorates. This dataset provides information on the amount (kg) of seeds (or cones, referred to as seeds in the text) collected in each district per year. The data have been collected for silver fir (*Abies alba*), European beech (*Fagus sylvatica*), European larch (*Larix deciduosa*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), sessile oak (*Quercus petraea*), and pedunculate oak (*Quercus robur*) from 1987 to 2022. Before 2008, oak harvests were not reported separately by species and records were therefore pooled for the entire time series. Seeds are collected from the ground or tree canopies (depending on the species) by local companies on behalf of the Polish State Forest, and each inspectorate has assigned seed collection sites. We obtained data for 431 districts (referred to as 'sites'). For each species, we have subset the data and used only sites that had less than 80% of zero records, which resulted in 237 sites in beech, 384 in oaks, 380 in pine, 79 in spruce, 93 in fir, and 138 in larch.

Data analysis

Intraspecific masting synchrony. We calculated distance-decay of whole-distribution seed production synchrony using non-parametric spatial covariance functions (Bjørnstad & Falck, 2021). First, for each pair of sites for a given species, we calculated a Spearman rank correlation between the (log-transformed) seed production time series. Next, we used the matrices of pairwise Spearman correlations as the response (synchrony variables), explained by the matrices of pairwise geographical distances between sites (Szymkowiak *et al.*, 2024b). To calculate the 95% confidence bands for each function, we used the standard bootstrapping procedure (Bjørnstad & Falck, 2021).

Interspecific masting synchrony. We calculated interspecific seed production synchrony using Spearman rank correlations for all pairwise species-species combinations. For each seed production series of species i, we calculated its synchrony with all (log-transformed) seed production series of species j at all sites at which species i and j co-occurred. Next, we calculated the distance-decay of interspecific masting synchrony for each pair of species. We used non-parametric spatial covariance functions, in which the matrix of pairwise synchrony between species i and j was explained by the matrix of pairwise distances between sites (Bjørnstad & Falck, 2021).

Tail-dependence in regional masting synchrony.

Categorization of masting into tails. Our framework follows that of Walter *et al.* (2022), modified by Szymkowiak *et al.* (2024b). Masting lower tail includes annual values of seed production ≤ 0.25, while upper those > 0.25, for seed production scaled within each species-site to values between 0 and 1. The categorization reflects the distribution of annual values of seed production (Fig. S6). The thresholds are arbitrary in the sense that masting is not 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; Szymkowiak *et al.*, 2024b).

Intraspecific tail-dependent 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 (≤ 0.25) and upper (> 0.25) tails 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 the partial Spearman correlation in both tails (Szymkowiak *et al.*, 2024b). 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 for each model species. Note that scaling of the mast 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 (Szymkowiak *et al.*, 2024b). To calculate 95% confidence bands for each function, we used the standard bootstrapping procedure (Bjørnstad & Falck, 2021).

We mapped tail-dependence in masting over the region using generalized linear mixed models, built separately for lower and upper tail synchrony. We included within-tail synchrony scaled between 0 and 1 as a response, while the site's latitude, longitude, and their interaction were included as fixed effects. We fitted the model with the Tweedie distribution and logit link function, and included site ID as a random intercept.

Interspecific tail-dependent masting synchrony. We used partial Spearman correlations to calculate interspecific synchrony of seed production in lower (≤ 0.25) and upper (> 0.25) tails between all pairs of species (Walter *et al.*, 2022). We calculated pairwise correlations in tails between the seed production series of species i and j at all sites at which both species co-occurred. Next, we used non-parametric spatial covariance functions to calculate the distance-decay of seed production synchrony for each species pair, separately for the lower and upper tails. We included the pairwise within-tail correlation matrices as the response and the pairwise matrices of between-site geographical distances as the explanatory matrices.

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Author Contributions Statement

All authors conceived the study. JSz and MB designed the study. JSz conducted the analysis. JSz and MB co-wrote the first draft of the manuscript. All authors contributed to the interpretation of the analysis, revised the draft, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data availability statement

The data supporting the results will be archived in a permanent repository upon acceptance.

