Short periods dominate mast seeding across diverse tree species

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Abstract

Mast seeding, synchronous and highly variable reproduction among perennial plants, profoundly impacts ecosystem dynamics and species interactions. However, the extent of periodicity in mast seeding, defined as cyclical but not strictly regular intervals between reproduction, remains poorly understood. Here, we used autoregressive analyses on seed production data from 556 populations across 20 tree species, with time series ranging from 10 to 62 years, to quantify the prevalence and length of masting periods. We found widespread periodicity, predominantly characterised by a short period of 2–3 years. Although periodicity was common, the signal was often weak, indicating limited explanatory and predictive power. This period length aligns with theoretical predictions that balance the ecological benefits of predator satiation, with costs such as missed reproductive opportunities. Extended period lengths (>4 years) were uncommon (2%), suggesting that longer periods may be less ecologically advantageous or subject to specific local conditions. Climate and elevation have limited and species-specific effects on period length and strength, implying local adaptation in cue sensitivity and resource accumulation. Our findings emphasise the adaptive value of short periods in mast seeding, likely reflecting consistent evolutionary constraints on reproductive timing across diverse ecological conditions.

keywords: | masting | masting period | seed production | periodicity | autoregressive model | resource pulses

Introduction

Mast seeding, or masting, is synchronous and highly variable reproduction among years by a population of perennial plants (Kelly, 1994; Bogdziewicz *et al.*, 2024). The seed pulses that result from masting influence plant recruitment, demographic processes, and ecosystem dynamics, including effects on seed consumers, their predators, and associated parasites (Ostfeld *et al.*, 2000; Hacket-Pain *et al.*, 2022; Seget *et al.*, 2022), as well as nutrient cycling and abundance of mycorrhizal fungi (Müller-Haubold *et al.*, 2015; Michaud *et al.*, 2024). Although masting can occur without periodicity — populations may vary and synchronise even when reproductive peaks are irregularly spaced — whether masting follows predictable periods has long interested ecologists and foresters (Elton, 1924). However, periods have been difficult to test largely due to analytical constraints (Bogdziewicz *et al.*, 2023). Exceptions include Allen *et al.* (2012), who applied ordinal time series analysis and detected a 7-year periodicity in seed production of New Zealand mountain beech (*Nothofagus solandri*), and Shibata *et al.* (2020), who used autoregressive models to show that warming reduced the period length in masting of Japanese oak (*Quercus crispula*) from 3–4 years to just 2 years. These studies show that, despite the inherent difficulties, it is possible to detect masting periods using a range of statistical approaches, which have also revealed potential links with climate. However, a broad-scale analysis comparing periodicity across populations of multiple species and climates remains limited.

Prior research has mostly centred on a related concept of masting return intervals, which refers to the average time between large seed production events. Return intervals provide a descriptive summary of the spacing between mast years but do not capture the underlying temporal dynamics of reproduction. Return interval studies have often reported longer masting periods, sometimes exceeding 5–10 years, particularly in tropical and temperate tree species. For example, return intervals for three North American oaks varied from 2 to 4 years (Sork *et al.*, 1993), while in tropical forests, Igarashi *et al.* (2024) reported 2 to 10 year return intervals in 18 dipterocarp species. In four temperate forest species, Nussbaumer *et al.* (2016) reported masting frequency (the reciprocal of return interval) ranging from 1.64 to 10 years. Some studies report ranges of typical masting return intervals, noting that return intervals are irregular over time (Övergaard *et al.*, 2007; Broome *et al.*, 2007; Wagner *et al.*, 2010). Moreover, numerous manuals and monographs used by foresters and wildlife managers include tables of species-specific masting return intervals (Burns *et al.*, 1990; Young & Young, 1992), because such information can optimise harvesting schedules, guide forest restoration, and support wildlife conservation dependent on mast resources (Kettle *et al.*, 2010; Köhnke *et al.*, 2020; Bregnard *et al.*, 2021). While the identification of return intervals may be of practical value, such assessments inevitably depend on the selected threshold defining a mast year (Bogdziewicz *et al.*, 2024). Because return intervals depend on arbitrary thresholds used to define mast years, they cannot reliably capture variation in masting behaviour across species or environmental gradients, including elevation. Here, we return to the original concept of masting periods, analysing autoregressive patterns (Bjørnstad *et al.*, 2008; Shibata *et al.*, 2020) in seed production across 556 populations of 20 tree species, offering a broad-scale evaluation of periods across and within species. Understanding these periods provides insight into temporal patterns of seed production, with implications for the evolutionary drivers of masting and broader ecosystem dynamics, such as resource availability and consumer–producer interactions.

From an evolutionary perspective, the period reflects the degree of reproductive delay, shaped by the cost–benefit balance of interannual variation in seed production (Bogdziewicz *et al.*, 2024). Major costs include missed reproductive opportunities, which can reduce population growth rates (Vacchiano *et al.*, 2021), and increased density-dependent seedling mortality associated with concentrating reproduction in large, intermittent events (Visser *et al.*, 2011; Huang *et al.*, 2021; Seget *et al.*, 2022). These constraints select against prolonged periods of reproductive delay (Bogdziewicz *et al.*, 2024), particularly in environments with low productivity and high background mortality, where the risks associated with delaying reproduction may be greater (Waller, 1979). In contrast, two major benefits, known as economies of scale, can favour delayed reproduction (Bogdziewicz *et al.*, 2024). First, alternating between years of low and high seed production allows plants to starve and then overwhelm scarce seed consumers, thereby reducing seed predation rates (Zwolak *et al.*, 2022). This mechanism is particularly effective against consumers with low mobility, high dietary specialization, and short lifespans, such as many insect species (Kelly & Sork, 2002; Zwolak *et al.*, 2022). For example, populations of seed-predating micromoths are often highly vulnerable to even a single year of seed scarcity (Yasaka *et al.*, 2003; Żywiec *et al.*, 2013). Secondly, large and synchronised flowering enhances pollination success by increasing floral density (Venner *et al.*, 2016; Szymkowiak *et al.*, 2025; Crone & Rapp, 2025). While reproductive delay and interannual variation in flowering do not directly improve pollination rates, they allow resource accumulation that helps populations exceed the flowering threshold needed for efficient pollination (Kelly *et al.*, 2001). Where species or populations cannot maintain high flowering effort every year, selection may favour delayed flowering that enables resource build-up (Kelly *et al.*, 2001; Bogdziewicz *et al.*, 2020; Kelly, 2020).

From a proximate perspective, periodicity arises from interactions between resource dynamics and weather cues (Satake & Bjørnstad, 2008; Kelly *et al.*, 2025). Resource budget models propose that plants must accumulate sufficient resources before high seed production occurs (Crone & Rapp, 2014). Then, high seed production occurs when adequate resources align with favourable weather cues, such as - in the case of species inhabiting boreal and temperate regions - warm conditions in preceding years (Bisi *et al.*, 2016; Nussbaumer *et al.*, 2018; Hirsch *et al.*, 2025). Because plant response to the weather cue depends on the levels of accumulated resources, resource dynamics play the role of both promoter and suppressor of reproduction, enabling plants to maintain periodic reproduction despite variability in cue frequency (Monks *et al.*, 2016; Kelly *et al.*, 2025). Specifically, low resource levels can suppress reproduction even when strong cues occur consecutively, thereby preventing successive high-seeding years and reducing the risk of seed overexploitation by consumer populations (Kelly *et al.*, 2000, 2013, 2025). Conversely, high accumulated resource levels enhance plant sensitivity to weather cues, allowing even moderate cues to trigger large seed production, thus preventing excessively delayed reproductive episodes (Kelly *et al.*, 2025). These processes can stabilise the periodicity of masting, optimising spacing between large-seeding years to maximise fitness benefits. However, environmental conditions influencing resource accumulation and weather cue frequency introduce stochastic variation into these patterns. Consequently, quantitative assessments of periodicity across multiple species are required to better understand how resource dynamics and cue frequency interact at broader ecological scales.

To explore how environmental conditions influence reproductive dynamics, we tested whether local climate and elevation affect masting periodicity. We expected warmer and wetter conditions characterised by higher mean annual temperature (MAT) and precipitation (MAP), or positive climatic water balance (CWB), to facilitate faster resource accumulation, resulting in shorter periods. Conversely, populations inhabiting colder or drier environments were expected to show longer periods, as resource build-up between reproductive events proceeds more slowly. With increasing elevation, we also expected longer periods due to the combined effects of lower temperatures, reduced nutrient cycling, and shorter growing seasons that constrain resource renewal.

Building on earlier methods (Bjørnstad *et al.*, 2008; Shibata *et al.*, 2020), we apply second-order autoregressive models to quantify periodicity and evaluate how period length varies across species and ecological contexts. We then relate these patterns to local climate and elevation, testing whether variation in environmental conditions corresponds to systematic differences in period length. Importantly, our focus on periodicity does not imply that masting events occur at strictly regular or predictable intervals. Aside from the two-year "alternate bearing" observed in a few species (Garcia *et al.*, 2021), there is little reason to expect strict periodicity in masting time series. Instead, periodicity arises from interactions between stochastic weather cues and internal plant resource dynamics, with period length shaped by selection processes.

