

# Forest tree fecundity declines as climate shifts

## Author list

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## 19 **Abstract**

20 Tree fecundity underpins regeneration and range tracking, yet may decline when climates exceed reproductive niches. How  
21 fecundity has changed under recent climate change remains unclear. Here, using Polish seed harvest data including 40,530  
22 observations for five species across 438 districts, we show a reduction in viable seed production by 32–65% across 34 years  
23 (*Quercus robur* & *Q. petraea* ~65%, *Pinus sylvestris* ~64%, *Abies alba* ~44%, *Fagus sylvatica* ~32%). Summer warming was  
24 the dominant driver, with hotter summers reducing fecundity across species. Growing-season moisture and spring temperature  
25 contributed little beyond local fecundity effects. Weather effects on fecundity varied with site climate, with the diverging  
26 within-site (transient) and across-site (equilibrium) responses suggesting local adaptation or acclimation capacity. Together, our  
27 results indicate warming-driven fecundity declines, suggesting that climate change has pushed populations beyond the optimum  
28 of their reproductive niches, while revealing management potential through informed provenance selection.

## 29 **Main Text**

### 30 **Introduction**

31 Tree reproduction governs the renewal of forest ecosystems, shaping composition and structure over long time scales [1–3].  
32 Fecundity can offset mortality and contributes to resilience, determining whether populations recover and how communities  
33 restructure after increasingly frequent disturbance [3, 4]. Because seed output determines both the supply of new individuals  
34 *in situ* and their dispersal potential, it links demography to range dynamics and the capacity of species to track shifting climate  
35 niches [5–8]. Fecundity also determines seed supply for nurseries: climate-driven shortfalls and variability in seed years can  
36 limit restoration plantings and assisted migration programs that depend on sufficient, provenance-appropriate collections [9, 10].  
37 In Europe, accelerating tree mortality and disturbance frequency increase reliance on successful reproduction and a need for  
38 reliable seed supply [11–14]. This motivates assessing whether reproduction is keeping pace, as reproductive processes may be  
39 more sensitive to climatic variation than survival or growth [15].

40 Across the few long-term records available, fecundity shows a generally declining trend that is associated with changing  
41 weather conditions during key phenological stages, while the disruption of masting dynamics (the characteristic synchronised  
42 year-to-year variability in seed production) causes viable seed crops to decline over time despite increased reproductive  
43 investment (Table 1). Positive trends exist but are context-specific. In *Nothofagus solandri*, increasing moisture without strong  
44 warming is associated with higher seed production [16]. In *Quercus crispula*, warmer springs have increased mast frequency,  
45 raising mean seed output while maintaining masting and its benefits (lower predation, sustained pollination) [17]. However,  
46 if cues occur too regularly, masting can collapse with consequent reductions in viable seeds [18]. In *Fagus sylvatica*, warmer  
47 summers increased the frequency of flower initiation, resulting in more regular seeding but fewer overall viable seeds because of  
48 reduced pollination efficiency and weaker predator satiation [19–21]. In *Picea engelmannii*, an apparent positive trend is driven  
49 by an exceptional mast year at the end of the time-series; nonetheless, its stable or positive trend likely reflects warming that has  
50 not yet moved the species towards a suboptimal region of its reproductive niche [22]. Overall, these cases suggest a coherent  
51 pattern: fecundity declines when sustained warming and shifts in moisture push populations away from the historical climatic  
52 optimum for reproduction, remains stable where climate change has not yet shifted populations outside the stable region of the  
53 fecundity performance curve, and increases when climatic change moves populations towards this optimum. This aligns with  
54 the expectation that sustained environmental change reduces fecundity as niche mismatch grows [23].

55 Because reproduction proceeds through successive phenological stages — flower initiation, pollination, and seed maturation  
56 — the climatic niche for fecundity is effectively partitioned among these phases, each with its own sensitivity to temperature  
57 and moisture [15, 24, 25]. In European beech, floral initiation is strongly driven by summer temperatures: cool summers two  
58 years prior and hot summers one year prior to flowering promote abundant initiation [26, 27]. Once initiation occurs, later stages  
59 proceed with relatively little climatic constraint [28]. In Norway spruce (*Picea abies*), cone production also correlates positively  
60 with summer temperature in the year before [29]. Temperate deciduous oaks (*Quercus* spp.) show greater complexity [30, 31].  
61 In oceanic climates, seed production is linked to floral initiation, whereas in more continental climates, pollination success  
62 has a larger effect and therefore seed crops show a stronger dependence on spring weather [31]. Rising spring temperatures  
63 can therefore enhance oak fecundity under some conditions [32], but reduced seeding stochasticity may also weaken predator  
64 satiation and therefore reduce viable seed counts [33]. Other stressors, e.g., drought and late spring frost, further modify  
65 reproductive responses. Prolonged drought can reduce reproduction in many species [15, 34, 35], though some maintain seed  
66 production at the expense of growth or defence [36–38]. Late spring frosts can destroy flower crops, with impacts varying across  
67 species and populations, for instance, through variation in flowering phenology [33, 39]. Thus, climate impacts on fecundity can  
68 emerge through stage-specific bottlenecks. Given stage-dependent sensitivities and the link between masting and seed viability,  
69 the attribution of temporal trends in fecundity requires stage-specific climatic metrics and, where possible, measures of viable  
70 rather than total seed output.

71 As climatic cues and vetoes affecting fecundity at each reproductive stage are episodic and spatially variable, tracking  
72 fecundity trends requires long-term and extensive observations. Such data are rarely available, because sustained, community-  
73 wide monitoring of seed production exceeds the scope of most research programs. Even if initiated today, new monitoring  
74 networks would fail to capture past changes that may already have altered forest reproductive capacity. Harvest records, widely  
75 used in ecology when scientific monitoring is not available [40–43], can provide retrospective insight. In Poland, the state  
76 forestry administration funds annual seed collection across all forest districts to supply regeneration and reforestation programs  
77 for the main tree species. Because collections occur mainly in near-rotation-age stands (i.e. mature stands approaching the  
78 typical harvest age), stand age is effectively constant. These records (40,530 observations spanning 34 years, 1988–2021)  
79 document both the mass of seed and cones collected (hereafter referred to as seeds for brevity) from seed stands in each  
80 district, and the demand driving collection intensity ('sampling effort'). Importantly, the harvest records comprise only sorted  
81 seeds (eliminating empty, underdeveloped, or infested seeds), thereby representing an estimate of viable seed crops instead  
82 of total seed output. Their interpretation requires caution, as harvests reflect not only seed availability but also forestation  
83 needs (including desired species composition), logistical capacity, and a gradual move toward natural regeneration that lowers  
84 sampling effort. Because collectors may sample multiple stands within a district, viable seed production might be overestimated  
85 when demand is high, while low demand for planting suppresses sampling effort. Since demand for seeds is documented, it  
86 can be incorporated into statistical analyses, allowing the separation of demand-driven fluctuations from biological trends in  
87 fecundity. With this adjustment, harvest records provide one of the few available windows into multi-decadal, community-wide  
88 reproductive dynamics in European forests.

89 Here, we use this nationwide dataset to examine temporal trends in fecundity for five dominant forest-forming species and  
90 their links to seasonal climate: European beech (*Fagus sylvatica*), silver fir (*Abies alba*), Scots pine (*Pinus sylvestris*), and  
91 oaks (pooled *Quercus petraea* and *Q. robur*). We test whether climatic change has reduced fecundity in European forests by  
92 pushing populations beyond the optimum range of their reproductive climatic niches. Specifically, we predict that (i) fecundity  
93 has declined across species, (ii) changes in seasonal climate, including summer and spring temperatures during phenologically

94 sensitive stages, explain much of this decline, and (iii) the magnitude and direction of these effects vary across local climates,  
95 reflecting population-specific reproductive niches and their thermal optima associated with local adaptations [44]. By testing  
96 these predictions, we provide a community-wide assessment of long-term fecundity change, quantifying how both temporal  
97 trends and local climatic context shape the reproductive response of Europe's dominant tree species to sustained environmental  
98 change. To provide an independent line of evidence, we also analyse temporal changes during this period in masting behaviour  
99 in the same taxa using the MASTREE+ dataset of reproductive effort [45].