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Supporting Information

Title

Jakub Szymkowiak*[1,2], Jessie Foest[1], Marcin K. Dyderski[3], Szymon Jastrzębowski[4], Maciej Barczyk[1], Andrew Hacket-Pain[5], Michał Bogdziewicz*[1]

[1]Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland.

[2]Population Ecology Research Unit, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland.

[3]Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, Kórnik, 62-035, Poland.

[4]Department of Silviculture and Forest Tree Genetics, Forest Research Institute, Braci Leśnej 3, Sękocin Stary, 05-090, Raszyn, Poland.

[5]Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom.

*corresponding authors: jakub.szymkowiak@amu.edu.pl, michalbogdziewicz@gmail.com

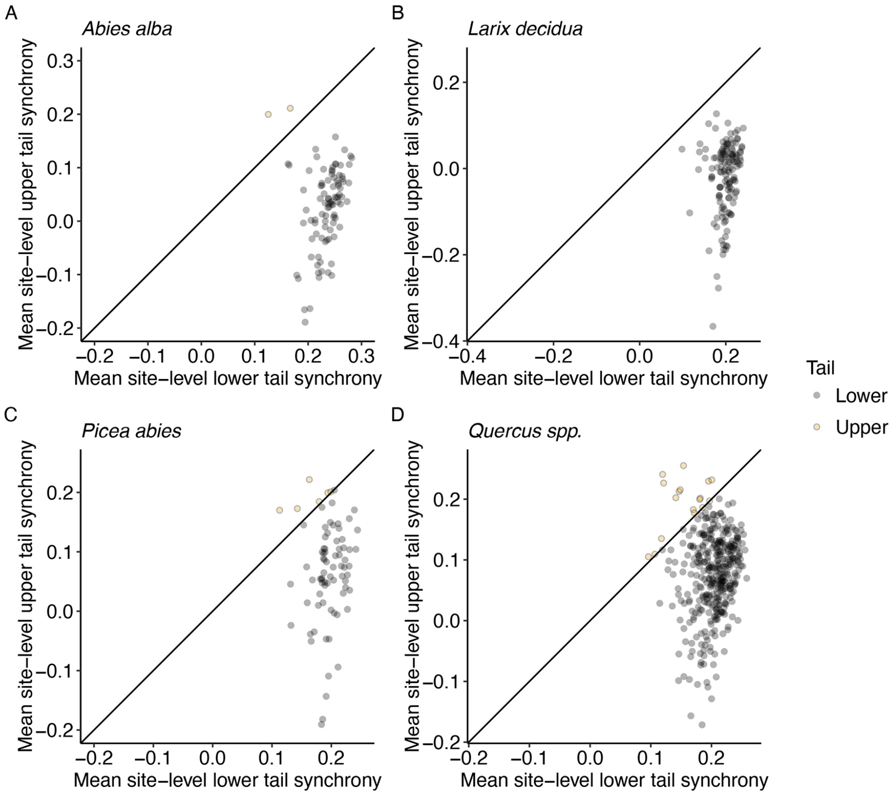

Figure S1: Tail-dependence in masting synchrony in the species studied. The panels show relationships between site-level mean synchrony of seed production in the lower and upper tail in (A) Silver fir, (B) European larch, (C) Norway spruce, and (D) oaks, with point size scaled according to tail dependence strength (difference between mean synchrony in the upper and lower tail).

