Forest fecundity declines as climate shifts

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Abstract

Tree fecundity underpins regeneration and range tracking, yet may decline when climates exceed reproductive niches. Using 34 years of Polish harvests (40,530 observations across 438 districts) spanning oaks (*Quercus robur*, *Q. petraea*), European beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*), and silver fir (*Abies alba*), we tested whether climate change has changed fecundity. Viable seed production declined by 32–65% across species (oaks ~65%, pine ~64%, fir ~44%, beech ~32%). Summer warming was the dominant driver, with hotter summers reducing fecundity across species. Growing-season moisture and spring temperature contributed little beyond local fecundity effects. Weather effects varied with climate, indicating diverging within-site (transient) and across-site (equilibrium) sensitivities. This suggests local adaptation or acclimation capacity, offering actionable management leverage. Together, our results show warming-driven fecundity declines, pushing populations beyond optimal ranges of their reproductive niches, and suggest potential scope for mitigation through informed provenance selection.

Introduction

Tree reproduction governs the renewal of forest ecosystems, shaping composition and structure over long time scales (1; 2; 3). Fecundity can offset mortality and contributes to resilience, determining whether populations recover and how communities restructure after increasingly frequent disturbance (3; 4). Because seed output determines both the supply of new individuals *in situ* and their dispersal potential, it links demography to range dynamics and the capacity of species to track shifting climate niches (5; 6; 7; 8). Fecundity also determines seed supply for nurseries: climate-driven shortfalls and variability in seed years can limit restoration plantings and assisted migration programs that depend on sufficient, provenance-appropriate collections (9; 10). In Europe, accelerating tree mortality and disturbance frequency increase reliance on successful reproduction and a need for reliable seed supply (11; 12; 13; 14). This suggests a central question: is reproduction keeping pace, when it is arguably more sensitive to climate variation than survival or growth (15)?

Across the few long-term records available, fecundity shows a generally declining trend that is associated with climatic conditions during key phenological stages, while the disruption of masting dynamics (the characteristic synchronised year-to-year variability in seed production) causes viable seed crops to decline over time despite increased reproductive investment in seeds (Table 1). Positive trends exist but are context-specific. In *Nothofagus solandri*, increasing moisture without strong warming is associated with higher seed production (16). In *Quercus crispula*, warmer springs have increased mast frequency, raising mean seed output while maintaining masting and its benefits (lower predation, sustained pollination) (17). However, if cues occur too regularly, masting can collapse with consequent reductions in viable seeds (18). In *Fagus sylvatica*, warmer summers increased the frequency of flower initiation, resulting in more regular seeding but fewer overall viable seeds (i.e., successfully pollinated and not predated) because of reduced pollination efficiency and weaker predator satiation (19; 20; 21). In *Picea engelmannii*, an apparent positive trend is driven by an exceptional mast year at the end of the time-series; nonetheless, its stable or positive reproduction likely reflects warming that has not yet moved the species towards a suboptimal region of its reproductive niche (22). Taken together, these cases suggest a coherent pattern: fecundity declines when sustained warming and shifts in moisture push populations away from the historical climatic optimum for reproduction, remains stable where climate change has not yet shifted populations outside the stable region of the fecundity performance curve, and increases when climatic change moves populations towards this optimum. This aligns with the expectation that sustained environmental change reduces fecundity as niche mismatch grows (23).

Because reproduction proceeds through successive phenological stages — flower initiation, pollination, and seed maturation

— the climatic niche for fecundity is effectively partitioned among these phases, each with its own sensitivity to temperature and moisture (15; 24; 25). In European beech, floral initiation is strongly driven by summer temperatures: cool summers two years prior and hot summers one year prior to flowering promote abundant initiation (26; 27). Once initiation occurs, later stages proceed with relatively little climatic constraint (28). In Norway spruce (*Picea abies*), cone production also correlates positively with summer temperature in the year before (29). Temperate deciduous oaks (*Quercus* spp.) show greater complexity (30; 31). In oceanic climates, seed production is linked to floral initiation, whereas in more continental climates, pollination success has a larger effect and therefore seed crops show a stronger dependence on spring weather (31). Rising spring temperatures can therefore enhance oak fecundity under some conditions (32), but reduced seeding stochasticity may also weaken predator satiation and therefore reduce viable seed counts (33). Other stressors, e.g., drought and late spring frost, further modify reproductive responses. Prolonged drought can reduce reproduction in many species (34; 15; 35), though some maintain seed production at the expense of growth or defence (36; 37; 38). Late spring frosts can eliminate flowers entirely, with impacts varying across species and populations, for instance, through variation in flowering phenology (33; 39). These patterns indicate that climate impacts on fecundity can emerge through stage-specific bottlenecks. Given these stage-dependent sensitivities and the link between masting and seed viability, attributing temporal trends in fecundity requires stage-specific climatic metrics and, where possible, measures of viable rather than total seed output.

As climatic cues and vetoes affecting fecundity at each reproductive stage are episodic and spatially variable, tracking fecundity trends demands observations that are both long-term and extensive. Such data are rarely available, because sustained, community-wide monitoring of seed production exceeds the scope of most research programs. Even if initiated today, new monitoring networks would fail to capture past changes that may already have altered forest reproductive capacity. Harvest records, widely used in ecology when scientific monitoring is not available (53; 54; 55; 56), can provide retrospective insight. In Poland, the state forestry administration funds annual seed collection across all forest districts to supply regeneration and reforestation programs for the main tree species. These records (40,530 observations spanning 34 years, 1988–2021) document both the mass of seed and cone collected (hereafter referred to as seeds for brevity) from seed stands in each district, and the demand driving collection intensity. Importantly, the harvest records comprise only sorted seeds (eliminating empty, underdeveloped, or infested seeds), thereby representing an estimate of viable seed crops as opposed to total seed output. Their interpretation requires caution, as harvests reflect not only seed availability but also reforestation needs and logistical capacity. Because collectors may sample multiple stands within a district, viable seed production might be overestimated when demand is high, while low demand for planting suppresses sampling effort. Since demand for seeds is documented, it can be incorporated into statistical analyses, allowing the separation of demand-driven fluctuations from biological trends in fecundity. With this adjustment, harvest records provide one of the few available windows into multi-decadal, community-wide reproductive dynamics in European forests.