## 100 **Fecundity declined across-species**

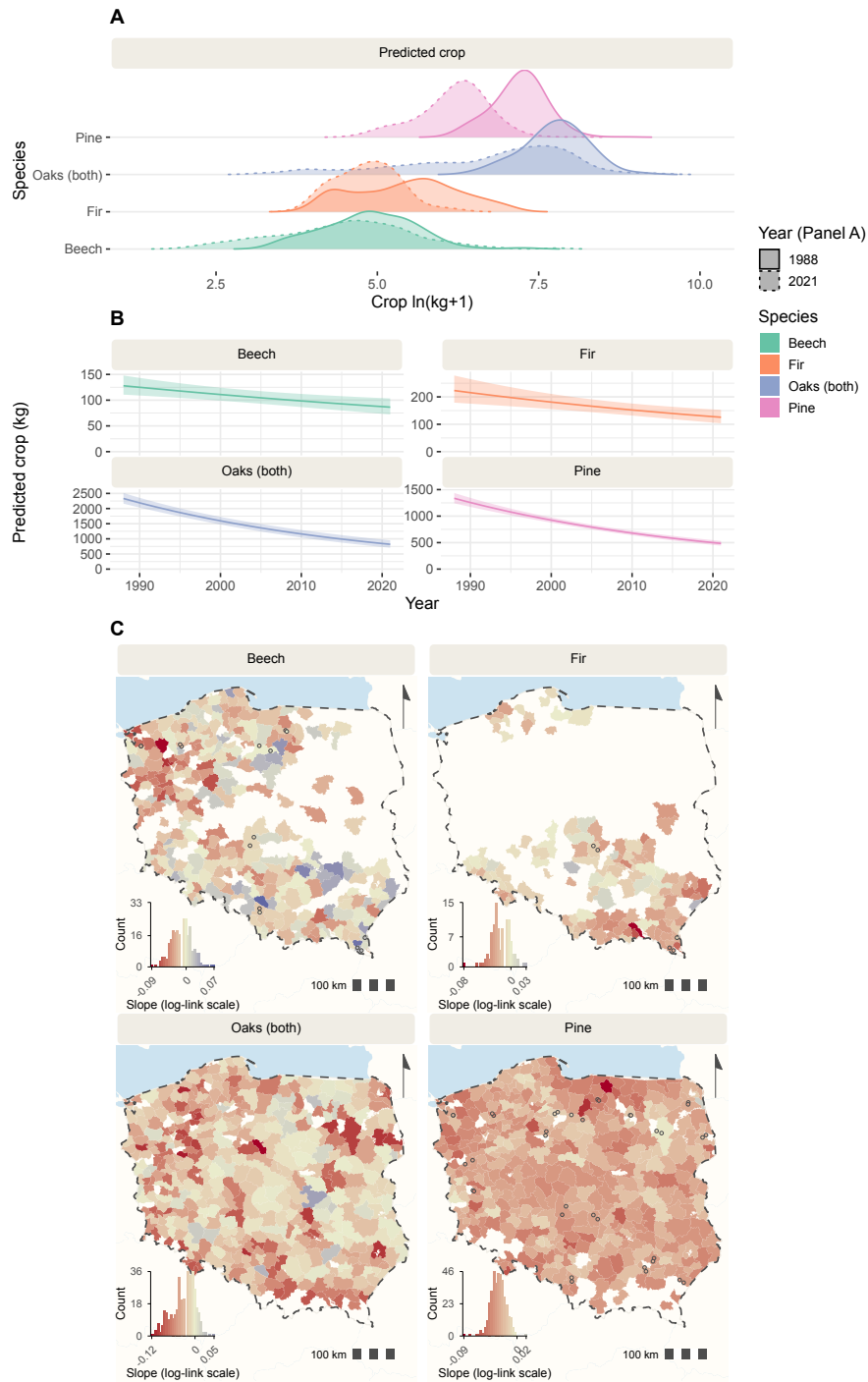
101 Consistent with our expectation of decreasing fecundity (i), our long-term dataset reveals a consistent decline in mean seed  
102 production over the past three decades across species (Fig. 1, Table S1; Methods 'TREND'). The oaks showed a decline of  
103  $-64.8\%$  ( $\pm 0.003$  SE), scots pine  $-63.7\%$  ( $\pm 0.004$  SE), and silver fir and European beech experienced more moderate declines  
104 of  $-43.7\%$  ( $\pm 0.05$  SE) and  $-32.5\%$  ( $\pm 0.08$  SE) respectively (Fig. 1). Spatially, fecundity declines across most populations  
105 (Fig. 1C), but trend magnitude is species-specific, with central Poland showing weaker declines or localised increases in some  
106 species. Further evidence of a fecundity decline comes from the independent MASTREE+ dataset (Methods 'MASTREE'),  
107 as inter-annual variability in seed production (CVp) declined across taxa ( $-0.02$  to  $-0.08$  SD year $^{-1}$ ; all  $p \leq 0.016$ ), and an  
108 increase in seed output in low seeding years occurred in all taxa ( $0.03$ – $0.04$  SD year $^{-1}$ ; all  $p < 0.0001$ ), except oak ( $-0.08$ ,  
109  $p = 0.94$ ) for which data availability limited inference (Extended Data Fig. 1).

## 110 **Fecundity trends are attributable to climate change**

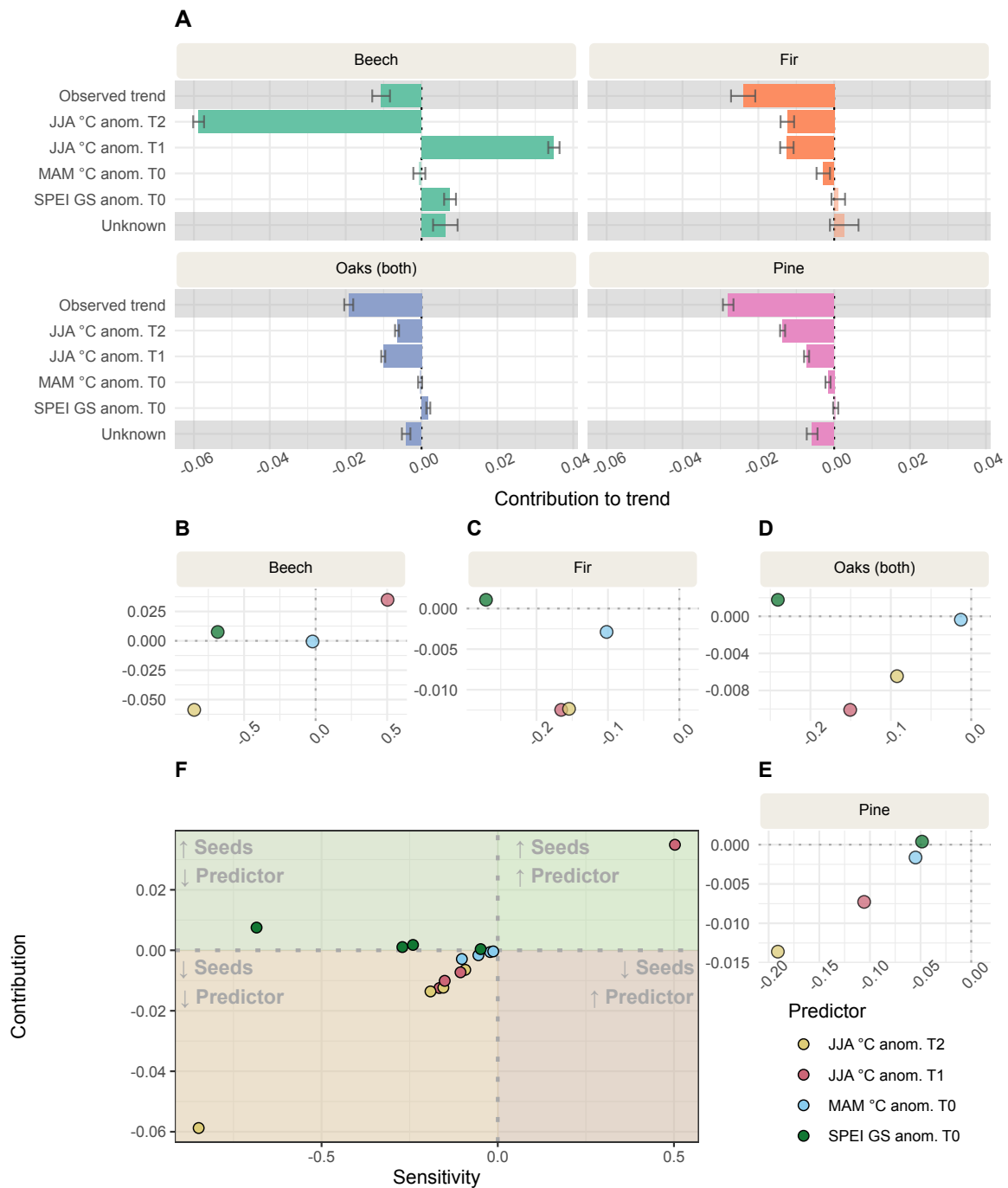
111 We used a temporal attribution framework [46] to evaluate how long-term trends in seed production are associated with climatic  
112 conditions during key phenological stages of flower-to-fruit development (prediction ii; See Methods 'TA'). In this framework,  
113 contribution captures how much each climatic predictor drives the fecundity temporal trend, while sensitivity quantifies the  
114 effect size of the predictor–response relationship. That is, how much seed production changes per unit change in a climatic  
115 predictor (Fig. 2B).

116 Climate during reproductive stages changed across populations of all species, with the strongest trends in summer temper-  
117 ature, followed by spring temperature and growing-season SPEI; the only exception was SPEI in fir, for which no significant  
118 temporal trend was detected (Table S3). Increases in summer temperature two years before seed production (T2) were consis-  
119 tently associated with lower seed output across species (Fig. 2). Warming in the summer one year before seed production (T1)  
120 also predicted lower output for most species; the exception was beech, where warmer T1 summers increased seed production  
121 (Fig. 2). Even in beech, however, the negative T2 effect dominated, yielding a net negative effect of summer warming on seed  
122 output. Species showed sensitivity to growing season moisture (SPEI) (Fig. 2, Table S2), but its contribution to long-term  
123 trends was limited. The modest contribution aligned with the smaller magnitude of change in this climate driver relative to the  
124 other variables (Table S3). In other words, SPEI patterns suggested an emerging risk, but have not been a primary driver to  
125 date. Minimum spring temperatures contributed little to temporal trends and showed weak sensitivity overall.