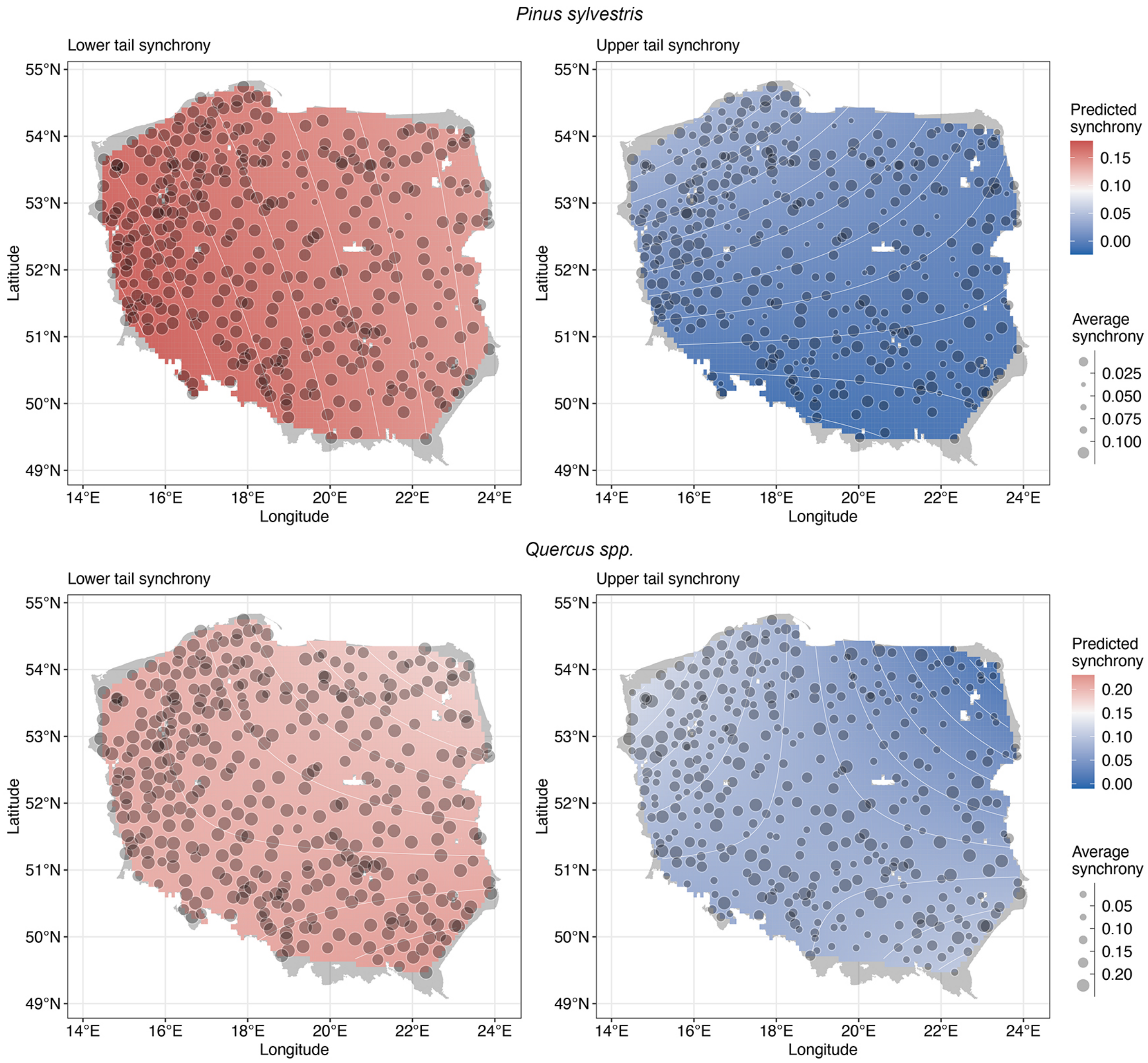

Figure S2: Maps of masting synchrony in *Pinus sylvestris* and *Quercus* spp. Points show sites with point size scaled according to the site-level mean synchrony of seed production in the lower and upper tails. The color gradient shows the spatial trend of seed production synchrony in a given tail, estimated based on a GLMM model (see Table S1 for model summary).