Materials and Methods

Seed production data We obtained data from MASTREE+, a database that records annual, population-level records in perennial plants' reproductive effort (Hacket-Pain *et al.*, 2022; Foest *et al.*, 2024). The species selected for analysis were those that met the following criteria: data were recorded on a continuous scale and included counts of seeds, fruits, or cones; data spanned a minimum of ten distinct locations, each representing either a stand or a patch (excluding regional-scale records); and each time series comprised at least ten years of data.

The final dataset included 20 species, encompassing 556 unique time series (Table S1). All species displayed substantial interannual variation in seed production in our dataset, with population-level coefficients of variation ranging from approximately 0.86 to 1.94. Elevation data were included for species with available information and sufficient variation, defined as multiple elevation points where differences in elevation across populations exceeded 100 meters. This threshold was chosen to ensure meaningful differentiation in elevation values, enabling the analysis to capture changes in climatic conditions. The dataset with elevation covered 10 species and 141 populations.

Climate data Mean annual temperature (MAT), mean annual precipitation (MAP), and climatic water balance were calculated for each unique location based on monthly data (1960–2020) from the corresponding 1/24° (4 km) resolution in the TerraClimate dataset (Abatzoglou *et al.*, 2018). The CWB values were taken directly from TerraClimate, where they are computed as precipitation minus reference evapotranspiration estimated using the Penman-Monteith equation. To evaluate the climatic representativeness of our sampled populations, we compared their mean annual temperature (MAT) and precipitation (MAP) values to the full climatic range of each species, defined as all grid cells within its native distribution. Climatic variables were obtained from WorldClim 2.1 (Fick & Hijmans, 2017). To assess the climatic representativeness of our sampled populations, we compared their mean annual temperature (MAT) and precipitation (MAP) values to the full climatic range of each species based on species distribution polygons.

These range maps were compiled from EUFORGEN for European taxa (EUFORGEN, 2020), GBIF occurrence-based polygons for globally distributed species (Global Biodiversity Information Facility, 2025), and digitized maps from the *Atlas of United States Trees* (Little, 1971–1978; Petry, 2024) for North American species. The average (±SD) coverage was 36.7% (13.7) for MAT and 35.5% (18.8) for MAP (Fig.S1).

Analysis To estimate the period length, we calculated the second-order autoregression (AR2) coefficients that relate current seed production (t) to past observations.The coefficients $1+a_1$ and a_2 describe the statistical dependence of current seed production (t) on values in preceding years within a second-order autoregressive process, capturing temporal autocorrelation rather than fixed biological delays. The AR(2) framework, first formalised by Royama (Tom Royama, 1992) and subsequently applied across diverse ecological time series, including insect outbreaks, rodent population cycles, ungulate dynamics, and tree reproduction (Bjørnstad *et al.*, 1995; Cornulier *et al.*, 2013; Ahrestani *et al.*, 2016; Shibata *et al.*, 2020), provides a simple and comparable way to quantify the presence and strength of cyclic temporal structure in population-level data. This structure may reflect interactions among underlying processes such as resource dynamics and climatic cues, but the model itself remains agnostic to their specific mechanisms. Species-level differences in reproductive schedules, including seed maturation time, are therefore reflected in variation in the estimated period length rather than in the coefficients themselves.

Each time series was fitted using the second-order autoregressive model

$$x_t = (1 + a_1)\, x_{t-1} + a_2\, x_{t-2} + \varepsilon_t,$$

where x_t represents log-transformed annual seed production in year t, and x_{t-1} and x_{t-2} denote values from one and two years prior, respectively. ε_t is the residual error term. Following Royama (1992) and Bjørnstad et al. (2008), the coefficients a_1 and a_2 were estimated using the Yule–Walker method implemented in the `stats::ar()` function in base R (R Core Team, 2020), ensuring consistent estimation across species.

Population dynamics were considered periodic when the estimated combinations of $1 + a_1$ and a_2 fell within the periodic region of the parabola diagram—that is, inside the left triangular stability region and below the parabolic boundary that defines oscillatory dynamics (see Fig. 1), following the stability criteria of Bjørnstad *et al.* (2008). Within this framework, gradients in period length can arise through two main parameter changes (for examples across populations, see Fig.S2). First, increasing the $1 + a_1$ coefficient, while a_2 remains within the periodic region, elongates the period length. The position of points in the parabola diagram determines the period length: points between lines 2 and 2, as well as 2 and 3, indicate a two-year period; between 3 and 4, a three-year period, and so on (Bjørnstad *et al.*, 1995, 2008; Cornulier *et al.*, 2013; Ahrestani *et al.*, 2016; Shibata *et al.*, 2020). Second, increasing a_2 while $1 + a_1$ remains negative shifts points leftward within the periodic region of the parabola diagram (Fig. 1). This change affects the strength of periodicity: more negative values of $a_2$indicate stronger cycles, whereas higher values correspond to weaker or more irregular periodicity, or even non-periodic dynamics.

Points falling outside the triangle or falling inside the top right side of the triangle above the parabola region (i.e. the white space), are considered as non-periodic (Fig. 1). Because negative values of the $1 + a_1$ term are common in masting time series (Pearse *et al.*, 2020; Foest *et al.*, 2025), many populations naturally fall within the periodic region of the AR(2) parameter space, reflecting genuine ecological structure. Additionally, we note that although period length takes integer values in years, it is a ratio-scale quantitative variable rather than an ordinal one: differences between successive values (e.g., 2→3 years and 3→4 years) are equivalent, and ratios are meaningful.

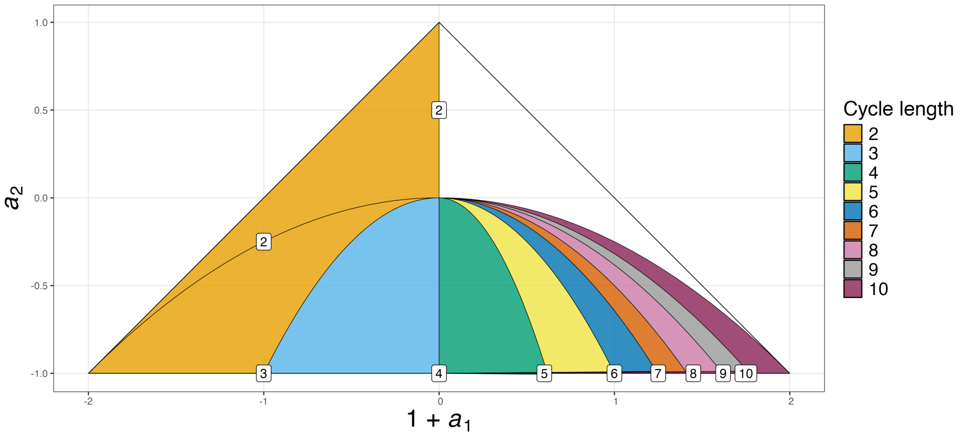

Figure 1: **Parabola plot** showing correspondence of combinations of $1 + a_1$ and a_2 coefficients values to period length. Coloured regions indicate oscillatory dynamics, with colours corresponding to different period lengths; white space indicates non-periodic dynamics. See Bjørnstad *et al.* (1995, 2008).

We used Bayesian second-order autoregressive models to analyse the relationships between climate variables and the autoregressive coefficients $1 + a_1$ and a_2 for each species separately. All predictors (MAT, MAP, and CWB) were centred and scaled prior to modelling to ensure comparability. Because these predictors were correlated, we fitted separate models for each climatic variable per species. Models were specified in `brms` (Bürkner, 2021) using the `bf()` and `brm()` functions, which allowed both autoregressive coefficients to be estimated simultaneously as multivariate responses. Default priors were used, and models were run with four MCMC chains of 10,000 iterations each (3,000 warm-up).To complement these analyses, we additionally fitted zero-truncated Poisson (ZTP) models treating period length as a discrete response, implemented in `glmmTMB` (Brooks *et al.*, 2017). All analyses were performed in R v.4.2.3 (R Core Team, 2020).

Results

Percentage of periodic populations Based on temporal autoregression coefficients, almost all populations (N = 525 out of 556) across the 20 analysed species exhibited periodic masting behaviour, with an overall prevalence of periodicity of approximately 95%. For eight species, all populations were periodic, including four conifers (*Picea engelmannii*, *Araucaria araucana*, *Abies amabilis*, *Abies alba*) and four deciduous species (*Quercus douglasii*, *Quercus cerris*, *Fagus sylvatica*, *Betula pubescens*).

For species that included both periodic and non-periodic time series, the proportion of periodic populations ranged from 90.0% in *Alnus incana* to 96.7% in *Quercus petraea*. Other species with relatively lower percentages of periodic populations included *Quercus robur* (90.9%) and *Pinus sylvestris* (91.1%). A detailed summary of species-level proportions is provided in the Supplementary Information (Fig.S3).