126

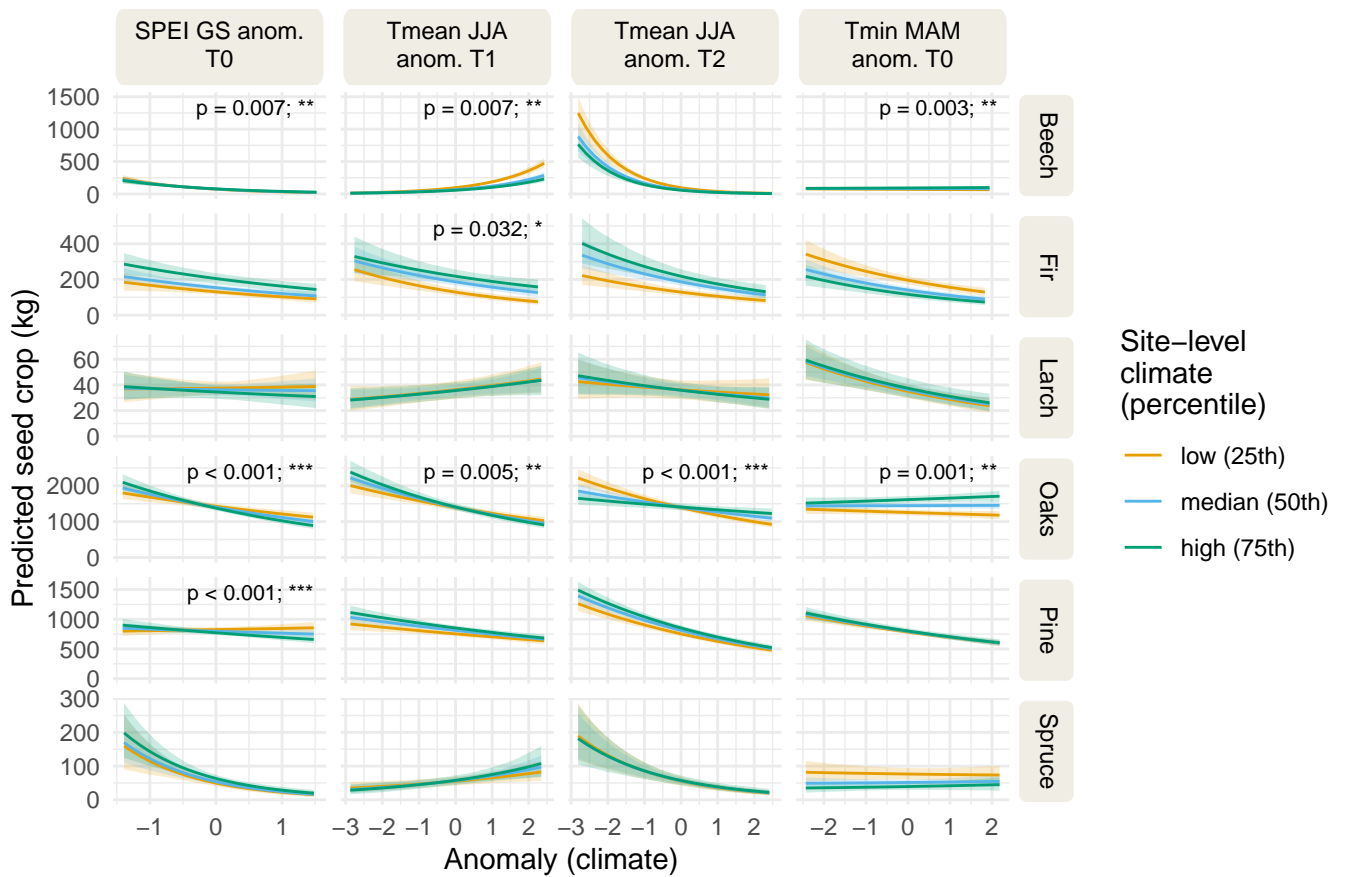


**Figure 1 | Over three decades, average seed crops have decreased across species.** A) Probability density functions of predicted seed crops at the site level at the start (solid line) and end (dotted line) of the study period across sites and species show the overall leftward shift in the predicted crop distributions across sites. Note that these are based on model predictions for each site and represent long-term changes in fecundity, rather than inter-annual variability in observed seed production. See Methods ('TREND'). Predictions are log-transformed for visualisation. B) species-specific panels show the general, across sites, declines in seed production over time. Shaded areas show 95% confidence intervals of the predicted mean response. For partial residuals, see Extended Data Fig. 3). C) Despite the general decline, there is spatial variation in temporal fecundity trends (Local patterns: red = declines, teal = increases. See inset histograms for species-specific legends) across forest district boundaries ('sites'; shown as polygons). Where forest district boundaries changed over time, coloured points mark the trend at each district's historic main administrative location, while the enclosing polygon colour shows the average of these sites. Trends were estimated using species-specific Tweedie-family generalised linear mixed-effects models with site-level random slopes on a log-link scale, and accounted for variation in sampling effort. Country boundaries are from Natural Earth.



**Figure 2 | Temporal changes in seasonal weather explain a large portion of observed temporal variation in fecundity.**

A) Contribution of changes in seasonal climate variables to observed long-term fecundity trends across species. Lagged summer temperature anomalies were the dominant drivers, while the unexplained component (“unknown”) was comparatively small. Whiskers show standard errors. B–E) Species-specific contributions and sensitivities plotted jointly for each seasonal predictor. This highlights potential risks from variables that have shown little temporal change but to which fecundity is highly sensitive such as growing season SPEI. Panel F) summarises patterns across species. See Methods ‘TA’ for analysis details.  $n = 40,530$  annual harvest values; species-specific sample sizes are given in Methods ‘Fecundity data’. Abbreviations: GS = growing season; anom. = anomaly relative to site mean climate; Tx = time lag (T0 = year of seed production); Tmean = mean temperature; Tmin = mean minimum temperature; JJA = summer months; MAM = spring months. GS = growing season; anom. = anomaly from mean climate; Tx = time lag, with T0 indicating the year of seed production; Tmean = mean temperature; Tmin = mean minimum temperature; JJA = summer months; MAM = spring months; SPEI = Standardised Precipitation-Evapotranspiration Index.



**Figure 3 | Weather effects on seed production depend on local climate.** Temporal deviations from a site its typical climate during reproductively sensitive phases are linked to variation in seed crop size, but the magnitude and direction of these effects differ across climates and taxa. Predicted seed production (back-transformed) was derived from bootstrapped GLMMs (1000 replicates per species and climate–anomaly combination) across gradients of climate anomalies for three representative site climates (line colours). Shaded ribbons show 95% confidence intervals around the predicted mean response. Two-sided p-values were derived from bootstrap coefficient distributions. See Methods ‘CF’ for analysis details. Abbreviations: GS = growing season; anom. = anomaly from mean climate; Tx = time lag, with T0 indicating the year of seed production; Tmean = mean temperature; Tmin = mean minimum temperature; JJA = summer months; MAM = spring months; SPEI = Standardised Precipitation-Evapotranspiration Index. Asterisks show significance levels for site × anomaly interactions:  $p < 0.001 = ***$ ,  $p < 0.01 = **$ ,  $p < 0.05 = *$ .

## Local climate modulates weather effects on fecundity

To test whether local climate mediates the effects of seasonal weather on fecundity (prediction iii), we fitted species-specific GLMMs with interactions between seasonal climate anomalies and site mean conditions (see Methods 'CF'). The estimated effects show that both the magnitude and sign of weather effects depend on overall climate and season (Fig. 3). Reported coefficients and standard errors are on the model (log-link) scale.

For nearly all species, there was a significant interaction between summer temperature in the year before seedfall (T1) and site mean summer temperatures (beech:  $-0.09 \pm 0.03$  SE,  $p = 0.007$ ; fir  $0.08 \pm 0.04$  SE,  $p = 0.03$ ; oak  $-0.07 \pm 0.03$  SE,  $p = 0.005$ ; site conditions are not centred), suggesting moderation by local climate. For instance Fig. 3 shows that high summer temperatures (T1) increased fecundity more strongly at cold sites in beech. Across the observed climate norms, high summer temperature anomalies (T1) reduced seed production in both fir and oak; the decline was strongest at colder sites for fir, but at warmer sites for oak. There was no site  $\times$  weather interaction for pine. Pines produced more seeds in warmer sites ( $0.16 \pm 0.04$  SE,  $p < 0.001$ ), but not in warmer years ( $0.48 \pm 0.42$  SE,  $p = 0.25$ ).

Temperature anomalies during the summer two years before seed production (T2) showed consistent but non-significant negative trends across species, with no significant site interactions. Oak was the exception: seed production was lower following hot summers, especially in cold sites ( $0.15 \pm 0.02$  SE,  $p < 0.001$ ; Fig. 3).

Spring temperature anomalies and site conditions also interacted to affect fecundity. In beech and oak, cooler springs reduced seed production in warmer sites, but cooler springs increased seed production in colder sites (beech:  $0.11 \pm 0.04$  SE,  $p = 0.003$ ; oak:  $0.08 \pm 0.022$  SE,  $p = 0.001$ ). No site  $\times$  weather interaction was observed for fir. Fir populations in warmer sites did produce fewer seeds ( $-0.59 \pm 0.13$  SE,  $p < 0.001$ ).

The effect of SPEI growing season anomaly on seed production depended, for most species, on site SPEI levels. For beech, drier sites (low SPEI) experienced stronger decreases in seed production in wet years (higher SPEI anomaly;  $4.74 \pm 1.55$  SE,  $p = 0.007$ ). Conversely, oak and pine showed that wet years in drier sites were associated with higher seed crops (oak  $-3.82 \pm 1.09$  SE,  $p < 0.001$ ; pine  $-3.87 \pm 0.99$  SE,  $p < 0.001$ ). Fir seed crops, moreover, were higher in wetter sites ( $7.17 \pm 1.46$  SE,  $p < 0.001$ ), with no significant weather interactions.

## Discussion

Our analysis of nationwide Polish harvest records reveals broad declines in fecundity across Europe's dominant tree species, with few regions showing stability or increase over the past three decades. These results support our prediction (i) that climatic change is eroding reproductive capacity where populations are pushed beyond their optimal climatic conditions. Declines were strongest in Scots pine and oaks and weaker, though evident, in European beech and silver fir. In European beech, the decline is consistent with disrupted masting, also detected in these populations [47], and an associated reduction in viable seed production due to increased seed predation and reduced pollination. We thereby extend species-level reports of reduced fecundity in temperate and boreal forests to the community scale [2, 16, 48, 49]. In Scots pine, marked fecundity declines combined with increasing climate-driven mortality suggest that reproductive output may become insufficient to offset population losses, although further research is needed to quantify downstream demographic consequences [50, 51]. Partial buffering in beech and fir likely reflects interspecific differences in reproductive thermal niches and stage-specific climatic sensitivity during flower–fruit development.