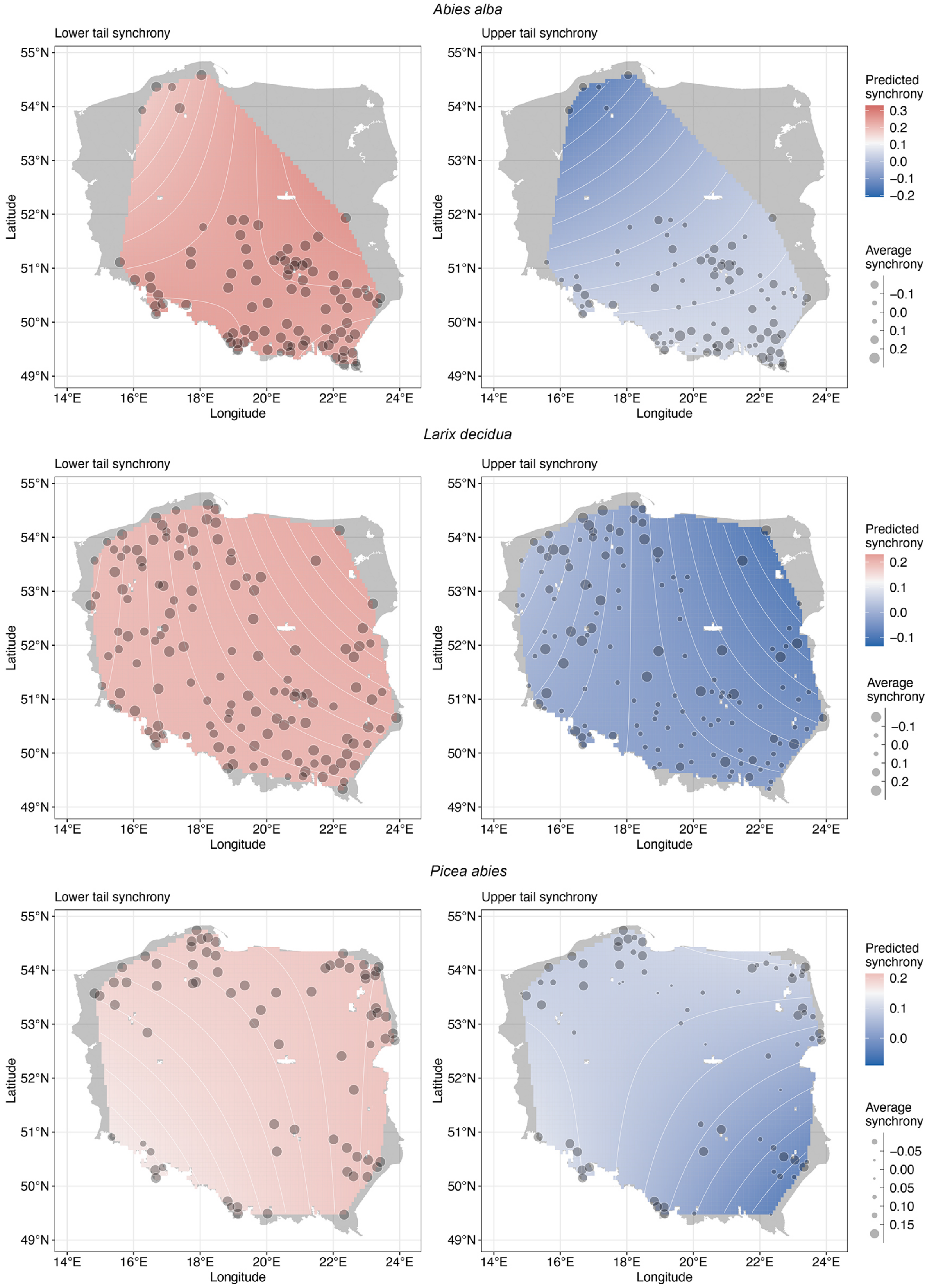

Figure S3: Maps of masting synchrony in *Abies alba*,*Larix decidua*, and *Picea abies* spp. Points show sites with point size scaled according to the site-level mean synchrony of seed production in the lower and upper tails. The color gradient illustrates the spatial trend of seed production synchrony in a given tail, estimated using a GLMM model (see Table S1 for model summary).