Variation in period length across species The average period length across species was 2.65 years (±0.49 SD) (Fig. 2), and was not correlated with the length of time series (Fig. S4). Note that even long time-series >40 years did not show differences in mean period length, although it was notable that longer period lengths were restricted to relatively short time-series (Fig.S4). Among the species analysed, *Quercus lobata* had the shortest period (2 ± 0 SD), showing highly consistent values across populations (all 11 populations had period = 2). In contrast, *Quercus cerris* had the longest period (3.27 ± 0.14 SD), also with relatively low variability. Most species exhibited period lengths closely centred around the overall mean, corresponding to a two- to three-year period. We found little evidence of longer period length, with only 15 time series showing periods longer than 4 years, mainly associated with *Pinus ponderosa* and *Pinus sylvestris* (Fig.2).

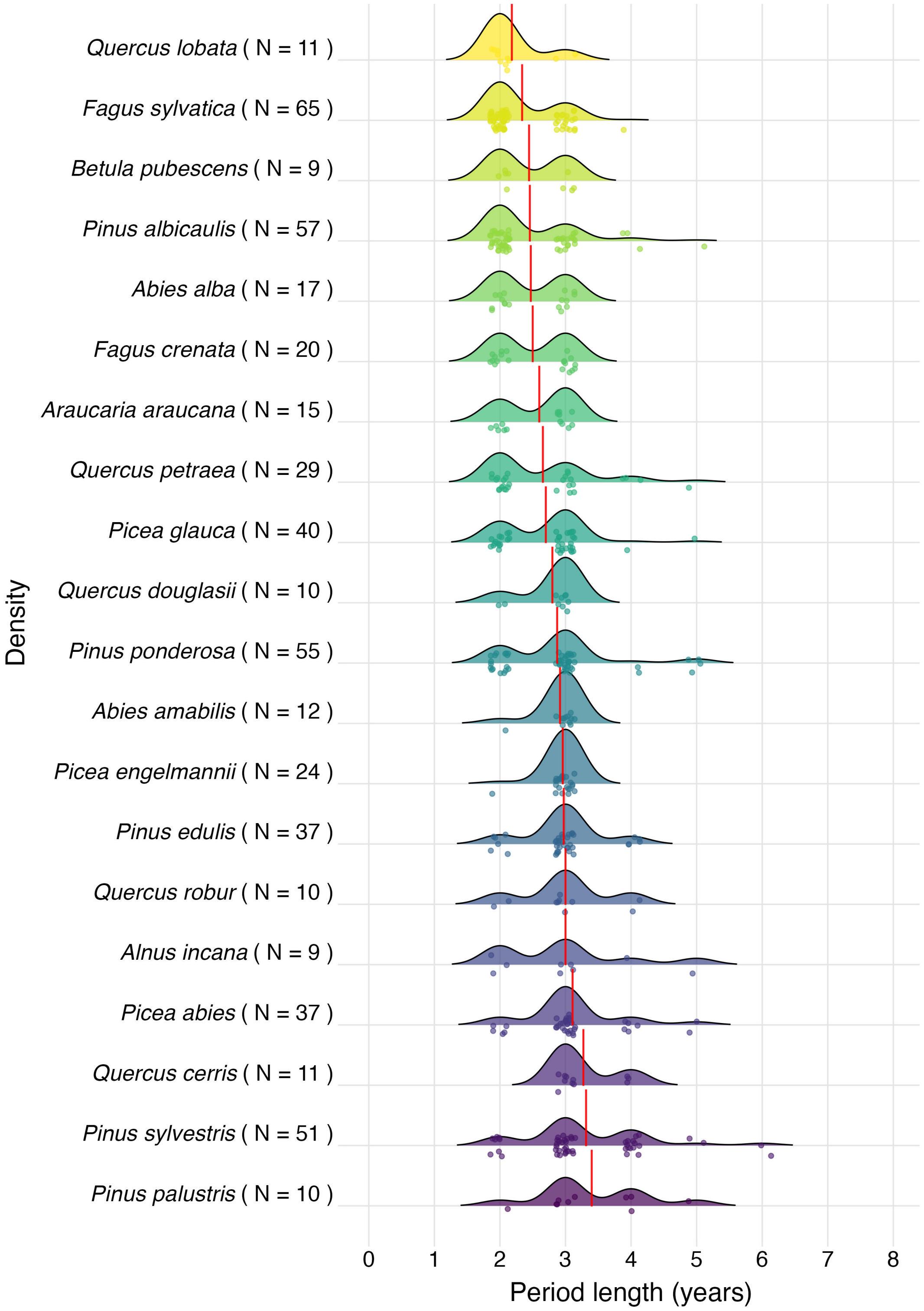

Figure 2: **Inter- and intra-specific variation in period length** (N = 525 periodic populations, 20 species). Each row represents the distribution of estimated period lengths (years) across populations of each species. Period length for each population was determined based on the position of the population $1+a_1$ and a_2 coefficients on the parabola plot (Fig. 1). Numbers in brackets indicate the number of studied populations. Each point corresponds to a single population. All presented values are integers, and jitter was added to decrease overlap. Red vertical lines represent the species-level means. Non-periodic populations are excluded from the graph. The $1+a_1$ and a_2 coefficients for each population are given in Fig. S5.

Period length and climate While some species show an association between mean annual temperature (MAT), mean annual precipitation (MAP), or climatic water balance (CWB) ($1+a_1$ and a_2), many do not exhibit a strong or consistent relationship. The diversity of slope directions and significance levels indicates that these associations are species-specific.

Higher MAT was associated with longer periods in only one species, *P. abies*, as indicated by a positive slope of MAT on $1 + a_1$. In contrast, higher MAT was associated with shorter periods in three species, *P. albicaulis*, *P. engelmannii*, and *A. incana*, as indicated by its negative effects on $1 + a_1$ (Fig. 3A). A positive a_2 slope with MAT in *P. abies* indicates that populations occurring in warmer conditions tend to show weaker periodicity and less regular reproductive dynamics.

Period length was also associated with MAP. Longer periods tended to occur under higher precipitation in four species—*P. albicaulis*, *F. sylvatica*, *F. crenata*, and *A. araucana*, as indicated by positive slopes of MAP on $1 + a_1$. Conversely, in five species, *Q. lobata*, *P. palustris*, *P. engelmannii*, *P. glauca*, and *A. incana*, shorter periods were associated with higher MAP, as indicated by its negative slopes on $1 + a_1$ (Fig. 3B). Positive slopes of a_2 in *F. crenata* and *A. araucana* indicate that although wetter conditions are associated with longer periods, periodicity tends to be weaker and reproduction less regular with increasing MAP.

Higher CWB values were associated with longer periods in *P. albicaulis* and *A. araucana*, as indicated by positive slopes of CWB on $1 + a_1$. However, in *A. araucana*, as well as *F. crenata*, the positive slope of$a_2$that, although wetter conditions were linked to longer periods, periodicity tended to weaken. In contrast, *Q. lobata*, *P. palustris*, *P. glauca*, *P. engelmannii*, and *A. incana* showed the opposite pattern, with shorter periods associated with more humid conditions (Fig. S6).

Although associations emerged in several species, most 95% credible intervals overlapped zero, indicating that climatic variables were only weakly associated with variation in period length across taxa. Complementary zero-truncated Poisson models yielded consistent results, showing similarly weak associations between period length and climate across species (Fig. S7).