Here, we use this nationwide dataset to examine temporal trends in fecundity for five dominant forest-forming species and their links to seasonal climate: European beech (*Fagus sylvatica*), silver fir (*Abies alba*), Scots pine (*Pinus sylvestris*), and oaks (pooled *Quercus petraea* and *Q. robur*). We test whether climatic change has reduced fecundity in European forests by pushing populations beyond the optimum range of the reproductive climatic niches. Specifically, we predict that (i) fecundity has declined across species, (ii) changes in seasonal climate, including summer and spring temperatures during phenologically sensitive stages, explain much of this decline, and (iii) the magnitude and direction of these effects vary across local climates, reflecting population-specific reproductive niches and their thermal optima associated with local adaptations (57). By testing these predictions, we provide a community-wide assessment of long-term fecundity change, quantifying how both temporal trends and local climatic context shape the reproductive response of Europe's dominant tree species to sustained environmental change.

Results

Fecundity declined across-species. In agreement with prediction (i), our long-term dataset reveals a consistent decline in mean seed production over the past three decades across all species (Fig. 1, Table S1). The oaks showed a decline of −64.8% (± 0.003 SE), scots pine −63.7% (± 0.004 SE), and silver fir and European beech experienced more moderate declines of −43.7% (± 0.05 SE) and −32.5% (± 0.08 SE) respectively (Fig. 1). Spatially, a consistent pattern of declining fecundity emerges across most populations (Fig. 1C), with the level of spatial heterogeneity varying by species. While many regions show negative trends in seed production, others, particularly in central Poland, exhibit milder declines or even localised increases.

Fecundity trends are attributable to climate change. We used a temporal attribution framework (58) to evaluate how long-term trends in seed production are associated with climatic conditions during the key phenological stages of flower-to-fruit development (prediction ii). Contribution captures how much each climatic predictor drives the fecundity temporal trend, while sensitivity quantifies the effect size of the predictor–response relationship. That is, how much seed production changes per unit change in a climatic predictor (Fig. 2B).

Increases in summer temperature two years before seed production (T2) were consistently associated with lower seed output across all species (Fig. 2). Warming in the summer one year before seed production (T1) also predicted lower output for most species; the exception was beech, where warmer T1 summers increased seed production (Fig. 2). Even in beech, however, the negative T2 effect dominated, yielding a net negative effect of summer warming on seed output. Species showed sensitivity to growing season moisture (SPEI) (Fig. 3, 2, Table S2), but its contribution to long-term trends was limited. The modest contribution aligned with the smaller magnitude of change in this climate driver relative to the other variables (Table S3). In other words, SPEI patterns suggested a potential emerging risk factor, although they have not been a primary driver of change to date. Minimum spring temperatures contributed little to temporal trends and showed weak sensitivity overall.

Local climate modulates effects of seasonal weather on seed production 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. The resulting effects show that both the magnitude and the sign of weather effects depend on overall climate and season (Fig. 3). All reported coefficients and standard errors are on the model (log-link) scale.

For nearly all species, effects of summer temperature in the year before seedfall (T1) varied with site mean summer temperatures (beech: -0.09 ± 0.03 SE, $p = 0.007$; fir 0.08 ± 0.04 SE, $p = 0.03$; oak -0.07 ± 0.03 SE, $p = 0.005$; site conditions are not centred), suggesting moderation by local climate. For instance, the increasing seed production related to high summer temperatures (T1) was stronger in cold sites for 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 intensified at warmer sites for oak. Pine produced more seeds in warmer sites (0.16 ± 0.04 SE, $p < 0.001$), but not in warmer years (0.48 ± 0.42 SE, $p = 0.25$).

Temperature anomalies during the summer two years before seed production (T2) generally showed consistent but non-significant negative trends across species. Oak was the exception: seed production was lower following hot summers, especially