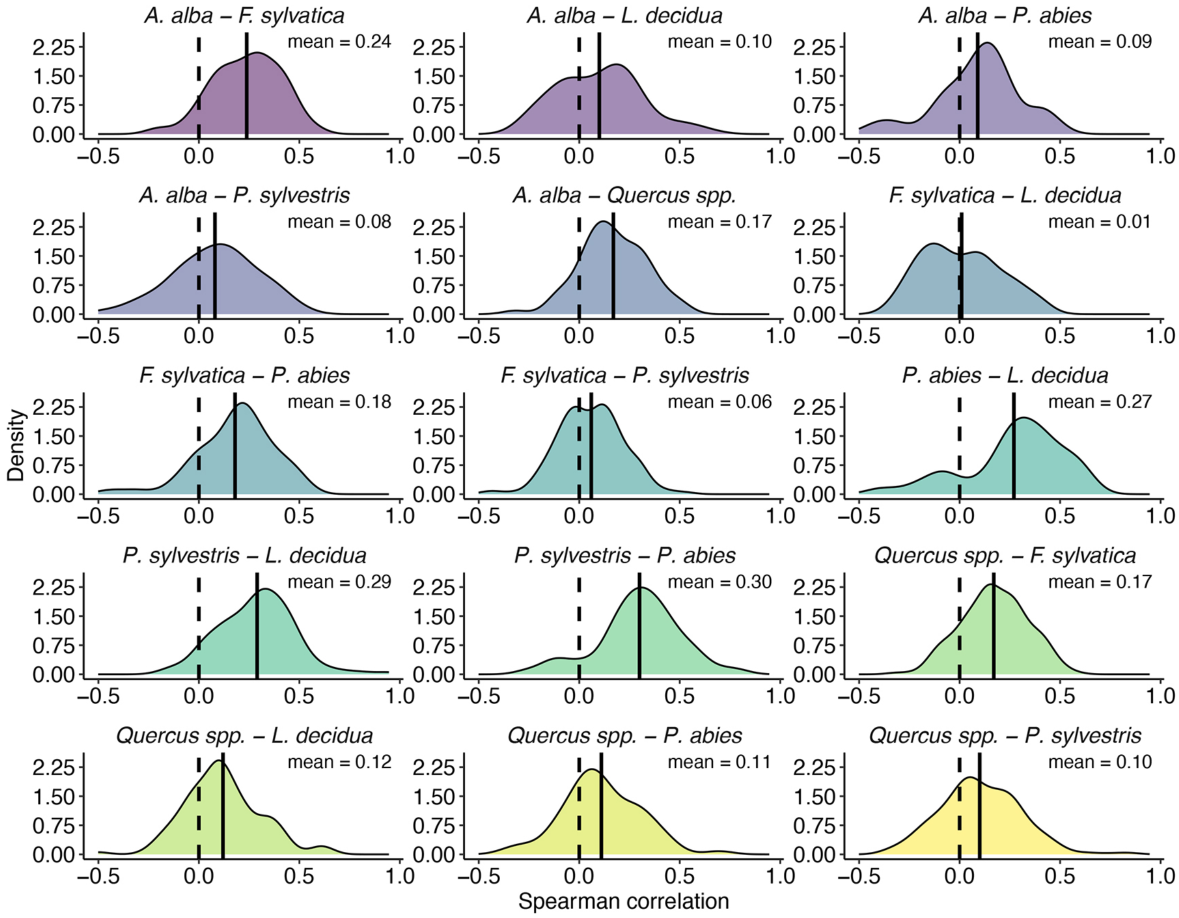

Figure S4: Local among-species masting synchrony. Density plots show the distributions of within-site synchrony, based on Spearman correlations, between all possible pairs of studied species. Vertical dashed lines indicate zeros, while the solid lines indicate pair-level mean synchrony.