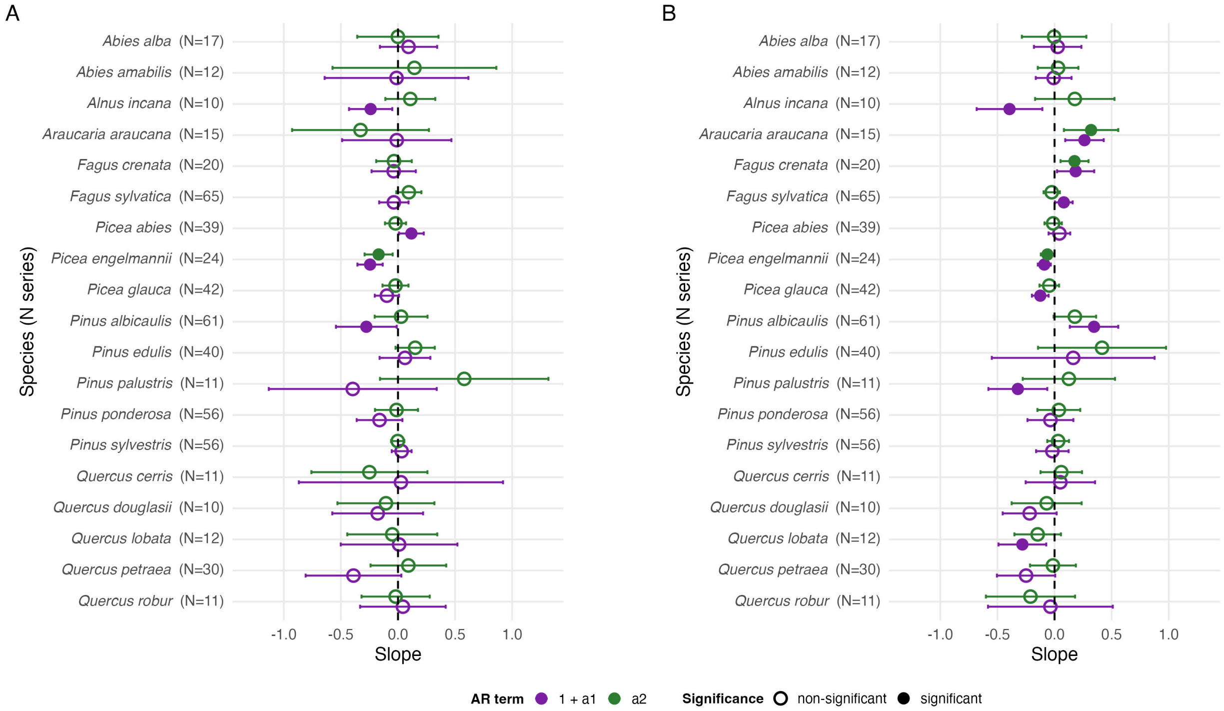

Figure 3: Associations between autoregressive coefficients $(1+a_1)$ and a_2 and local climate (MAT: mean annual temperature and MAP: mean annual precipitation) across 525 populations representing 19 species. Results for *B. pubescens* are not shown due to model convergence issues. Panel A shows MAT, while panel B shows MAP. Rows represent individual species. Each point shows the estimated slope for a standardised climatic predictor, with error bars indicating 95% confidence intervals. Significant effects are shown as filled circles, while non-significant effects are shown as empty circles. Positive slopes of $1+a_1$ are associated with longer period lengths, whereas negative slopes are associated with shorter period lengths. Positive slopes of a_2 indicate weaker or less regular periodicity, while negative slopes indicate stronger or more regular periodicity. To aid interpretation of these slopes, we provide a supplementary Figure S8 illustrating how fitted $1+a_1$ and a_2 values from the same models move across the parabola in *Fagus sylvatica* along MAT and MAP gradients. Results for climatic water balance (CWB) are provided in Fig. S6.

Period length and elevation The associations between elevation and autoregressive coefficients $1+a_1$ and a_2 were generally weak, though statistically significant in seven species (Fig. S9). At higher altitudes, estimated periods tended to be longer in four species—*A. araucana*, *F. sylvatica*, *P. engelmannii*, and *P. albicaulis*, as indicated by positive relationships with $1+a_1$, and with shorter periods in two species, *P. abies* and *P. glauca*. The strength of periodicity tended to weaken with increasing elevation in *F. crenata* and *P. engelmannii*, as reflected by positive relationships with a_2, but became stronger in *P. glauca*, which showed a negative relationship with a_2. In other species, the associations between elevation and both $1+a_1$ and a_2 were not significant (Fig. S9). Overall, although several species exhibited significant associations, these patterns were weak, suggesting that elevation is only weakly linked to variation in masting period. Complementary zero-truncated Poisson models of period length(Fig.S10) showed similarly limited associations.

Discussion

Our findings reveal that periodicity is widespread across diverse tree taxa. Specifically, the 20 species—including angiosperms and gymnosperms from boreal, temperate, and Mediterranean biomes—consistently fell into parameter space that indicated periodicity, with a relatively short mean period length of 2–3 years. We interpret this as evidence that common ecological factors, most likely the economies of scale and the inherent costs of delayed reproduction, play key roles in governing masting behaviour across broad phylogenetic and environmental settings. This suggests that the selective pressures favouring reproductive delay converge to a similar outcome across species.

The mean period length of 2–3 years fits well with predictions based on economies of scale. Interannual variation in seed production can effectively reduce seed predation by insects, whose short life spans mean that a delay of just 1–2 years is sufficient to lock them into periods of starvation and satiation (Zwolak *et al.*, 2022). Prolonging the delay would increase the costs, such as missed reproductive opportunities (Rees *et al.*, 2002; Visser *et al.*, 2011; Tachiki & Iwasa, 2010), possibly with little additional benefit to reproductive success. In contrast, extending the period length specifically to starve and satiate consumers with longer lifespans, such as generalist vertebrates, is unlikely to be effective. These animals are typically mobile and capable of exploiting alternative resources or migrating to areas of higher seed availability during periods of scarcity, making predator satiation less viable as a strategy against them (Curran & Leighton, 2000; Bogdziewicz *et al.*, 2022; Zwolak *et al.*, 2022). Similarly, while accumulating resources to reach a critical flower density is essential for successful pollination (Kelly *et al.*, 2001), extending the delay beyond what is necessary increases the costs of missed reproductive opportunities. Recent findings further suggest that the interaction between resource levels and cue strength allows plants to fine-tune this delay, providing a proximate mechanism to maintain the period length at the desired level (Monks *et al.*, 2016; Ascoli *et al.*, 2017; Kelly *et al.*, 2025). Importantly, reliance on stochastic weather cues remains crucial, as regular periods could enable seed predators to predict and exploit seed pulses, for example, through diapause (Maeto & Ozaki, 2003; Pélisson *et al.*, 2012).

Period length is only one among many metrics used to describe mast seeding patterns, alongside more frequently used synchrony among individuals and interannual variation in seed production (CV) (Koenig *et al.*, 2003; Lamontagne & Boutin, 2007; Qiu *et al.*, 2023). Natural selection acts on physiological traits influencing reproductive synchrony and variability at the proximate level, such as sensitivity to environmental cues (Kelly *et al.*, 2013; Bogdziewicz *et al.*, 2020). These physiological traits produce seed production patterns that enhance fitness at the ultimate level, primarily through economies of scale (Kelly, 1994; Pearse *et al.*, 2016; Pesendorfer *et al.*, 2021). Various combinations of reproductive synchrony and individual variability can generate a similar population-level period length, meaning that this pattern arises from group-level dynamics rather than direct selection on period length itself. For example, low synchrony but high variability among individual trees could yield similar periodicity as high synchrony with moderate variability (Koenig *et al.*, 2003), a pattern reflected in our data by the weak correlation between CV and period length (Fig. S11). The specific ecological context, particularly seed predator mobility, generation time, and feeding behaviour, shapes these combinations (Koenig *et al.*, 2003; Bogdziewicz *et al.*, 2021). Relatively immobile predators, like micromoths, may be satiated by seed production from single trees, reducing selective pressure for synchrony (Nilsson & Wastljung, 1987; Satake *et al.*, 2004). In turn, mobile predators might be attracted to large seed crops, potentially selecting against high interannual variability or synchrony (Koenig *et al.*, 2003). Despite these different selective contexts, period lengths frequently converge around 2–3 years, reflecting common costs and benefits associated with masting strategies.

Notably, we found little evidence supporting long period length. Only 15 time series exhibited periods exceeding four years, and these were generally derived from relatively short datasets compared to the period lengths identified. This scarcity of long periods contrasts with some reports in the literature indicating longer masting periods (Maki, 1952; Wagner *et al.*, 2010). Such discrepancies might arise from masting periods being identified based on arbitrary thresholds to define mast years (Bogdziewicz *et al.*, 2024). Conversely, our findings of predominantly short periods (2–3 years) align with the results of (Qiu *et al.*, 2023), who identified periodicity averaging around three years in 142 species. Furthermore, the detected periods, when present, were often weak (see, e.g., Fig.S2) suggesting that these inherent periods account for only a modest fraction of total variability in seed production. Consequently, the periodicity identified here might offer limited utility for predicting future seed crops. While our analysis supports the presence of underlying periods in many species, the weakness and variability of these signals cautions against characterizing masting as strictly periodical. Nevertheless, forecasting models that increasingly link seed production to weather variability (Journé *et al.*, 2023; Wion *et al.*, 2025) could potentially benefit from incorporating patterns indicating a higher likelihood of masting events as more time passes since the last occurrence.

The effects of local climate on period length were generally weak or absent, as observed in seven species lacking clear climatic associations. This finding is consistent with recent work showing that intraspecific variation in masting behaviour is often unrelated to climate, with no consistent support for the environmental stress hypothesis across species or masting metrics (Foest *et al.*, 2025). One possible explanation is that climate ranges within species were too narrow to detect consistent effects. However, most species in our dataset exhibited substantial within-species variation in both MAT and MAP, and sampled populations span large portions of the species' climatic ranges, including those with weak or absent association, making this explanation unlikely (Figure S1). Superficially, our results appear to contrast with a recent large-scale synthesis reporting longer masting periods in drier climates (Qiu *et al.*, 2023). However, period lengths in that study varied only narrowly (most 2.5–3.5 years), so any aridity effect is small and consistent with convergence toward a common period across climates.