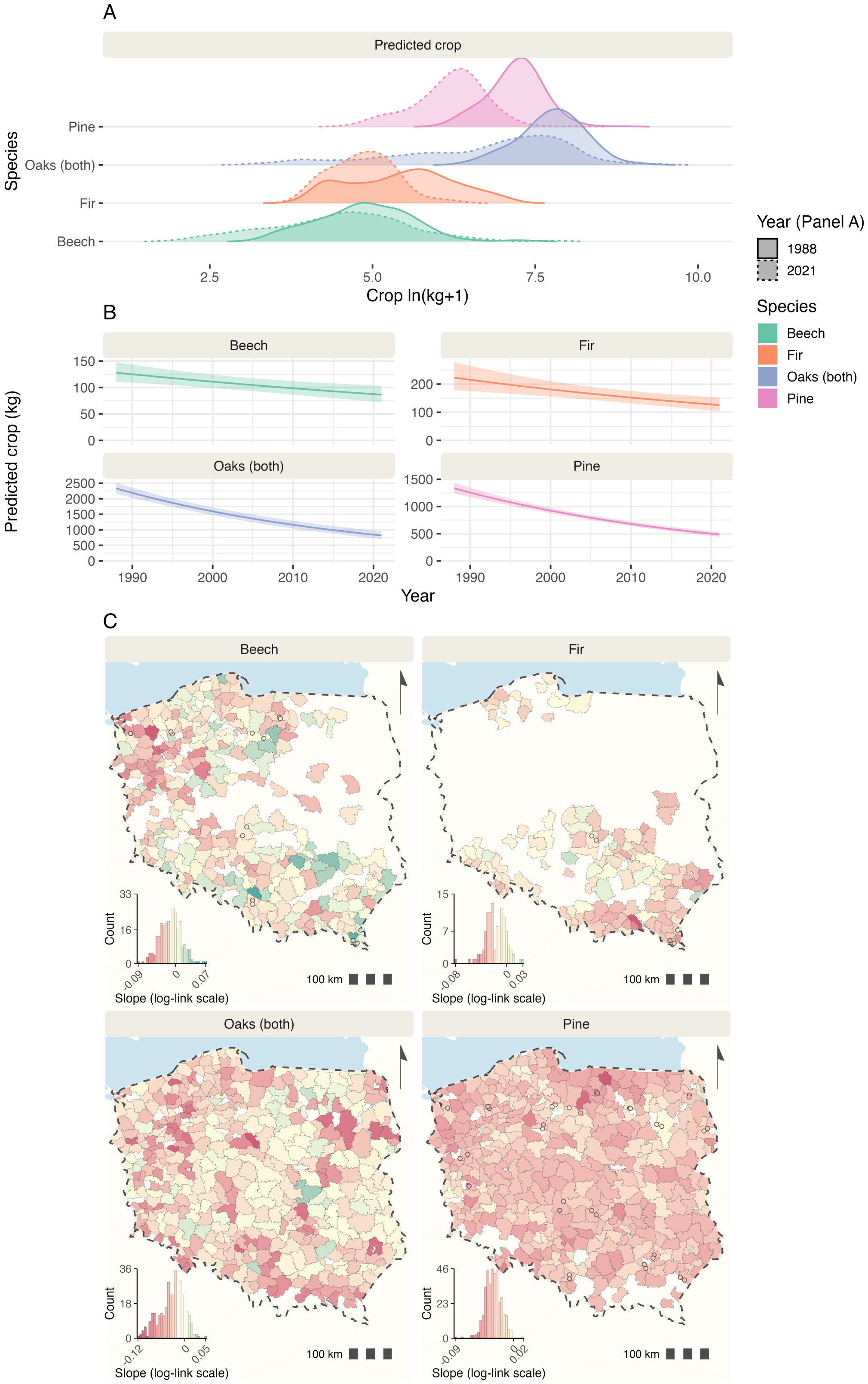

Figure 1: **Over three decades, average seed crops have decreased across species.** A) Probability density functions of predicted seed crops at the start (solid line) and end (dotted line) of the study period across sites and species show the overall leftward shift in the predicted crop distributions across sites. Predictions are log-transformed for visualisation. B) species-specific panels show the general, across sites, declines in seed production over time. For partial residuals, see Fig. S2). 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. See Methods for details.