Because harvest records reflect both biological supply and forestation demand ('sampling effort'), we accounted for temporal variation in demand to isolate biological trends. The negative trends persisted, indicating that declining seed availability cannot solely be attributed to fluctuations in sampling effort. Some uncertainty remains when effort and biology share trends. For

165 instance, sampling effort declined over time (Extended Data Fig. 2), likely reflecting a shift from planting to natural regeneration  
166 and increased use of broadleaves, which may reduce detection of high seed-crop years in the later part of the series. However,  
167 supplementary analyses of independent MASTREE+ data for the same species and period show a decline in masting, implying  
168 fewer viable seeds were produced even if total seed production increased, because masting enhances pollination efficiency and  
169 predator satiation [52]. Together, these results support a widespread decline in forest fecundity. Additionally, the direction  
170 and magnitude of our declines align with independent evidence of large fecundity losses: a >50% decline in viable seeds in  
171 European beech in the UK [21], a 40% decline in cone production in pinyon pine in New Mexico [48], and an 80% decline  
172 in fruit production in Gabon [53]. The scale of change matches or exceeds contemporary declines in growth and increases in  
173 mortality [54–56], consistent with the view that fecundity is a strongly climate-sensitive demographic rate [15] and an early  
174 signal of population stress driving forest restructuring under ongoing environmental change.

175 Consistent with prediction (ii), long-term fecundity declines are tied to changes in seasonal climate during phenologically  
176 sensitive stages. Across species, warmer summers two years before seed production were associated with lower seed output,  
177 indicating a negative sensitivity of flower initiation to elevated temperature. In beech, seed production declined with summer  
178 warming two years before reproduction, consistent with the species' requirement for cool summers during floral initiation  
179 [27, 57]. Warmer summers one year before reproduction partly offset this decline by promoting flowering initiation [19, 21],  
180 yet the net contribution of summer warming remained negative. The magnitude of fecundity decline is comparable to trends  
181 associated with masting breakdown, including increased seed predation and reduced pollination success in beech [21]. Other  
182 species showed no such offset, with both T2 and T1 warming linked to fecundity declines. While warm springs were locally  
183 associated with reduced seed production — potentially due to mismatched pollen release or spring frost damage [33, 58, 59] —  
184 long-term declines were not closely linked to spring temperature trends in any species. This aligns with the absence of regional  
185 trends in late frost damage [60]. Although drought severity (SPEI) has increased, it did not emerge as a consistent driver of  
186 fecundity trends. Weak overall effects of spring temperature and SPEI likely reflect opposing site-level responses that cancel out  
187 when aggregated regionally, suggesting that these variables may still shape local-scale trends. Together, these results indicate  
188 that multiple reproductive stages constrain long-term fecundity, with the dominant bottlenecks differing among species [25].

189 Consistent with prediction (iii), local climate modulates how seasonal weather anomalies affect fecundity. By comparing  
190 within-site responses to short-term climate anomalies with across-site responses to long-term climatic means (Fig. 3), we  
191 distinguish fast ecological processes such as phenotypic plasticity and phenological adjustment from slower responses driven  
192 by acclimation or local adaptation [44, 61]. Temporal ('within site') sensitivities thus represent "transient" responses to changes  
193 in weather, while across site patterns approximate "equilibrium" responses emerging after prolonged exposure to local climatic  
194 regimes [44]. Such patterns often differ in magnitude or sign; for instance, ponderosa pine grows faster in warmer sites but  
195 shows reduced growth in unusually hot years [62, 63]. Here, fir fecundity was unaffected by short-term drought anomalies  
196 but was higher in wetter sites, implying that persistent drying will reduce reproduction not through increasing annual drought  
197 damage, but through gradual reorganisation of populations toward a low-fecundity equilibrium. Beech showed the opposite  
198 pattern, i.e., higher reproduction in dry years but no advantage at dry sites, suggesting that positive short-term responses to  
199 drought will not persist over the long term. This divergence between temporal and spatial patterns is consistent with past  
200 studies, which compared beech seed production responses to within-site anomalies and among-site variation in precipitation  
201 [64, 65]. More generally, across many species–anomaly combinations, spatial effects of climate were modest, suggesting that  
202 local adaptation or acclimatisation may help populations maintain similar performance across climate gradients, even if notable  
203 site-level differences remain for some species [44]. From a management perspective, local adaptation offers near-term buffering

204 capacity. However, climate change mitigation via provenance selection or translocation would require careful, small-scale  
205 testing given associated risks of interventions [66].

206 While we focus on fecundity, seedling recruitment is also sensitive to climate variability, particularly to drought and  
207 temperature extremes during germination and early establishment [67–69]. For instance, in ponderosa pine (*Pinus ponderosa*)  
208 and Douglas fir (*Pseudotsuga menziesii*), recruitment is non-linearly related to moisture, with recent conditions falling below  
209 thresholds for successful regeneration in many sites [70]. Increased seed supply can partially buffer negative climate effects on  
210 regeneration [71], but if fecundity declines in parallel with decreasing climatic suitability for establishment, these effects will  
211 interact, potentially accelerating population decline [72]. Recruitment studies that reconstruct past reproductive output from  
212 age structures and regeneration records [70, 73–75] could help test whether reduced seed availability is already constraining  
213 forest renewal, and how this interacts with climate effects on seedling establishment. Given the observed fecundity declines  
214 and reports of seedling mortality following increasingly severe drought [51], such analyses are urgent. Other factors, such as  
215 changes in forest structure and age, atmospheric CO<sub>2</sub> or nitrogen deposition and air pollution may also influence long-term  
216 fecundity patterns and warrant further study.

217 We document a multi-decadal decline in viable seed production across Europe’s dominant temperate forest-forming trees,  
218 after adjusting harvest records for sampling effort. The pattern is consistent with our theoretical framework: climatic change  
219 reduces fecundity as populations are pushed beyond their reproductive climatic optima (prediction i), with declines largely  
220 attributable to seasonal thermal conditions during phenologically sensitive stages, especially summer warming (prediction ii),  
221 and with effect sizes moderated by local climate (prediction iii). Because our records reflect viable seed crops, the decline  
222 indicates reduced effective reproductive output. Since reproduction underpins regeneration, community structure, range tracking,  
223 and the seed supply required by nurseries [3, 7, 76], continuing declines in fecundity elevate renewal risk [72], especially where  
224 establishment is already constrained by drought and heat [70]. Simultaneously, contrasts between spatial and temporal patterns  
225 suggest that slow response processes (acclimation and adaptation) may partly offset negative trends if given sufficient time; an  
226 outcome that depends critically on the pace of environmental change [44]. The next step is to integrate fecundity trends with  
227 long-term recruitment and demographic data to determine whether the declines documented here, especially in combination  
228 with shifting climatic suitability for seedling establishment, are translating into reduced regeneration.

## 229 **Acknowledgements**

230 This study was funded by the European Union (ERC, ForestFuture, grant no. 101039066 to M.B.; Marie Skłodowska-Curie  
231 Actions, FECUND, grant no. 101244227 to J.F.) and by the Foundation for Polish Science (START, to J.F.). Views and  
232 opinions expressed are those of the authors only and do not necessarily reflect those of the European Union or the European  
233 Research Council. Neither the European Union nor the granting authority can be held responsible for them. We thank the  
234 Directorate-General of State Forests for providing data on the abundance of seeds of major forest-forming species.

## 235 **Author Contributions Statement**

236 JJF, MB, and JSz designed the study. MKD and JJF performed seed crop data preparation (cleaning), and SJ and MKD provided  
237 context on data collection protocols. JJF conducted the formal analysis and visualisation. All authors contributed to the data  
238 interpretation. JJF and MB wrote the first draft of the manuscript, and all authors revised the text.

239 **Competing Interests Statement**

240 No competing interests to declare.

241 **Tables**

**Table 1** | Literature summary on temporal trends in tree reproduction across species and regions. Articles were retrieved from Scopus using the query '(fecundity OR "seed production") AND tree\* AND trend,' where the asterisk is a truncation wildcard. The table was supplemented with sources from our own review of the literature. T = temperature, P = precipitation.