This limited effect of climate on period length may instead reflect local adaptation, with the thresholds for climatic cues triggering high-seeding years varying across sites (Kon *et al.*, 2005; Foest *et al.*, 2025). For example, species responding to warm temperatures might not exhibit lower cue frequencies at colder sites, as the "warm" threshold may adjust to local climate norms (Foest *et al.*, 2024). Similarly, local adaptation may affect how climate influences resource dynamics, making absolute climatic values less predictive of resource accumulation rates (Piper & Fajardo, 2024). When climate influences period length, temperature and precipitation can function as reproductive cues or vetoes (Kelly *et al.*, 2013; Bogdziewicz *et al.*, 2019). Warmer temperatures may shorten period length by frequently triggering seed production (Shibata *et al.*, 2020), although colder conditions, such as late frosts, could lengthen masting period by inhibiting reproduction (Inouye, 2008; Schermer *et al.*, 2020). Similarly, precipitation variability is likely to influence reproductive dynamics; drought conditions can correspond with longer masting periods by limiting resources, whereas excessive precipitation may reduce pollination success, leading to longer resource accumulation periods between mast events (Espelta *et al.*, 2008; Fleurot *et al.*, 2024). Thus, the relationship between climate and period length appears complex and influenced by species-specific adaptations and local environmental contexts.

In summary, our analyses highlight the widespread occurrence of periodicity in masting across diverse tree species, predominantly converging toward a 2–3 year period length. This consistent periodicity highlights the adaptive balance between the advantages of predator satiation, primarily targeting specialised insect seed predators, and the risks associated with prolonged reproductive delays, such as resource loss or missed reproductive opportunities. The limited effect of climatic variables on periodicity across species suggests that local adaptation likely modulates plant sensitivity to weather cues, complicating broad-scale predictions of masting behaviour under changing climates. Interestingly, the rarity of longer masting periods challenges previous assumptions derived from return interval studies, indicating that prolonged periods may be ecologically exceptional rather than typical.

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Author Contributions Statement

KK, MB, JSz, AHP, JF, DA designed the study. KK, Jsz, TS, MS conducted the analysis. KK developed the first manuscript draft under the direction and input of MB. All authors contributed to the interpretation of the analysis, revised the draft, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data availability statement

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

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Supporting Information

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Title: Short periods dominate mast seeding across diverse tree species

Table S1: **Summary of per-species sample size in our study. Reproduction (seed/cones, depending on species) was monitored annually; thus time series length is given in years.**

Species name	Number of populations	Mean time series length	Maximal time series length
Abies alba	17	18	25
Abies amabilis	12	11	12
Alnus incana	10	18	22
Araucaria araucana	15	16	18
Betula pubescens	9	13	17
Fagus crenata	23	17	24
Fagus sylvatica	65	29	43
Picea abies	39	22	40
Picea engelmannii	24	36	41
Picea glauca	42	24	57
Pinus albicaulis	61	22	33
Pinus edulis	40	16	20
Pinus palustris	11	47	62
Pinus ponderosa	57	16	31
Pinus sylvestris	57	21	45
Quercus cerris	11	25	31
Quercus douglasii	10	30	41
Quercus lobata	12	27	41
Quercus petraea	30	13	23
Quercus robur	11	16	27

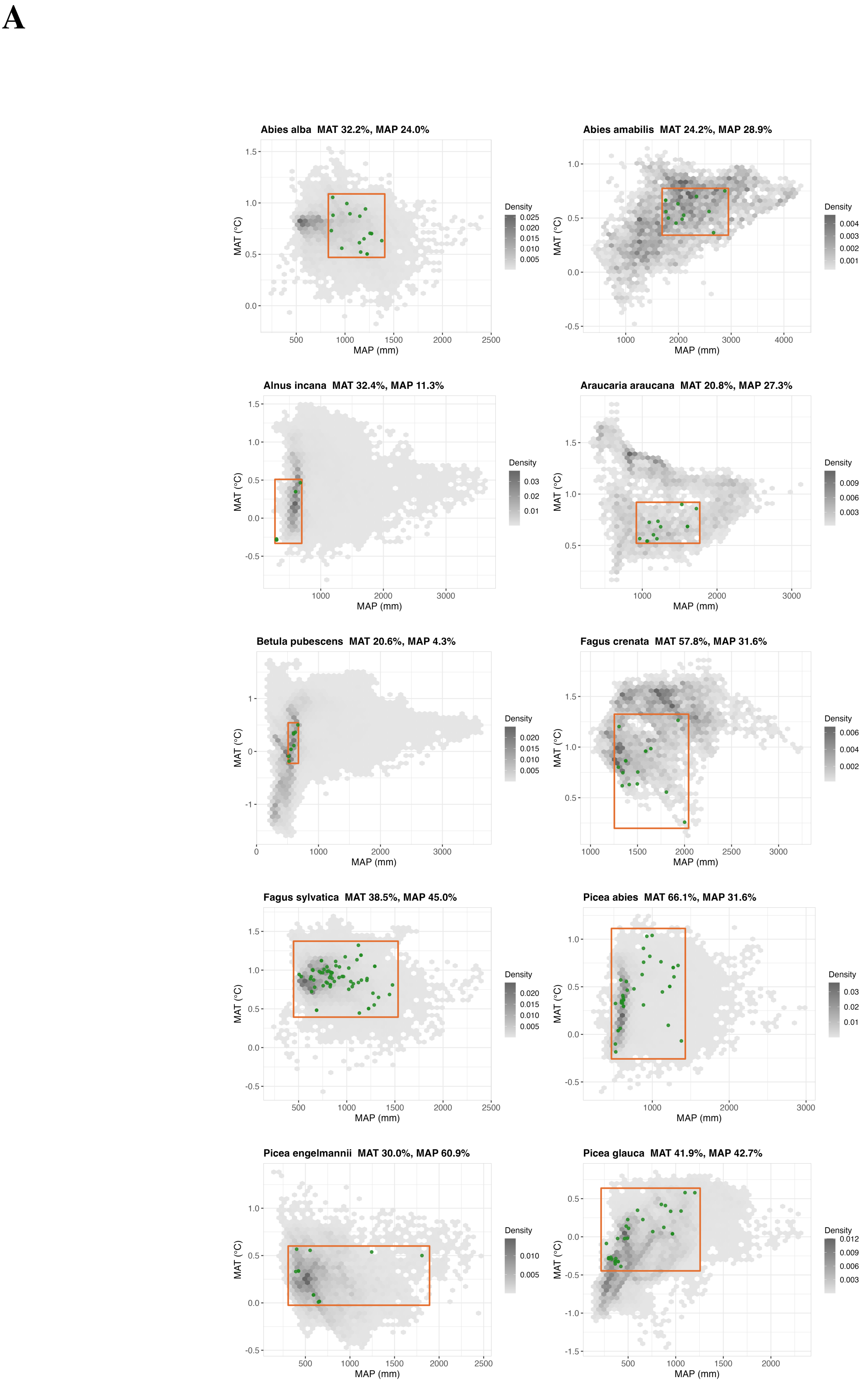

Figure S1: Climatic coverage of sampled populations relative to each species' full climatic distribution (A). Each green point represents one population; grey shading represents species-level climatic density estimated from WorldClim 2.1 (1 km resolution). Orange rectangles delineate the range of mean annual temperature (MAT) and precipitation (MAP) represented in our sampling. Numbers in panel titles indicate the percentage of the total species climatic range covered by the sample (MAT, MAP respectively).