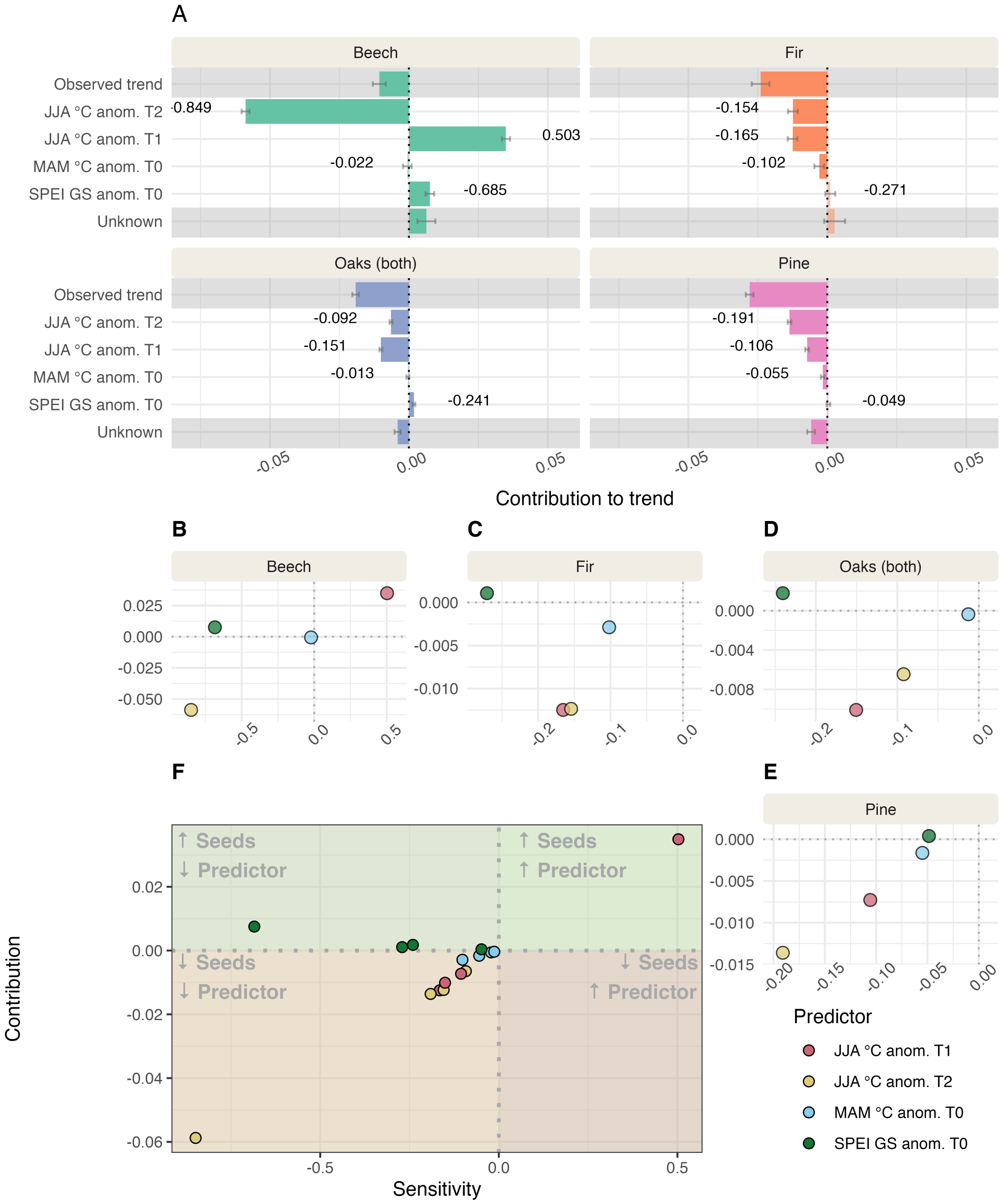

Figure 2: **Temporal changes in seasonal weather explain a large portion of observed temporal variation in fecundity.** A) Contribution of changes in seasonal climate variables to observed long-term fecundity trends across species. Lagged summer temperature anomalies were the dominant drivers, while the unexplained component ("unknown") was comparatively small. Sensitivities of fecundity to each predictor (effect size per unit change) are shown as labels next to the plot bars. (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. 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.

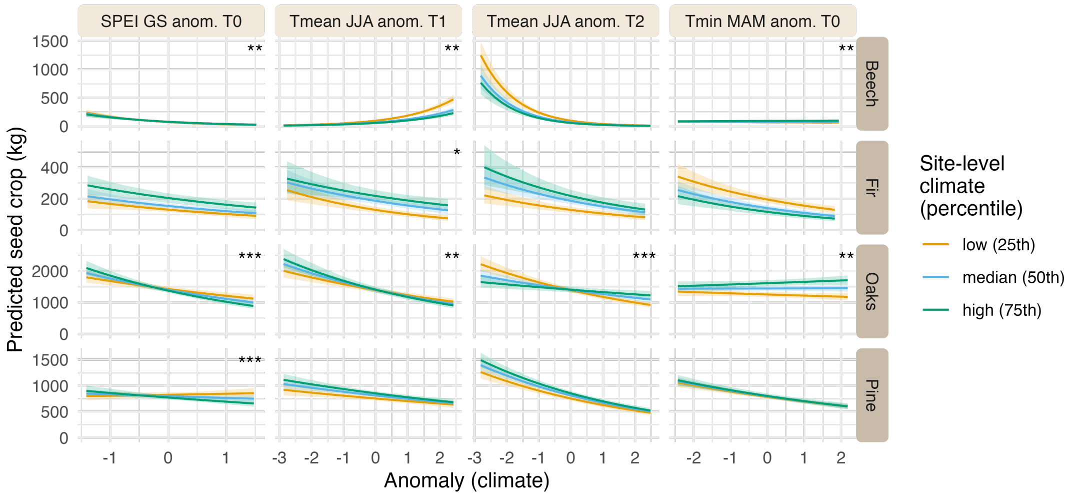

Figure 3: **Weather effects on seed production depend on local climate**. Temporal deviations from a site its typical climate during reproductively sensitive phases are linked to variation in seed crop size, but the magnitude and direction of these effects differ across climates and taxa. Predicted seed 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. 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. Asterices show significance levels for site × anomaly interactions: $p < 0.001$ = ***, $p < 0.01$ = **, $p < 0.05$ = *.

in cold sites (0.15 ± 0.02 SE, $p < 0.001$; Fig. 3).

Spring temperature anomalies and site conditions also influenced seed production. In beech and oak, cooler springs reduced seed production in warmer sites, but these cooler years increased seed production in colder sites (beech: 0.11 ± 0.04 SE, $p = 0.003$; oak: 0.08 ± 0.022 SE, $p = 0.001$). Fir populations in warmer sites produced fewer seeds (-0.59 ± 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 ± 1.55 SE, $p = 0.007$). Conversely, oak and pine showed that wet years in drier sites were associated with higher seed crops (oak -3.81 ± 1.09 SE, $p < 0.001$; pine -3.87 ± 0.99 SE, $p < 0.001$). Fir seed crops, moreover, were higher in wetter sites (7.17 ± 1.46 SE, $p < 0.001$).

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 (59), 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 (44; 16; 2; 45). 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 (60; 61). 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 reforestation demand ('sampling effort'), we accounted for temporal variation in demand to isolate biological trends. The negative trajectories persisted, indicating that declining seed availability cannot solely be attributed to fluctuations in collection effort. Some uncertainty remains when effort and biology share trends, but the direction and magnitude of our declines align with independent evidence of large fecundity losses: a >50% decline in viable seeds in European beech in the UK (21), and a 40% decline in cone production in pinyon pine in New Mexico (44), and an 80% decline in fruit production in Gabon (50). The scale of these changes matches or exceeds contemporary declines in growth and increases in mortality (62; 63; 64), consistent with the view that fecundity is a strongly climate-sensitive demographic rate (15) and an early signal of population stress driving forest restructuring under ongoing environmental change.