Species	Level	Linked to	Direction	Study	Sites	Location	Period
<i>Beilschmiedia tawa</i>	Species	Summer & winter T, P	-	[77]	6	New Zealand	1986-2020
<i>Fagus sylvatica</i>	Species	Summer T, tree size	-	[78, 79]	12	UK	1980-2020
<i>Fagus sylvatica</i>	Species	Summer T	viable, + total -	[19]	50	Europe	1980-2022
<i>Nothofagus solandri</i>	Species	Summer T & P	viable, + total + (great- est at high eleva- tion)	[16, 80]	3	New Zealand	1965-2009
<i>Pinus edulis</i>	Species	Summer T (cone initiation)	-	[48]	9	USA	1969-2012
<i>Pinus edulis</i>	Species	Climatic water deficit, monsoonal ity	- (hind- cast)	[49]	16	USA	1900-2024
<i>Picea engelmannii</i>	Species	Summer T, spring snow	+	[22]	13	USA	1970-2010
<i>Pinus pinea</i>	Species (harvest)	T & P throughout cone development	-	[81]	58	Spain	1960-2000
<i>Pinus sibirica</i>	Species	Spring T, September T	-	[82]	1	Russia	1990 - 2019
<i>Quercus crispula</i>	Species	Growing season T	+	[17]	1	Japan	1980-2017
<i>Quercus petraea</i> (& <i>Q. robur</i> ; ns)	Species	Spring T	+	[32]	28	France	1994-2007
3 <i>Quercus</i> species ( <i>Q. chapmanii</i> , <i>Q. geminata</i> , <i>Q. inopinata</i> )	Species	Spring P & fire	-	[83]	1	USA	1988-2018
68 plant species	Community	VPD, minimum relative humidity	Shrubs: -, Herbs, vines, trees & palms): NS, Over- all: NS	[84]	1	China	2014-2020
73 tropical tree species	Community	Not tested	-	[53]	1	Gabon	1986-2018
81 tropical tree and liana species	Community	El Niño events	Flowers +, Seeds: NS	[85]	1	Panama	1987-2005
123 tree species	Community	Tree size, Spring minimum T, summer T, moisture deficit	West: -, East: +	[4]	653	North America	~1960--2020
203 plant species	Community	Night T, Vapour pressure deficit	-	[86]	1	Ecuador	1960-2000
363 plant species	Community	Not tested	-	[23]	205	World	1900-2014

242 **Figure Legends/Captions**

243 **Fig 1: Over three decades, average seed crops have decreased across species.** A) Probability density functions of predicted  
244 seed crops at the site level at the start (solid line) and end (dotted line) of the study period across sites and species show

245 the overall leftward shift in the predicted crop distributions across sites. Note that these are based on model predictions for  
246 each site and represent long-term changes in fecundity, rather than inter-annual variability in observed seed production. See  
247 Methods ('TREND'). Predictions are log-transformed for visualisation. B) species-specific panels show the general, across  
248 sites, declines in seed production over time. Shaded areas show 95% confidence intervals of the predicted mean response. For  
249 partial residuals, see Extended Data Fig. 3). C) Despite the general decline, there is spatial variation in temporal fecundity  
250 trends (Local patterns: red = declines, teal = increases. See inset histograms for species-specific legends) across forest district  
251 boundaries ('sites'; shown as polygons). Where forest district boundaries changed over time, coloured points mark the trend at  
252 each district's historic main administrative location, while the enclosing polygon colour shows the average of these sites. Trends  
253 were estimated using species-specific Tweedie-family generalised linear mixed-effects models with site-level random slopes on  
254 a log-link scale, and accounted for variation in sampling effort. Country boundaries are from Natural Earth.

255 **Fig 2: Temporal changes in seasonal weather explain a large portion of observed temporal variation in fecundity.** A)  
256 Contribution of changes in seasonal climate variables to observed long-term fecundity trends across species. Lagged summer  
257 temperature anomalies were the dominant drivers, while the unexplained component ("unknown") was comparatively small.  
258 Whiskers show standard errors. B–E) Species-specific contributions and sensitivities plotted jointly for each seasonal predictor.  
259 This highlights potential risks from variables that have shown little temporal change but to which fecundity is highly sensitive  
260 such as growing season SPEI. Panel F) summarises patterns across species. See Methods 'TA' for analysis details. n= 40,530  
261 annual harvest values; species-specific sample sizes are given in Methods 'Fecundity data'. Abbreviations: GS = growing season;  
262 anom. = anomaly relative to site mean climate; Tx = time lag (T0 = year of seed production); Tmean = mean temperature;  
263 Tmin = mean minimum temperature; JJA = summer months; MAM = spring months. GS = growing season; anom. = anomaly  
264 from mean climate; Tx = time lag, with T0 indicating the year of seed production; Tmean = mean temperature; Tmin = mean  
265 minimum temperature; JJA = summer months; MAM = spring months; SPEI = Standardised Precipitation-Evapotranspiration  
266 Index.

267 **Fig 3: Weather effects on seed production depend on local climate.** Temporal deviations from a site its typical climate  
268 during reproductively sensitive phases are linked to variation in seed crop size, but the magnitude and direction of these  
269 effects differ across climates and taxa. Predicted seed production (back-transformed) was derived from bootstrapped GLMMs  
270 (1000 replicates per species and climate–anomaly combination) across gradients of climate anomalies for three representative  
271 site climates (line colours). Shaded ribbons show 95% confidence intervals around the predicted mean response. Two-sided  
272 p-values were derived from bootstrap coefficient distributions. See Methods 'CF' for analysis details. Abbreviations: GS =  
273 growing season; anom. = anomaly from mean climate; Tx = time lag, with T0 indicating the year of seed production; Tmean =  
274 mean temperature; Tmin = mean minimum temperature; JJA = summer months; MAM = spring months; SPEI = Standardised  
275 Precipitation-Evapotranspiration Index. Asterices show significance levels for site × anomaly interactions: p < 0.001 = \*\*\*, p  
276 < 0.01 = \*\*, p < 0.05 = \*.

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## 486 **Methods**

487 The data and code supporting the findings of this study are available at Figshare [87].

### 488 **Fecundity data**

489 Annual seed harvests were reported by local forest districts (*Nadleśnictwa*, referred to as 'sites') to the Polish State Forests,  
490 based on collections from 1988-2021 by contracted crews from the ground or canopy within designated seed stands. However,  
491 since analyses were conducted at the species level, results are independent of collection methods. Each site contains one or more  
492 seed stands per species, and foresters collect from as many of these stands within site boundaries as needed to meet demand.  
493 Before reporting, seeds underwent quality assessment following the nation-wide and unified protocol. Samples of each lot were  
494 evaluated for purity, including exclusion of empty seeds, species-specific debris (e.g., husks, needles), foreign material, and  
495 seeds damaged or infested by insects. Empty seeds were removed by sorting or air separation; in beech, sorting was typically  
496 done by hand to remove infested seeds. The degree of pre-cleaning varied among species, and in some cases small but viable  
497 seeds may have been excluded, or empty seeds retained. As a result, reported harvests are post-sorting seed lots (by weight),  
498 and reflect an estimate of viable seed yield rather than total seed production.

499 The dataset (438 sites, n=40,530 annual observations) records the mass (kg) of seeds (or cones, for conifers; hereafter  
500 'seeds') harvested annually for Silver fir (*Abies alba*; 123 sites, n=4,085), European beech (*Fagus sylvatica*; 290 sites, n=9,661),  
501 Scots pine (*Pinus sylvestris*; 401 sites, n= 13,272), Sessile oak (*Quercus petraea*), and Pedunculate oak (*Quercus robur*). Prior  
502 to 2007-2008, depending on the site, oak harvests were not reported separately for these two species, and records were therefore  
503 pooled (407 sites, n=13,512). The dataset also includes annual seed demand (kg) at the site level. Demand is calculated by  
504 the State Forests administration as the product of the planned artificial regeneration area for each species and fixed, species-  
505 specific conversion coefficients that reflect target planting density and standardised nursery sowing rates. These conversion  
506 coefficients are used uniformly across Poland and have remained unchanged over time; however, annual demand itself varies  
507 spatio-temporally with the planned regeneration area and available seed stocks as demand is reduced when stock levels of  
508 previously collected seeds are high. Demand is not influenced by private nurseries. Seed collection from forest stands by third  
509 parties is prohibited, and seeds are not exported. Thus, demand can be interpreted as a composite index of sampling effort.

510 We excluded time-series consisting of >90% seed harvest values of zero to avoid model convergence issues. Lowering this  
511 threshold to 80% or 50%, does not change the results qualitatively. The proportion of zero values across time-series is provided  
512 in Fig. S1. We analysed all time-series of these five species spanning more than a decade (mean: 33.19 years; Fig. S2).  
513 Site boundaries for each species are shown in Fig. 1C. If demand values were missing but the recorded seed harvest was zero,  
514 demand was set to zero (1,488 observations). If a harvest had taken place but demand was missing, we imputed the site-level  
515 mean demand for the focal species (1,625 observations).

## 516 **Climate data**

517 We obtained high-resolution (2.5') historical monthly climate data (1960–2021) for Europe from the WorldClim database  
518 (v. 2.1; [88]), including minimum and maximum temperature and precipitation. Mean monthly temperature was calculated  
519 by averaging Tmin and Tmax raster layers. For each grid cell, we then calculated mean temperature and total precipitation  
520 per season (December-February 'DJF', March-May 'MAM', June-August 'JJA', September-November 'SON') and per year.  
521 Potential evapotranspiration (PET) was estimated using the Thornthwaite method based on temperature, and combined with  
522 precipitation to compute the Standardised Precipitation-Evapotranspiration Index (SPEI) at a 1-month scale using the SPEI  
523 package (v. 1.8.1; [89]). To harmonise seasonal definitions, December was reassigned to the subsequent year, allowing each  
524 winter season to span December through February.

## 525 **Data analysis**

526 All models were built in R (v. 4.4.1) using glmmTMB (v. 1.1.10) unless indicated differently and validated with DHARMA  
527 (v.0.4.7; [90-92]). Throughout the analyses, we used Tweedie distribution models because they accommodate both zero-inflation  
528 and overdispersion, which are common features of reproductive data. The Tweedie family also offers flexibility across a range of  
529 data-generating processes, and applying the same distribution across all temporal attribution models (e.g. reproduction trends  
530 and climate effects) ensured consistency and comparability, making it the preferred choice.

531 **Spatio-temporal trends ('TREND')** *Reproductive trends.* To visualise spatio-temporal variation in seed production.  
532 (Fig. 1), we fitted a Tweedie family GLMM for each species with year,  $\ln[\text{kg} + 1]$ -transformed demand, and previous-year harvest  
533 as fixed effects, and allowed the effect of year to vary by site with a random slope. Including demand yields demand-adjusted  
534 fecundity trends and climate effects that are conditional on the observed variation in demand.