B

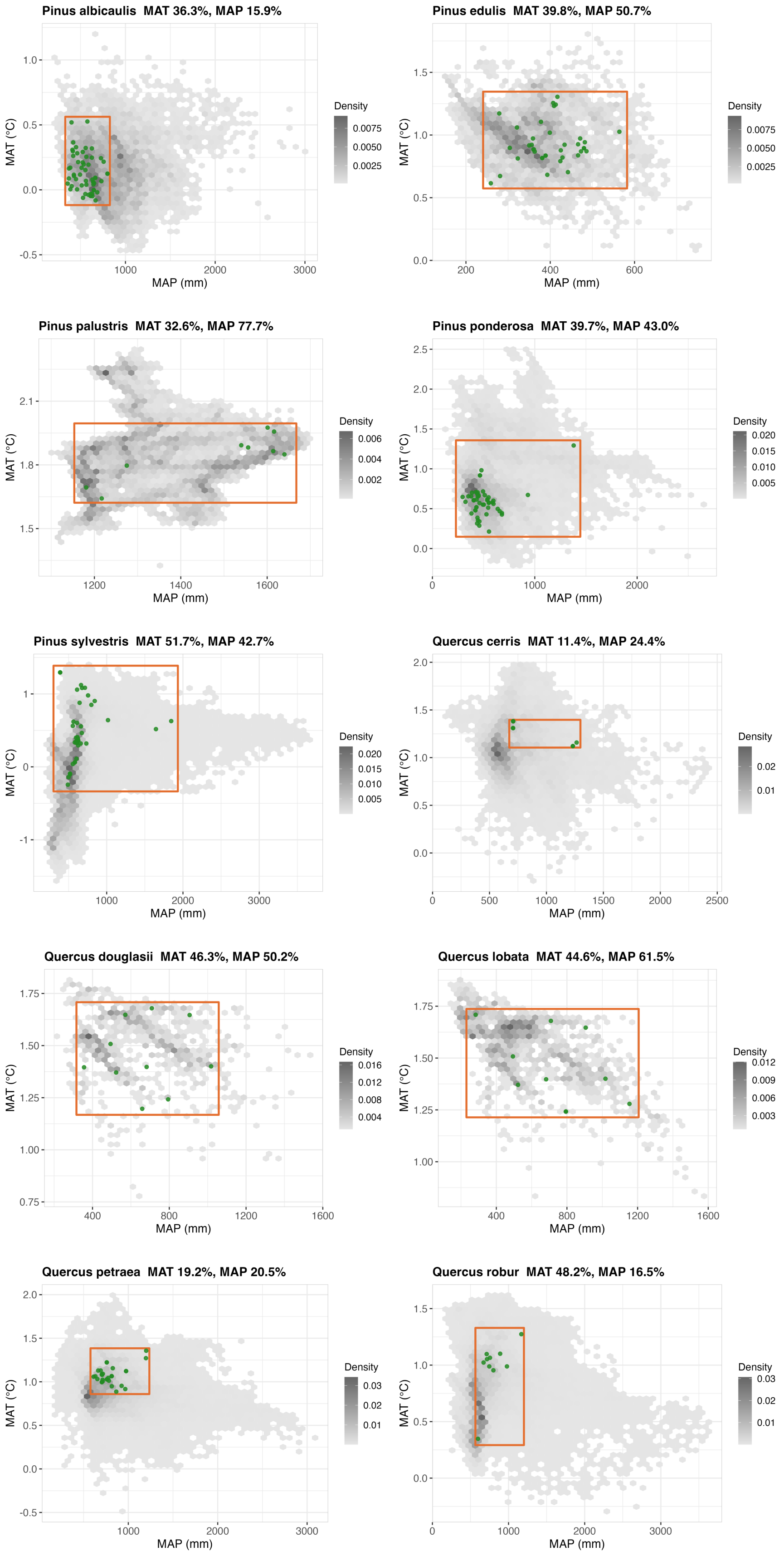

Figure S1: Climatic coverage of sampled populations (continued, B).

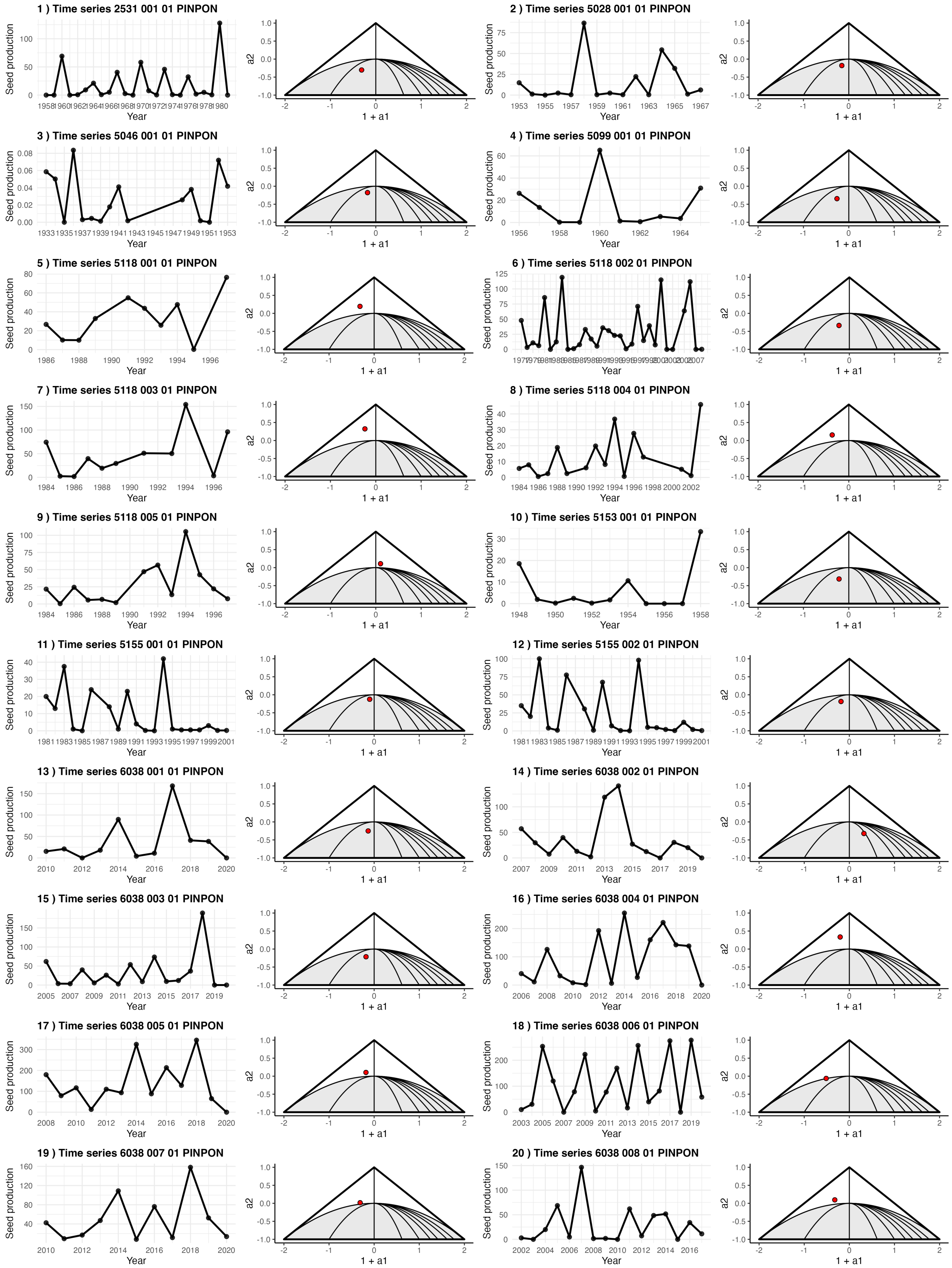

Figure S2: Time series of seed production and respective parabola plots for 20 populations of *Pinus ponderosa*. Each row contains two populations, with time series graphs (first and third columns) showing interannual variation in seed production and parabola plots (second and fourth columns) showing the period length of given time series based on $1 + a_1$ and a_2 coefficients from AR2 model.

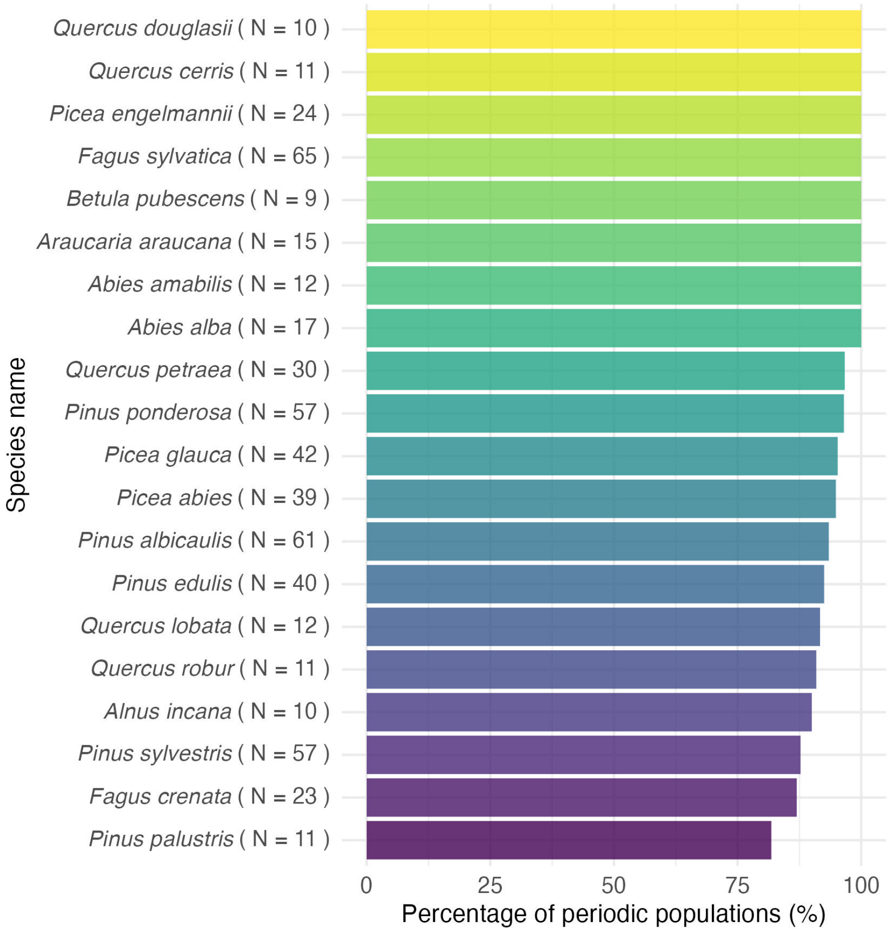

Figure S3: **Percentage of periodic populations across species studied** (N = 525 periodic populations, 20 species). The x-axis shows the percentage of periodic populations for each species. Whether a time series was categorised as periodic or not is based on whether a_1 and a_2 coefficients fell within the periodic region of the parabola plot (Fig. 1). The minimum time series length for each population was 10 years, with an average of 20 years (Table S1).