Consistent with prediction (ii), linking fecundity trends to seasonal climate during phenologically sensitive stages shows that climate change drives long-term declines via stage-specific sensitivities. Across all species, warmer summers two years before seed production were associated with lower seed output, indicating a negative sensitivity of flower initiation to elevated temperature. In beech, seed production declined with summer warming two years before reproduction, consistent with the species' requirement for cool summers during floral initiation (27; 65). Warmer summers one year before reproduction partly offset this decline by promoting flowering initiation (21; 19), yet the net contribution of summer warming remained negative. The magnitude of fecundity decline is comparable to trends associated with masting breakdown, including increased seed predation and reduced pollination success in beech (21). Other species showed no such offset, with both T2 and T1 warming linked to declines in fecundity. While warm springs were locally associated with reduced seed production — potentially due to mismatched pollen release or spring frost damage (66; 67; 33) — long-term declines were not closely linked to spring temperature trends in any species. This aligns with the absence of regional trends in late frost damage (68). Although drought severity (SPEI) has increased, it did not emerge as a consistent driver of fecundity trends. Weak overall effects of spring temperature and SPEI likely reflect opposing site-level responses that cancel out when aggregated regionally, suggesting that these variables may still shape local-scale trends. Together, these results indicate that multiple reproductive stages constrain long-term fecundity, with the dominant bottlenecks differing among species (25).

Consistent with prediction (iii), our analyses reveal that local climate modulates how seasonal weather anomalies affect fecundity. By comparing within-site responses to short-term climate anomalies with across-site responses to long-term climatic means, we distinguish fast ecological processes such as phenotypic plasticity and phenological adjustment from slower responses driven by acclimation or local adaptation (69; 57). Temporal sensitivities thus represent "transient" responses to interannual variability, while spatial sensitivities approximate "equilibrium" responses emerging after prolonged exposure to local climatic regimes (57). Such sensitivities often differ in magnitude or sign; for instance, ponderosa pine grows faster in warmer sites but shows reduced growth in unusually hot years (70; 71). Here, fir fecundity was unaffected by short-term drought anomalies but was higher in wetter sites, implying that persistent drying will reduce reproduction not through increasing annual drought damage, but through gradual reorganisation of populations toward a low-fecundity equilibrium. Beech showed the opposite pattern, i.e., higher reproduction in dry years but no advantage at dry sites, suggesting that positive short-term responses to drought will not persist over the long term. This divergence between temporal and spatial patterns is consistent with past studies, which compared beech seed production responses to within-site anomalies and among-site variation in precipitation (72; 73). More generally, across many species–anomaly combinations, spatial effects of climate were modest, suggesting that local adaptation or acclimatisation may help populations maintain similar performance across climate gradients, even if notable site-level differences remain for some species (57). From a management perspective, local adaptation offers near-term buffering capacity. However, climate change mitigation via provenance selection or translocation would require careful, small-scale testing given associated risks of interventions (74).

While we focus on fecundity, seedling recruitment is also sensitive to climate variability, particularly to drought and temperature extremes during germination and early establishment (75; 76; 77). For instance, in ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*), recruitment is non-linearly related to moisture, with recent conditions falling below thresholds for successful regeneration in many sites (78). In these systems, increased seed supply can partially buffer negative climate effects on regeneration (79). However, if fecundity declines occur in parallel with decreasing climatic suitability for establishment, these effects will interact, potentially accelerating population decline (80). Recruitment studies that reconstruct past reproductive output from age structures and regeneration records (78; 81; 82; 83) offer a means to test whether reduced seed availability is already constraining forest renewal, and how this interacts with climate effects on seedling establishment. Given the observed declines in fecundity and reports of seedling mortality following increasingly severe drought (61), such analyses are now urgently needed. Other factors, such as changes in forest structure and age, atmospheric CO_2 or nitrogen deposition and air pollution may also influence long-term fecundity patterns and represent important directions for future research.

We document a multi-decadal decline in viable seed production across Europe's dominant temperate forest-forming trees, after adjusting harvest records for sampling effort. The pattern is consistent with our theoretical framework: climatic change reduces fecundity as populations are pushed beyond their reproductive climatic niches (prediction i), with declines largely attributable to seasonal thermal conditions during phenologically sensitive stages, especially summer warming (prediction ii), and with effect sizes moderated by local climate (prediction iii). Because the records reflect sorted (viable) seed crops, the decline indicates reduced effective reproductive output rather than changes in total seed fall alone. Given that reproduction underpins regeneration, community structure, range tracking, and the seed supply required by nurseries (7; 84; 3), continuing declines in fecundity elevate renewal risk (80), especially where establishment is already constrained by drought and heat (78). At the same time, contrasts between spatial and temporal patterns in our results suggest that slow response processes (acclimation and adaptation) may partly offset negative trends if given sufficient time; an outcome that depends critically on the pace of environmental change (57). The next step is to integrate fecundity trends with long-term recruitment and demographic data to determine whether the declines documented here, especially in combination with shifting climatic suitability for seedling establishment, are translating into reduced regeneration.

Methods

Fecundity data

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

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

We excluded time-series consisting of >90% seed harvest values of zero to avoid model convergence issues. Lowering this threshold to 80% or 50%, does not change the results qualitatively. The proportion of zero values across time-series is provided in Fig. S3. We analysed all time-series of these five species spanning more than a decade (mean: 33.19 years; Fig. S4). Site boundaries for each species are shown in Fig. 1C. If demand values were missing but the recorded seed harvest was zero, demand was set to zero (1,488 observations). If a harvest had taken place but demand was missing, we imputed the site-level mean demand for the focal species (1,625 observations).