535 **Climate-fecundity relationships ('CF')** We assessed how seasonal climate influenced seed production for four  
536 climatic variables linked to reproduction: mean spring minimum temperature, summer mean temperature at one- and two-year  
537 lags, and growing-season (April–September) SPEI (Fig. 3).

538 For each species, we fitted Tweedie GLMMs of seed crop size (kg) with fixed effects for the interaction between climate  
539 anomalies and their corresponding site-specific long-term means of each time-series. Anomalies were defined as the difference  
540 between the observed value of a climatic variable and its site-specific long-term mean. The two-year lagged summer temperature  
541 anomaly was interacted with the one-year summer site mean rather than the two-year mean to avoid collinearity between site  
542 means (Spearman's  $\rho > 0.99$ ). We controlled for variation in harvesting effort by including log-transformed seed demand ( $\ln[\text{kg}$   
543  $+ 1]$ ) as a covariate, and accounted for temporal autocorrelation in seed production by including the previous-year seed crop.  
544 Site was included as a random intercept.

545 Uncertainty was quantified using a block bootstrap, which preserves temporal dependence. For each species–anomaly pair,  
546 we resampled the data in contiguous 10-year blocks drawn from all sites combined (sampling with replacement from valid site  
547  $\times$  block-start year combinations) to preserve within-block temporal dependence while allowing site composition to vary among  
548 replicates. Each resample was refitted 1000 times. For visualisation, we generated partial-dependence predictions across the  
549 observed anomaly range at three levels of the site mean (25th, 50th, and 75th percentiles). For inference, we pooled the 4000  
550 bootstrap fits per species to summarise effects.

551 **Temporal attribution modelling ('TA')** We used a temporal attribution framework [46] to assess how long-term  
552 trends in seed production are associated with climatic conditions, using Tweedie log-link GLMMs with site as a random intercept  
553 in all models (Fig. 2).

554 We first quantified observed temporal trends in seed production by fitting "total trend" models for each species similar to  
555 the RT models, except for the simpler random effect structure. These models adjusted for previous-year seed crops and  $\ln[\text{kg} +$   
556  $1]$ -transformed seed demand. We also fitted "predictor trend" models for each climatic anomaly variable with the predictor as a  
557 function of time.

558 For each species, we then fitted a "process" model as described in [Climate-fecundity relationships \('CF'\)](#), to which we  
559 added species-specific zero-inflation and dispersion components to ensure model convergence in subsequent models dependent  
560 on the model output. For pine, the zero inflation formula included the previous-year seed production. For all other species  
561 (i.e., beech, oak), zero inflation depended solely on previous-year seed production. Dispersion was modelled as a function of  
562 log-transformed seed demand ( $\ln[\text{kg} + 1]$ ) in all species except pine, where it was held constant to ensure model stability.

563 From the fitted process model, we generated predictions for all observations, and fitted a "full prediction" trend model to  
564 these predictions to quantify the overall temporal trend explained by the predictors. For temporal counterfactuals, we held each  
565 climate predictor at its site-specific long-term mean (with other variables varying as observed), and refit a "fixed predictor"  
566 trend model.

567 We calculated the contribution of that predictor as the log-scale difference between the full-prediction trend and the fixed-  
568 predictor trend. Sensitivity was calculated by taking the difference between the full- and fixed-predictor trends on the response  
569 scale divided by the predictor's temporal slope. The "unknown" contribution was the residual difference between the observed  
570 total temporal trend in seed production (from the "total trend" model) and the sum of individual predictor contributions.

571 **Sampling effort trend ('DEMAND')** To test whether there was a temporal trend in sampling effort, we fitted species-  
572 specific Tweedie family GLMMs of log-transformed demand ( $\ln[\text{kg}+1]$ ) as a function of time, with site included as a random  
573 intercept. Sampling effort declined over time in all species (Extended Data Fig. 2).

574 **MASTREE+ reproductive trends ('MASTREE')** We used the MASTREE+ database to quantify temporal trends  
575 in masting for the focal species over the period 1988–present [45]. We retained continuous seed, fruit or cone production time-  
576 series of at least 20 years, covering the period of 1988 to 2022. The final dataset contained annual reproduction observations for  
577 the five species: *Abies alba* (n=456 across 16 sites), *Fagus sylvatica* (n=1,602 across 54 sites), *Pinus sylvestris* (n=594 across  
578 19 sites), *Quercus petraea* (n=45 across 2 sites), and *Quercus robur* (n=47 across 2 sites).

579 For each time-series we calculated 10-year moving-window metrics of reproductive variability, given its links to viable  
580 seed counts [52], including the coefficient of variation (CVp) and the 25th percentile of reproduction (representing crop size in  
581 low seeding years).

582 To focus on temporal changes within populations, these metrics were standardised within each time-series (since scaling  
583 removes time-series averages, no random factor was used to capture between-time-series differences). We then fitted Gaussian  
584 linear models to test for temporal trends, with standardised CVp or the lower quantile as response variables and year, species,  
585 and their interaction as fixed effects. Trends for each species were estimated from marginal slopes of the 'year' predictor using  
586 emmeans (v. 1.10.5; [93]).