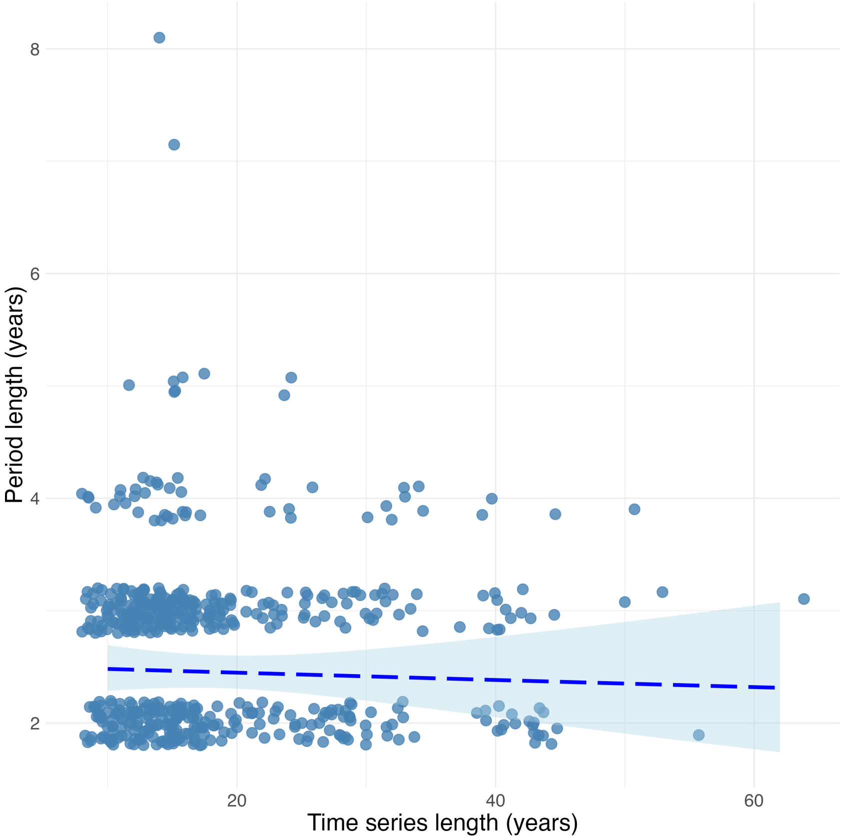

Figure S4: Relationship between period length and time series length. Each point represents an individual time series. A zero-truncated Poisson generalized linear model (GLM) was fitted to examine the relationship between period length as a response variable and time series length as an explanatory variable. The model showed no significant effect of time series length on period length (p = 0.681). The blue line represents model predictions, with 95% confidence intervals.

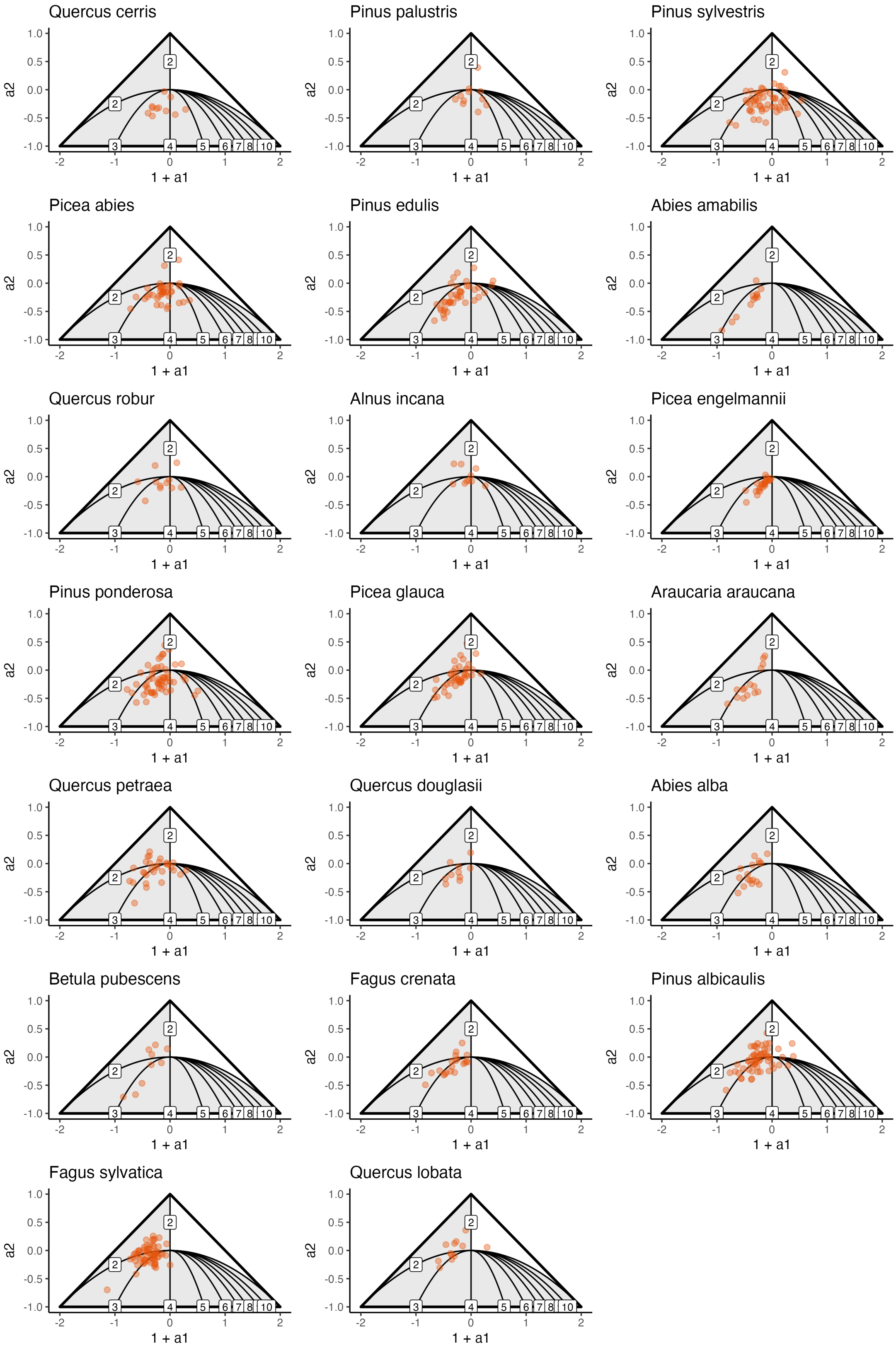

Figure S5: Temporal autoregression coefficients across studied species (N = 20). Each dot shows one population.