Climate data

We obtained high-resolution (2.5‘) historical monthly climate data (1960–2021) for Europe from the WorldClim database (v. 2.1; (85)), including minimum and maximum temperature and precipitation. Mean monthly temperature was calculated by averaging Tmin and Tmax raster layers. For each grid cell, we then calculated mean temperature and total precipitation per season (December-February ’DJF’, March-May ’MAM’, June-August ’JJA’, September-November ’SON’) and per year. Potential evapotranspiration (PET) was estimated using the Thornthwaite method based on temperature, and combined with precipitation to compute the Standardised Precipitation-Evapotranspiration Index (SPEI) at a 1-month scale using the `SPEI` package (v. 1.8.1; (86)). To harmonise seasonal definitions, December was reassigned to the subsequent year, allowing each winter season to span December through February.

Data analysis

All models were built in R (v. 4.4.1) using glmmTMB (v. 1.1.10) unless indicated differently and validated with DHARMa (v.0.4.7; (87; 88; 89)). Throughout the analyses, we used Tweedie distribution models because they accommodate both zero-inflation and overdispersion, which are common features of reproductive data. The Tweedie family also offers flexibility across a range of data-generating processes, and applying the same distribution across all temporal attribution models (e.g. reproduction trends and climate effects) ensured consistency and comparability, making it the preferred choice.

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

Spatial diversity in climate trends. We mapped spatial variation in long-term trends in climate variables (i.e. summer temperature, spring temperature, growing season SPEI) by calculating per-cell temporal slopes from WorldClim raster stacks (from 19988-2021). For each grid cell, a linear trend was fitted using the `stats` package to the annual time-series, and the resulting slope ($^\circ$C year^{-1}, SPEI index year^{-1}) was assigned to the cell.

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

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

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

Temporal attribution modelling We used a temporal attribution framework (58) to assess how long-term trends in seed production are associated with climatic conditions, using Tweedie log-link GLMMs with site as a random intercept in all models.

We first quantified observed temporal trends in seed production by fitting “total trend” models for each species. These models adjusted for previous-year seed crops and ln[kg + 1]-transformed seed demand. We also fitted predictor trend models for each climatic anomaly variable.

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

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

We calculated the contribution of that predictor as the log-scale difference between the full-prediction trend and the fixed-predictor trend. Sensitivity was calculated by taking the difference between the full- and fixed-predictor trends on the response scale divided by the predictor’s temporal slope. The “unknown” contribution was the residual difference between the observed "total" temporal trend in seed production and the sum of individual predictor contributions.

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Contributions

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

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.

Code availability statement

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

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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
Beilschmiedia tawa	Species	Summer & winter T, P	-	(40)	6	New Zealand	1986-2020
Fagus sylvatica	Species	Summer T, tree size	- viable, + total	(41; 42)	12	UK	1980–2020
Fagus sylvatica	Species	Summer T	- viable, + total	(19)	50	Europe	1980–2022
Nothofagus solandri	Species	Summer T & P	+ (greatest at high elevation)	(43; 16)	3	New Zealand	1965–2009
Pinus edulis	Species	Summer T (cone initiation)	-	(44)	9	USA	1969–2012
Pinus edulis	Species	Climatic water deficit, monsoonality	- (hindcast)	(45)	16	USA	1900–2024
Picea engelmannii	Species	Summer T, spring snow	+	(22)	13	USA	1970–2010
Pinus pinea	Species (harvest)	T & P throughout cone development	-	(46)	58	Spain	1960–2000
Pinus sibirica	Species	Spring T, September T	-	(47)	1	Russia	1990 - 2019
Quercus crispula	Species	Growing season T	+	(17)	1	Japan	1980–2017
Quercus petraea (& *Q. robur*; ns)	Species	Spring T	+	(32)	28	France	1994–2007
3 *Quercus* species (*Q. chapmanii, Q. geminata, Q. inopina*)	Species	Spring P & fire	-	(48)	1	USA	1988–2018
68 plant species	Community	VPD, minimum relative humidity	Shrubs: -, Herbs, vines, trees & palms): NS, Overall: NS	(49)	1	China	2014–2020
73 tropical tree species	Community	Not tested	-	(50)	1	Gabon	1986–2018
81 tropical tree and liana species	Community	El Niño events	Flowers +, Seeds: NS	(51)	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	-	(52)	1	Ecuador	1960–2000
363 plant species	Community	Not tested	-	(23)	205	World	1900–2014

Extended data

Forest fecundity declines as climate shifts

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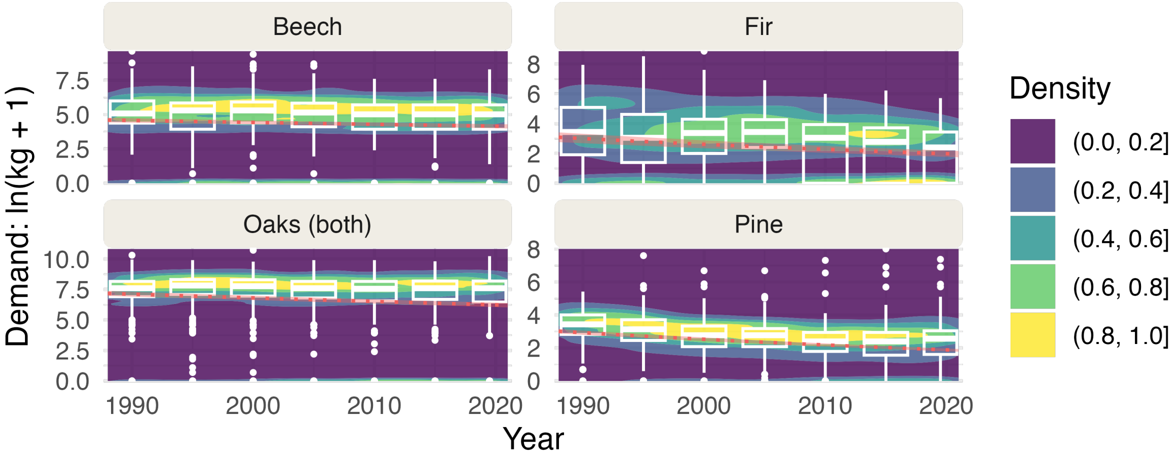

Figure S1: **Observed seed crop demand over time.** The colour shows the density of seed site-level, annual demand observations (scaled between 0 and 1 to allow for comparison between species). The box plots summarise seed demand observations by 5-year time windows, while red dotted lines show statistically 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.