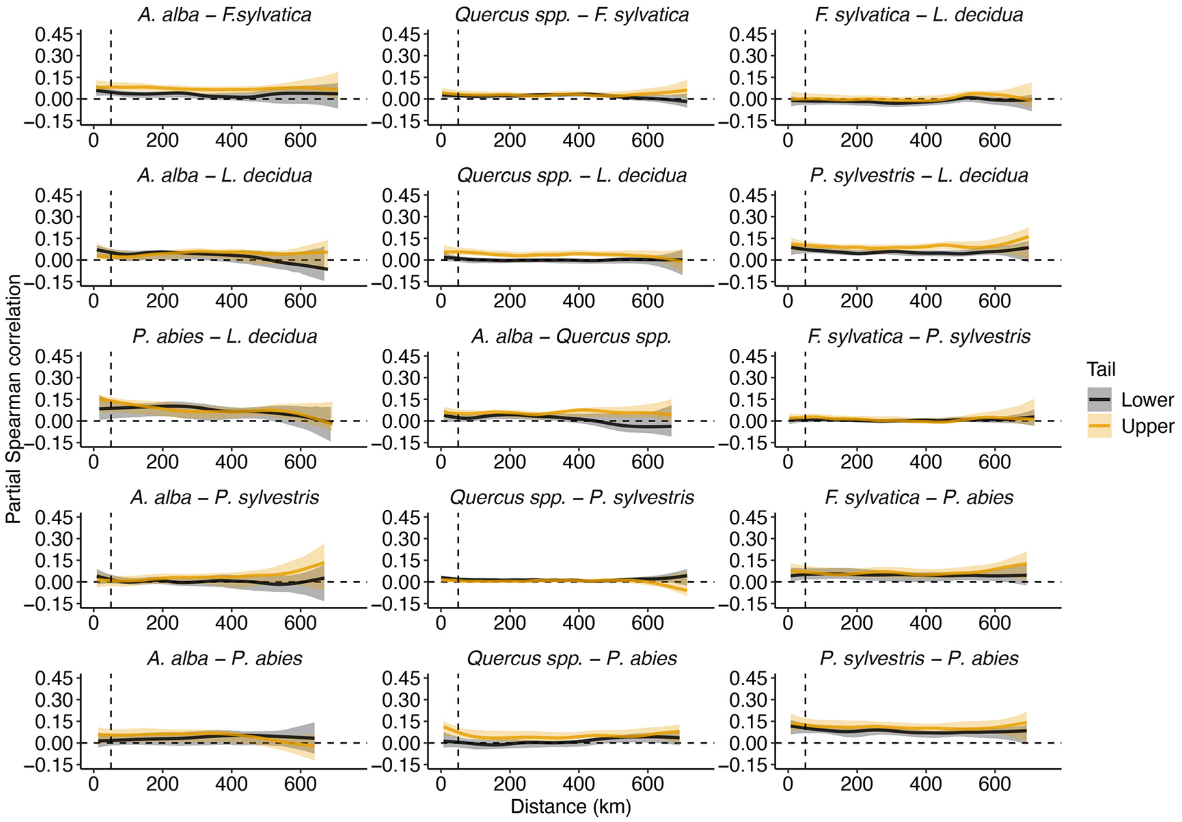

Figure S5: Distance dependence of regional among-species masting synchrony for each species pair in lower and upper tails, based on partial Spearman correlation. The synchrony is based on annual (1987-2022) observations of seed production across 431 sites, but the specific number of sites per species varies due to range differences (see Methods).