587 **Data Availability**

588 The data supporting the findings of this study are available at Figshare [87].

589 **Code Availability**

590 The code supporting the findings of this study is available at Figshare [87].

591 **Methods-only references**

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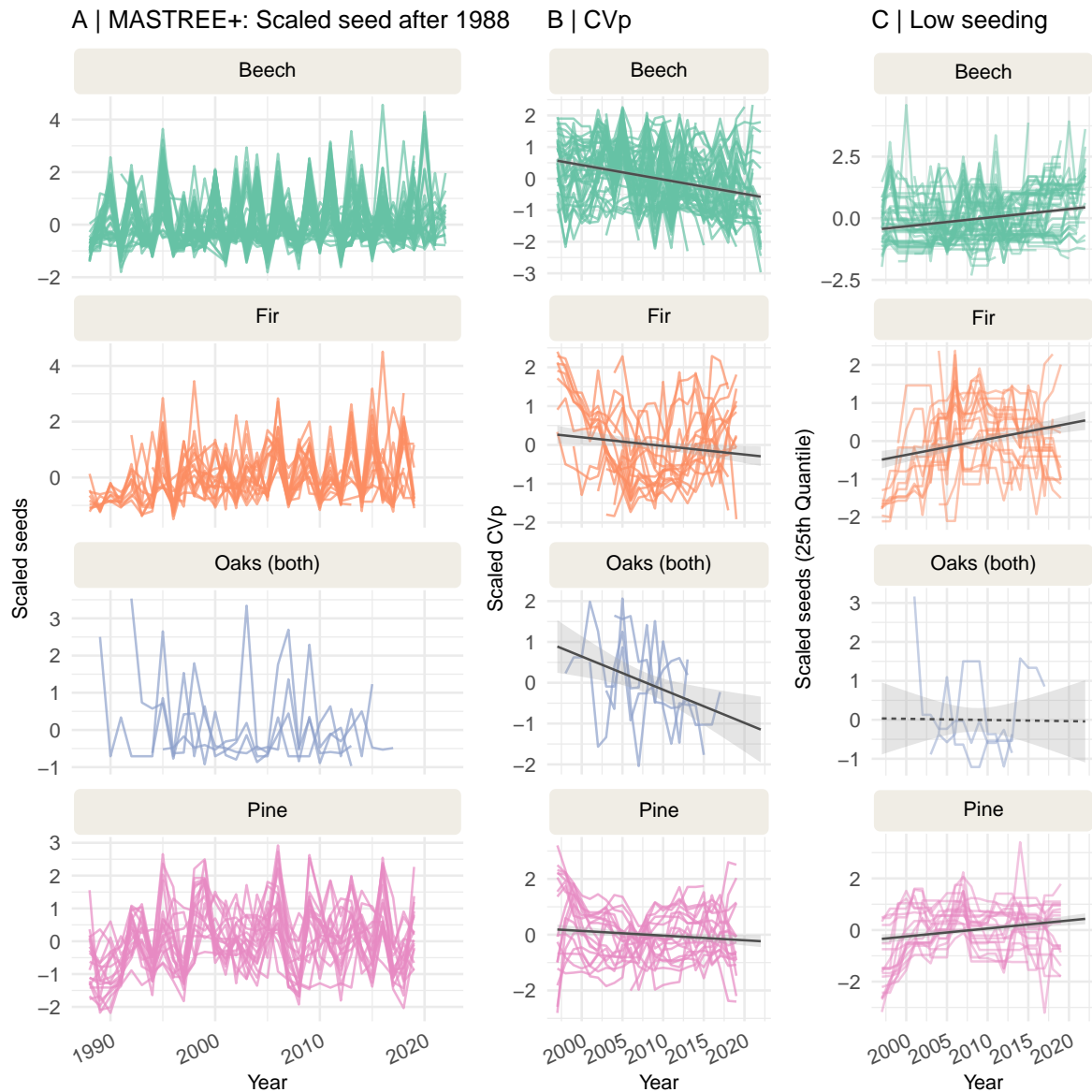
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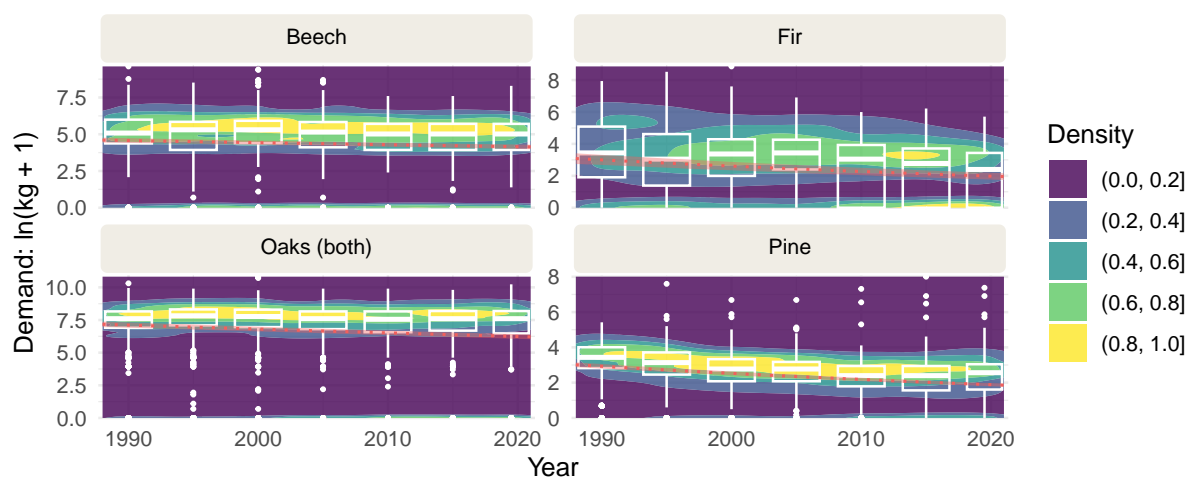
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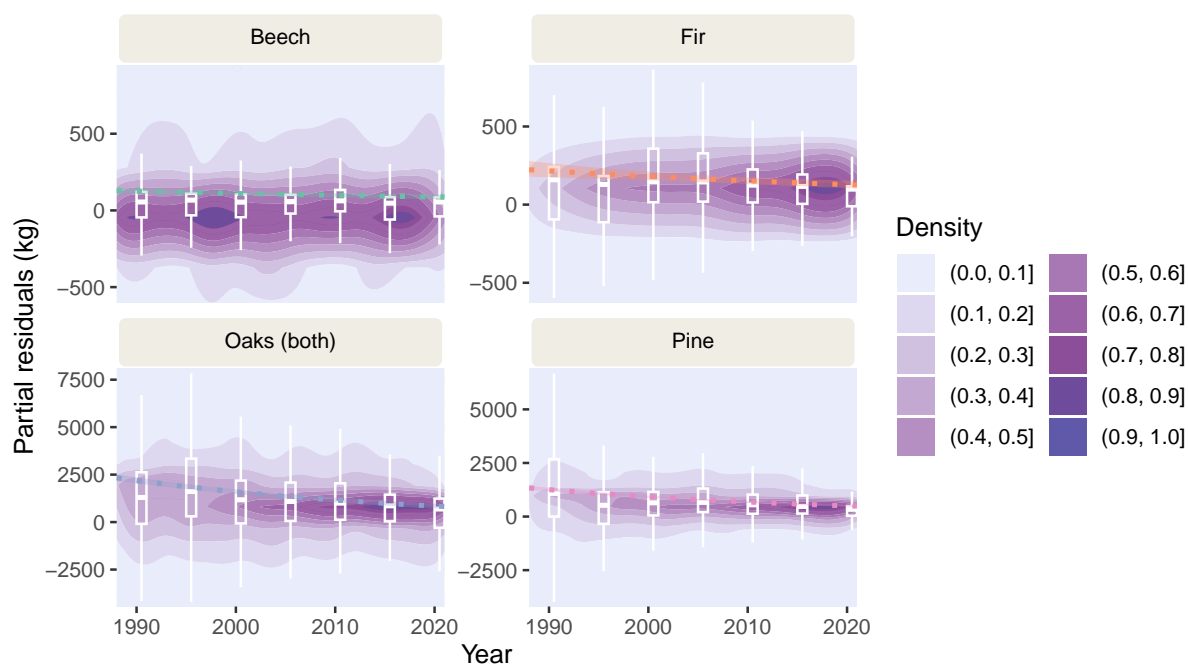
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**Figure 1 | Trends in MASTREE+ reproductive effort indicate a weakening of masting across the studied taxa consistent with declining fecundity.** Coloured lines show time-series data, whereas grey lines show predictions (significant: solid, not significant: dashed) obtained with linear models, and the shaded ribbons show 95% confidence intervals. A) Long-term ( $\geq 20$  years) time-series of scaled continuous observations of seeds, fruits and cones (labelled 'seeds'). B) Inter-annual variability in seed production (CVp) declined significantly in all taxa over time. C) Seed production in low seeding years (25th percentile) increased in all taxa except oak (dashed line), for which data availability was limited. Time-series in B-C were scaled at the time-series level and calculated with 10-year moving windows before regression. For details on data and analysis, see Methods 'MASTREE'.

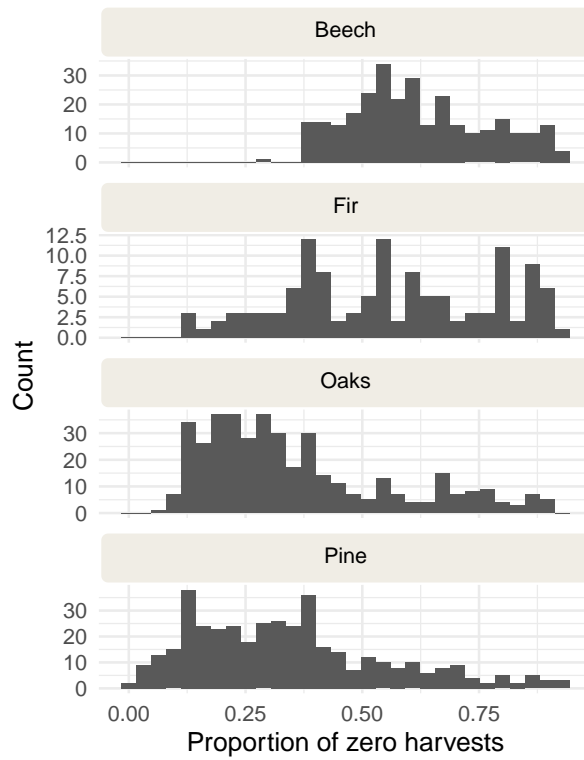


**Figure 2 | Observed seed crop demand (sampling effort) over time.** The colour shows the density of seed site-level, annual demand observations (scaled between 0 and 1 to allow for comparison between species). The box plots summarise seed demand observations by 5-year time windows, while red dotted lines show statistically significant linear trends as extracted from species-specific Tweedy family GLMMs of demand as a function of time with site included as a random intercept. The shaded red ribbons show 95% confidence intervals around these trends. For details on the analysis, see Methods 'DEMAND'.

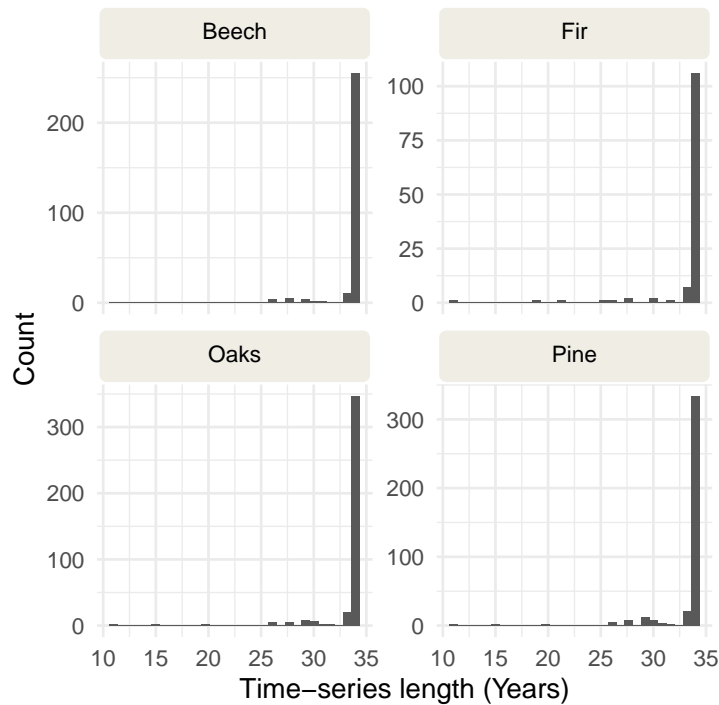


**Figure 3 | Partial residuals around long-term trend in fecundity.** Filled contour maps show normalised densities (scaled between 0–1) of partial residuals of seed production over time (i.e. fixed effect of time plus model residuals). Panels are cropped to regions with normalised density > 0.1 to highlight the predominant variation. Boxplots summarise partial residuals within 5-year windows, and the coloured dashed line reproduces the species-specific predicted trend from Fig. 1B. The shaded ribbons show 95% confidence intervals around these predicted trends. The results come from species-specific Tweedie-family generalised linear mixed-effects models, including random slopes of time effects by site. For details on the analysis, see Methods 'TREND'.





**Figure S1 | Distribution of the proportion of zero harvests (kg)** across Polish harvest time-series for beech, fir, oak, and pine. Each panel shows the number of time-series with a given proportion of years with zero harvest relative to the length of the time-series.



**Figure S2 | Distribution of the lengths of Polish harvest time-series** across sites for beech, fir, oak, and pine. Panels indicate the number of sites with time-series of varying durations (years) for each taxon.

**Table S1 | Temporal trends in fecundity show decline in harvest crop size for all species.** Results were obtained with 4 species-specific Tweedie family GLMMs, showing how harvest crops change with each year since the start of the time-series (1988 = 1). The model accounted for natural log transformed seed demand, and temporal autocorrelation in seed harvests through 1 year lagged harvests (Seeds T1). Site was included as a random effect. See Methods 'TA' for further detail.