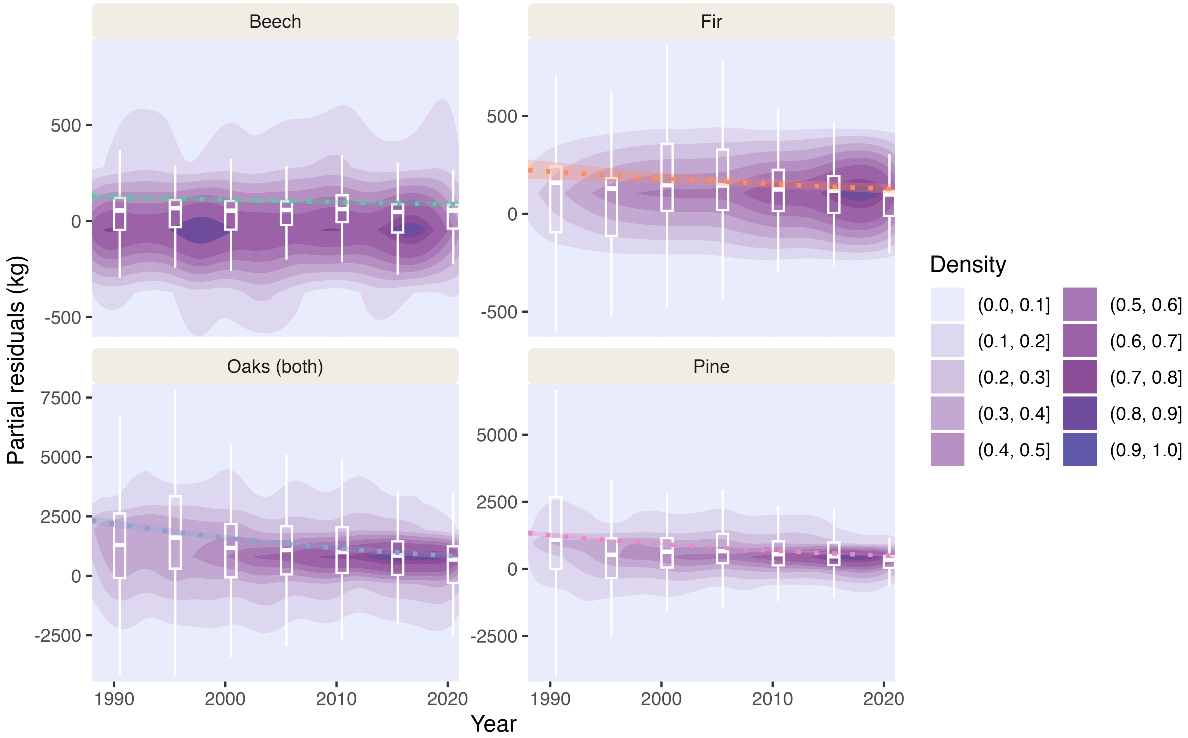

Figure S2: **Partial residuals around long-term trend in fecundity** Filled contour maps show normalised densities (scaled between 0–1) of partial residuals of seed production over time (i.e. fixed effect of time plus model residuals). Panels are cropped to regions with normalised density > 0.1 to highlight the predominant variation. 5-Year boxplots summarise partial residuals within 5-year windows, and the coloured dashed line reproduces the species-specific predicted trend from Fig. 1B. The results come from species-specific Tweedie-family generalised linear mixed-effects models, including random slopes of time effects by site. See Methods for further detail.