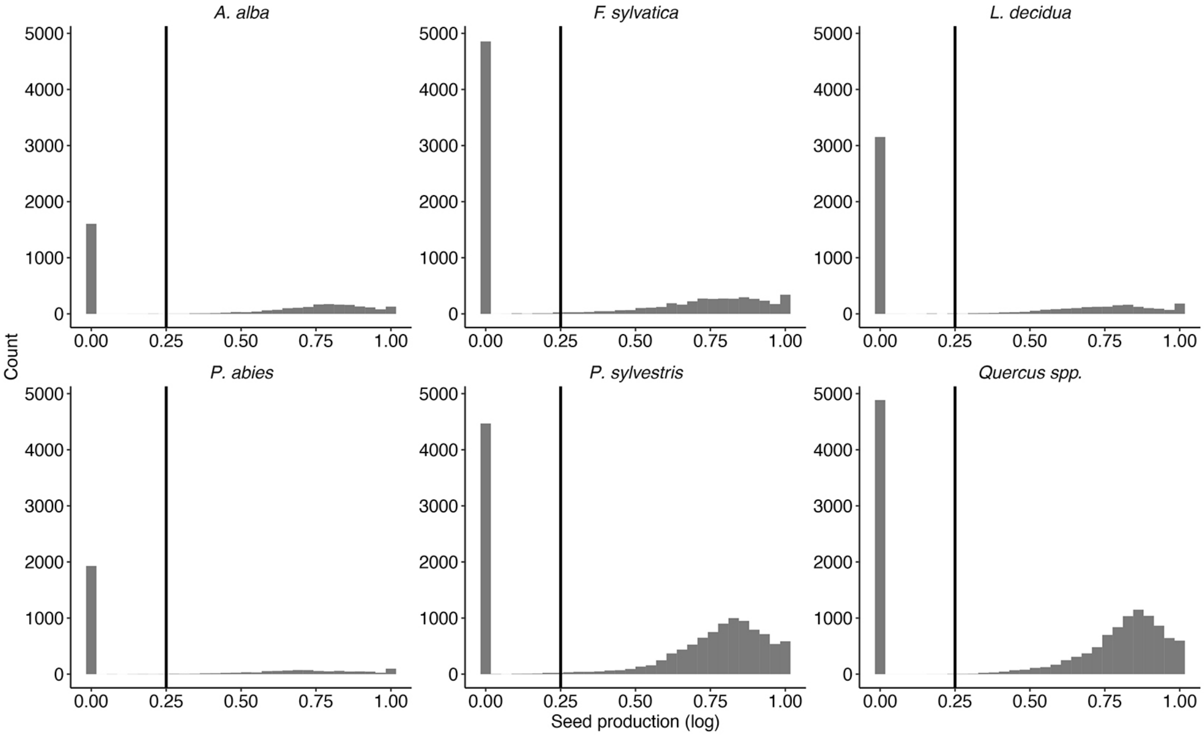

Figure S6: Categorization of masting into tails. Distribution of annual seed production values scaled within each site to fall between 0 and 1. The vertical solid lines show the categorization of masting into lower (left) and upper (right) tails.

Table S1: Spatial gradients of tail-dependent masting synchrony. The results of generalized linear mixed models testing for spatial trends of seed production synchrony in the lower and upper tails in the studied species. The models included within-tail pairwise synchrony of masting scaled between 0 and 1 as a response, while the site's spatial coordinates and their interaction were fitted as fixed effects. We fitted the models with the Tweedie distribution and logit link function, including site ID as a random intercept. Results are visualized in Fig. 2, Fig. S2, and Fig. S3.

Model term	**Lower tail**			**Upper tail**		
	Chisq	**d.f.**	**p**	**Chisq**	**d.f.**	**p**
Fagus sylvatica						
Latitude	36.88	1	<0.001	57.66	1	<0.001
Longitude	11.17	1	<0.001	14.55	1	<0.001
Latitude x Longitude	11.67	1	<0.001	0.65	1	0.421
***Quercus* spp.**						
Latitude	21.04	1	<0.001	2.89	1	0.089
Longitude	6.60	1	0.01	15.66	1	<0.001
Latitude x Longitude	7.50	1	0.006	15.12	1	<0.001
Pinus sylvestris						
Latitude	2.02	1	0.155	3.45	1	0.063
Longitude	28.49	1	<0.001	1.05	1	0.306
Latitude x Longitude	0.25	1	0.620	0.48	1	0.487
Abies alba						
Latitude	3.86	1	0.049	23.68	1	<0.001
Longitude	0.001	1	0.975	1.07	1	0.300
Latitude x Longitude	19.10	1	<0.001	3.34	1	0.068
Larix decidua						
Latitude	1.18	1	0.278	0.15	1	0.697
Longitude	3.66	1	0.056	8.08	1	0.004
Latitude x Longitude	0.83	1	0.362	2.30	1	0.130
Picea abies						
Latitude	4.10	1	0.043	8.75	1	0.003
Longitude	13.27	1	<0.001	4.55	1	0.033
Latitude x Longitude	3.27	1	0.071	7.52	1	0.006