Species	Term	Estimate (SE)	p
Beech	Intercept	3.172 (0.109)	< 0.001
Beech	Year	-0.011 (0.002)	< 0.001
Beech	ln(Demand+1)	0.428 (0.016)	< 0.001
Beech	Seeds T1	-3.673e-04 (5.988e-06)	< 0.001
Fir	Intercept	3.73 (0.129)	< 0.001
Fir	Year	-0.024 (0.003)	< 0.001
Fir	ln(Demand+1)	0.647 (0.024)	< 0.001
Fir	Seeds T1	4.764e-08 (9.034e-06)	0.996
Oaks (both)	Intercept	5.943 (0.071)	< 0.001
Oaks (both)	Year	-0.019 (0.001)	< 0.001
Oaks (both)	ln(Demand+1)	0.253 (0.007)	< 0.001
Oaks (both)	Seeds T1	-1.155e-05 (2.518e-06)	< 0.001
Pine	Intercept	5.817 (0.066)	< 0.001
Pine	Year	-0.028 (0.001)	< 0.001
Pine	ln(Demand+1)	0.512 (0.017)	< 0.001
Pine	Seeds T1	7.279e-05 (3.839e-06)	< 0.001

**Table S2 | Relationships between fecundity and spatio-temporal climatic variation.** Results were obtained with species-specific Tweedie family GLMMs, and show how harvest crops change with spatial ("Site") and temporal ("anom." = Anomaly) variation in climatic conditions during sensitive stages. Anomalies were added in interaction (":") with site-level mean climate. The model accounted for natural log transformed seed demand, and temporal autocorrelation in seed harvests through 1 year lagged harvests. Site was included as a random effect. JJA = June-August, MAM = March-May, GS = Growing season. SPEI = Standardised Precipitation Evapotranspiration Index. Tx indicates lag (e.g. T1 is a variable that was lagged 1 year). See Methods 'TA' for further detail.

Species	Term	Estimate (SE)	p
Beech	Intercept	11.381 (1.869)	< 0.001
Beech	JJA °C anom. T1	2.256 (0.52)	< 0.001
Beech	Site JJA °C	-0.528 (0.128)	< 0.001
Beech	JJA °C anom. T2	-0.546 (0.489)	0.264
Beech	MAM °C anom. T0	-0.668 (0.132)	< 0.001
Beech	Site MAM °C	0.356 (0.153)	0.02
Beech	SPEI GS anom. T0	0.036 (0.226)	0.874
Beech	Site SPEI GS	3.306 (1.7)	0.052
Beech	ln(Demand+1)	0.404 (0.017)	< 0.001
Beech	Seeds T1	-2.146e-04 (9.397e-06)	< 0.001
Beech	JJA anom. T1:Site JJA °C	-0.092 (0.029)	0.002
Beech	Site JJA °C:JJA anom. T2	-0.013 (0.028)	0.64
Beech	MAM anom. T0:Site MAM °C	0.178 (0.036)	< 0.001
Beech	SPEI GS anom. T0:Site SPEI GS	4.288 (1.509)	0.004
Fir	Intercept	1.132 (2.038)	0.579
Fir	JJA °C anom. T1	-1.902 (0.515)	< 0.001
Fir	Site JJA °C	0.266 (0.144)	0.066
Fir	JJA °C anom. T2	0.047 (0.497)	0.925
Fir	MAM °C anom. T0	-0.189 (0.128)	0.141
Fir	Site MAM °C	-0.396 (0.187)	0.034
Fir	SPEI GS anom. T0	-0.048 (0.187)	0.799
Fir	Site SPEI GS	7.601 (1.656)	< 0.001
Fir	ln(Demand+1)	0.605 (0.024)	< 0.001
Fir	Seeds T1	4.320e-06 (7.885e-06)	0.584
Fir	JJA anom. T1:Site JJA °C	0.097 (0.029)	< 0.001
Fir	Site JJA °C:JJA anom. T2	-0.013 (0.028)	0.645

Fir	MAM anom. T0:Site MAM °C	-0.012 (0.039)	0.754
Fir	SPEI GS anom. T0:Site SPEI GS	0.92 (1.55)	0.553
Oaks (both)	Intercept	3.953 (1.342)	0.003
Oaks (both)	JJA °C anom. T1	0.564 (0.349)	0.106
Oaks (both)	Site JJA °C	0.005 (0.088)	0.95
Oaks (both)	JJA °C anom. T2	-2.433 (0.346)	< 0.001
Oaks (both)	MAM °C anom. T0	-0.29 (0.092)	0.002
Oaks (both)	Site MAM °C	0.323 (0.105)	0.002
Oaks (both)	SPEI GS anom. T0	-0.755 (0.142)	< 0.001
Oaks (both)	Site SPEI GS	0.171 (1.307)	0.896
Oaks (both)	ln(Demand+1)	0.318 (0.011)	< 0.001
Oaks (both)	Seeds T1	-7.080e-06 (2.396e-06)	0.003
Oaks (both)	JJA anom. T1:Site JJA °C	-0.04 (0.019)	0.039
Oaks (both)	Site JJA °C:JJA anom. T2	0.129 (0.019)	< 0.001
Oaks (both)	MAM anom. T0:Site MAM °C	0.072 (0.024)	0.003
Oaks (both)	SPEI GS anom. T0:Site SPEI GS	-3.539 (0.907)	< 0.001
Pine	Intercept	6.012 (0.901)	< 0.001
Pine	JJA °C anom. T1	0.134 (0.349)	0.701
Pine	Site JJA °C	-0.059 (0.058)	0.313
Pine	JJA °C anom. T2	-0.041 (0.338)	0.903
Pine	MAM °C anom. T0	-0.13 (0.088)	0.137
Pine	Site MAM °C	0.157 (0.068)	0.022
Pine	SPEI GS anom. T0	-0.784 (0.165)	< 0.001
Pine	Site SPEI GS	-1.096 (0.911)	0.229
Pine	ln(Demand+1)	0.439 (0.016)	< 0.001
Pine	Seeds T1	6.716e-05 (3.754e-06)	< 0.001
Pine	JJA anom. T1:Site JJA °C	-0.014 (0.019)	0.472
Pine	Site JJA °C:JJA anom. T2	-0.009 (0.019)	0.635
Pine	MAM anom. T0:Site MAM °C	-0.002 (0.023)	0.921
Pine	SPEI GS anom. T0:Site SPEI GS	-4.938 (1.048)	< 0.001

**Table S3 | Temporal trends in weather during reproductive stages.** Results were obtained with 4 species-specific Tweedie family GLMMs (N.B. family was chosen for consistency with the other variables in the temporal attribution framework), showing how each climatic variable ("Predictor") has changed per year since the start of the time-series (1988 = 1). Site was included as a random effect. JJA = June-August, MAM = March-May, GS = Growing season. SPEI = Standardised Precipitation Evapotranspiration Index. Tx indicates lag (e.g. T1 is a variable that was lagged 1 year). See Methods 'TA' for further detail.

Species	Predictor	Term	Estimate (SE)	p
Beech	JJA °C anom. T1	Intercept	-2.294 (0.034)	< 0.001
Beech	JJA °C anom. T1	Year	0.067 (0.001)	< 0.001
Beech	JJA °C anom. T2	Intercept	-2.35 (0.035)	< 0.001
Beech	JJA °C anom. T2	Year	0.07 (0.001)	< 0.001
Beech	MAM °C anom. T0	Intercept	-1.506 (0.033)	< 0.001
Beech	MAM °C anom. T0	Year	0.026 (0.002)	< 0.001
Beech	SPEI GS anom. T0	Intercept	-1.517 (0.032)	< 0.001
Beech	SPEI GS anom. T0	Year	-0.011 (0.002)	< 0.001
Fir	JJA °C anom. T1	Intercept	-2.445 (0.054)	< 0.001
Fir	JJA °C anom. T1	Year	0.072 (0.002)	< 0.001
Fir	JJA °C anom. T2	Intercept	-2.531 (0.055)	< 0.001
Fir	JJA °C anom. T2	Year	0.077 (0.002)	< 0.001
Fir	MAM °C anom. T0	Intercept	-1.551 (0.05)	< 0.001
Fir	MAM °C anom. T0	Year	0.027 (0.002)	< 0.001
Fir	SPEI GS anom. T0	Intercept	-1.673 (0.052)	< 0.001
Fir	SPEI GS anom. T0	Year	-0.004 (0.003)	0.155
Oaks (both)	JJA °C anom. T1	Intercept	-2.277 (0.029)	< 0.001
Oaks (both)	JJA °C anom. T1	Year	0.066 (0.001)	< 0.001
Oaks (both)	JJA °C anom. T2	Intercept	-2.328 (0.03)	< 0.001
Oaks (both)	JJA °C anom. T2	Year	0.069 (0.001)	< 0.001
Oaks (both)	MAM °C anom. T0	Intercept	-1.53 (0.029)	< 0.001
Oaks (both)	MAM °C anom. T0	Year	0.028 (0.001)	< 0.001
Oaks (both)	SPEI GS anom. T0	Intercept	-1.592 (0.028)	< 0.001
Oaks (both)	SPEI GS anom. T0	Year	-0.007 (0.001)	< 0.001
Pine	JJA °C anom. T1	Intercept	-2.268 (0.029)	< 0.001
Pine	JJA °C anom. T1	Year	0.066 (0.001)	< 0.001
Pine	JJA °C anom. T2	Intercept	-2.314 (0.03)	< 0.001

Pine	JJA °C anom. T2	Year	0.068 (0.001)	< 0.001
Pine	MAM °C anom. T0	Intercept	-1.535 (0.029)	< 0.001
Pine	MAM °C anom. T0	Year	0.028 (0.001)	< 0.001
Pine	SPEI GS anom. T0	Intercept	-1.584 (0.028)	< 0.001
Pine	SPEI GS anom. T0	Year	-0.008 (0.001)	< 0.001

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