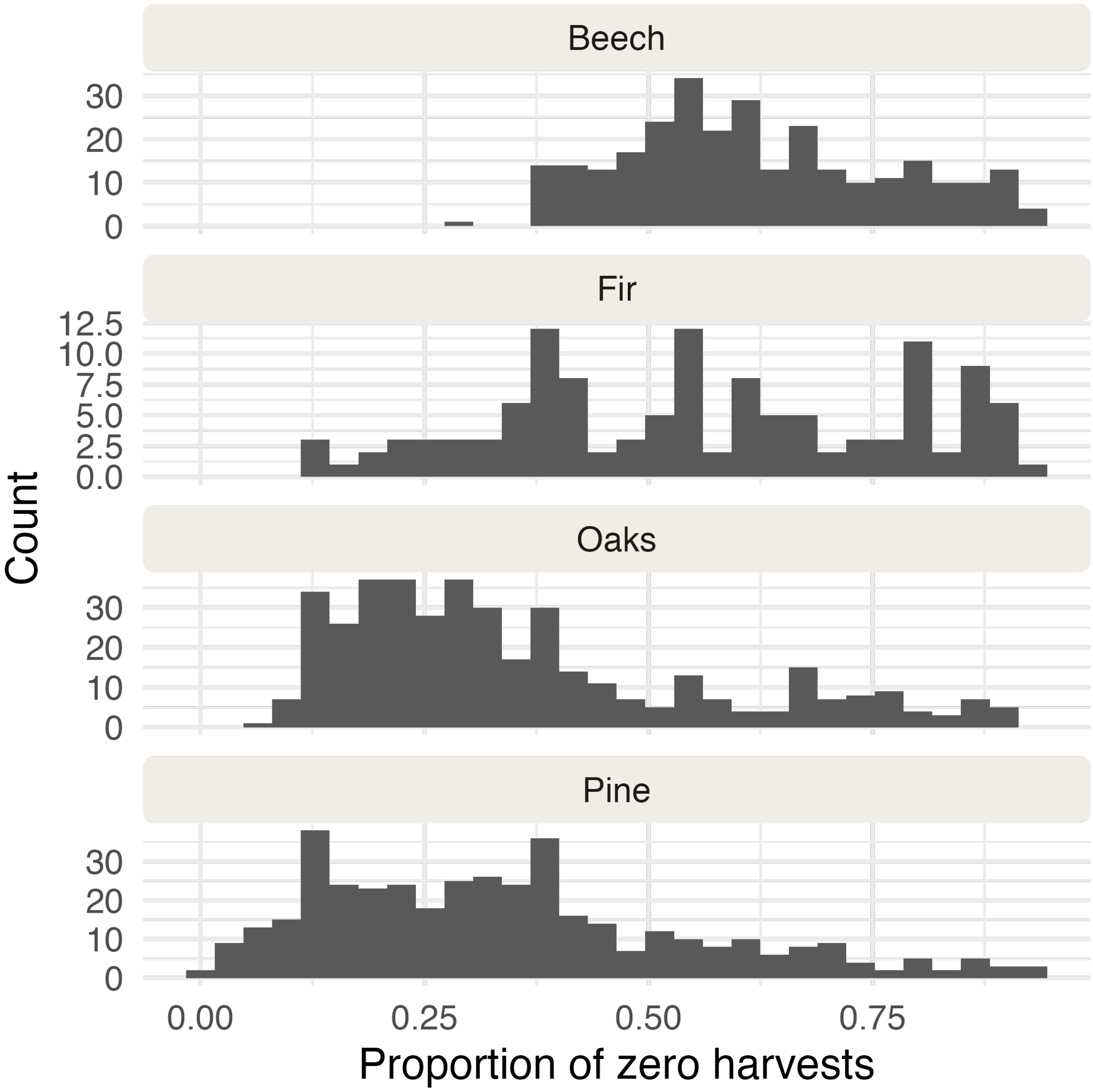

Figure S3: **Distribution of the proportion of zero harvests** across time series for beech, fir, oak, and pine. Each panel shows the frequency of time series with a given proportion of years with zero harvest.

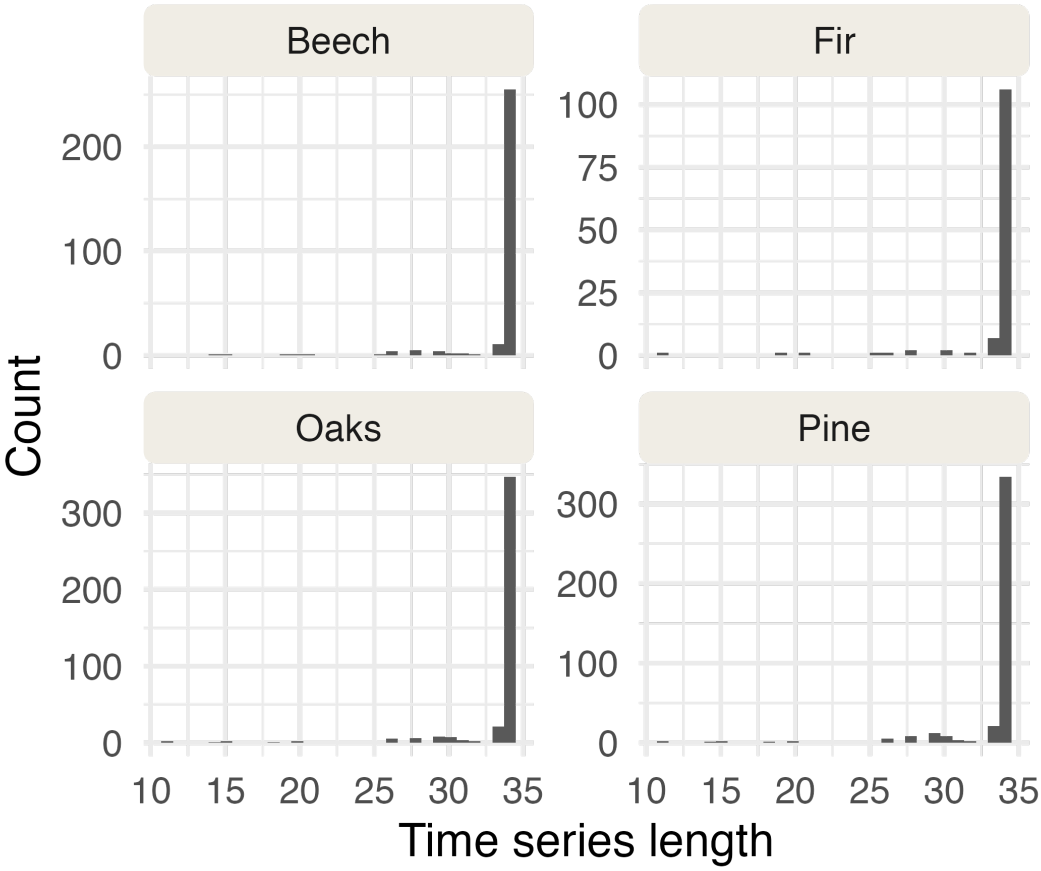

Figure S4: **Distribution of time-series length in years** across sites for beech, fir, oak, and pine.

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.

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 4 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).

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).

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