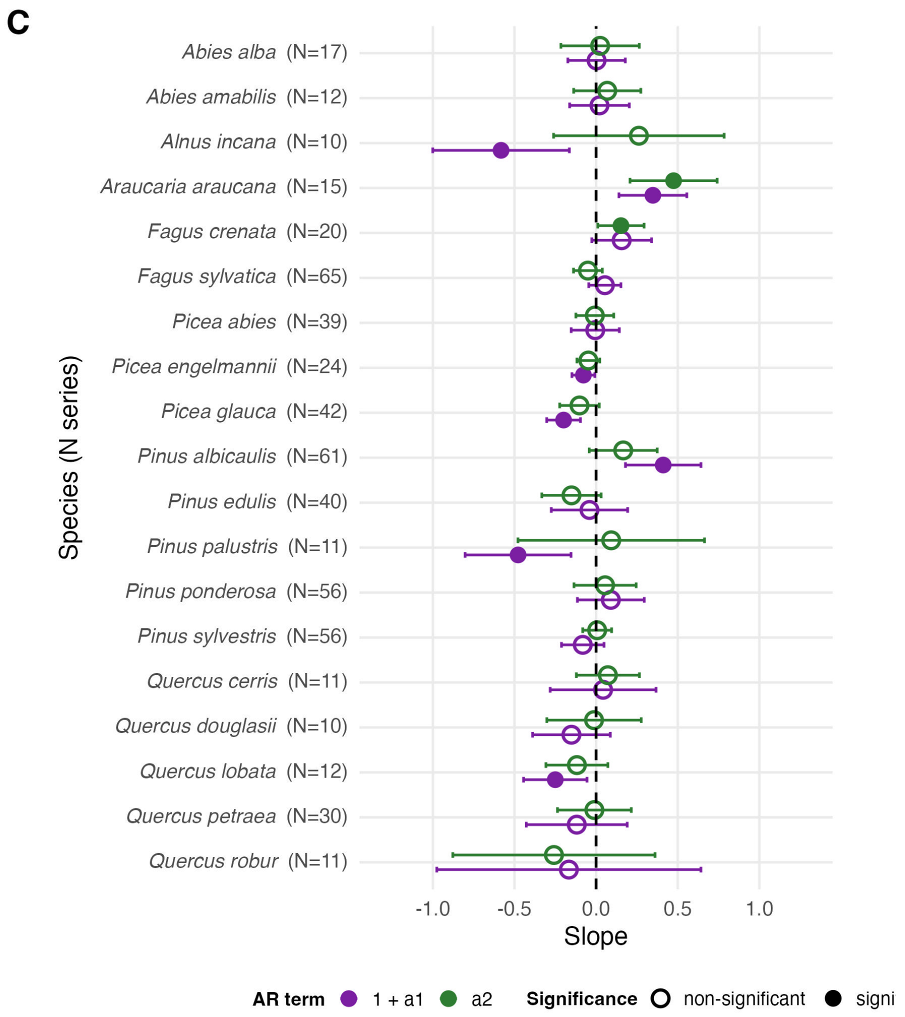

Figure S6: Associations between autoregressive coefficients $(1+a_1)$ and a_2 and climatic water balance (CWB) across 525 populations representing 19 species. Results for *B. pubescens* are not shown due to insufficient sample size for convergence. Each row represents a species. Points show estimated slopes for standardised CWB, with error bars indicating 95% confidence intervals. Significant effects are shown as filled circles, while non-significant effects are shown as empty circles. Positive slopes of $1+a_1$ are associated with longer period lengths, whereas negative slopes are associated with shorter period lengths. Positive slopes of a_2 indicate weaker or less regular periodicity, while negative slopes indicate stronger or more regular periodicity.

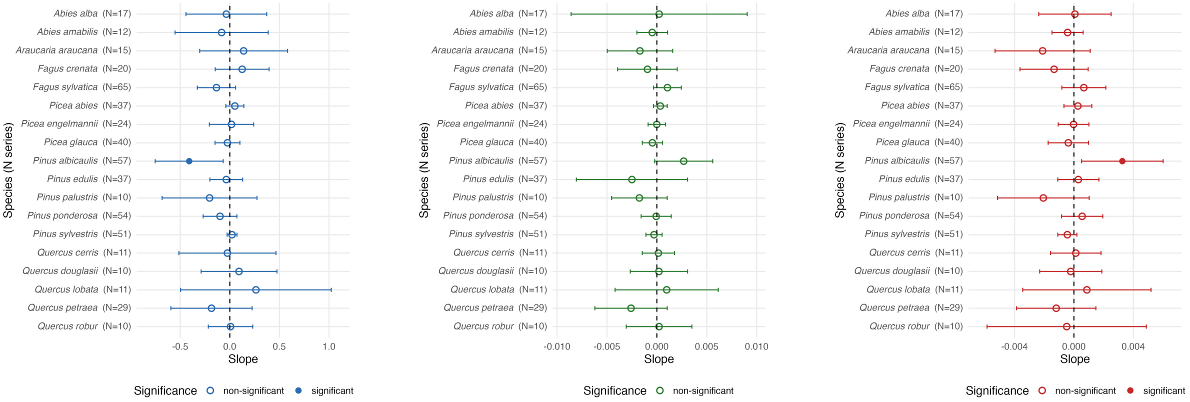

Figure S7: Relationship between climatic variables and masting period length from per-species truncated Poisson models. Each panel shows species-level slopes (±95% confidence intervals) from truncated Poisson regressions fitted with period length as the response and (A) mean annual temperature (MAT), (B) mean annual precipitation (MAP), or (C) climatic water balance (CWB) as predictors. Positive slopes indicate a tendency toward longer masting periods with increasing climatic values, while negative slopes indicate shorter periods. Models were fitted separately for each species using the `glmmTMB()` function from the `glmmTMB` R package. Significant effects are shown as filled circles, while non-significant effects are shown as empty circles.

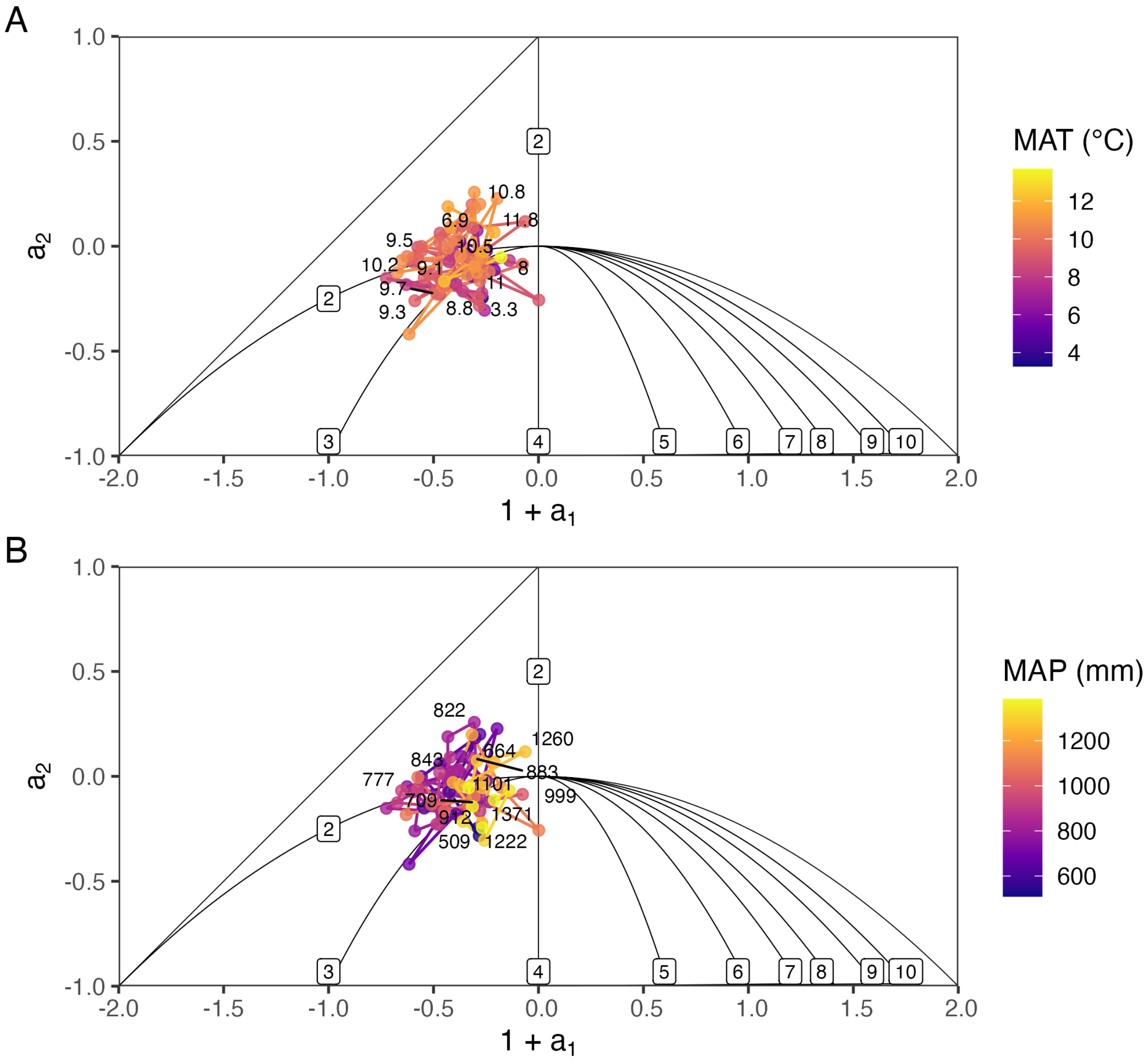

Figure S8: **Climatic variation in fitted $1+a_1$ and a_2 values for *Fagus sylvatica*.** The panels show how fitted $1+a_1$ and a_2 coefficients from the same climate–AR(2) models used in Fig. 4 vary along real climatic gradients for *Fagus sylvatica*. Populations are ordered from cold to warm in the MAT panel (A) and from dry to wet in the MAP panel (B), and plotted within the parabola plot according to their fitted coefficients. Consistent with Fig.3, the MAT effect for *Fagus sylvatica* was non-significant, and fitted $1+a_1$ and a_2 values show no systematic movement across the parabola. In contrast, MAP showed a significant positive effect, and fitted values display a clear directional shift across the parabola with increasing precipitation. This visualisation shows the same pattern as the whisker plot: no directional shift with MAT, and a gradual positive progression with MAP.

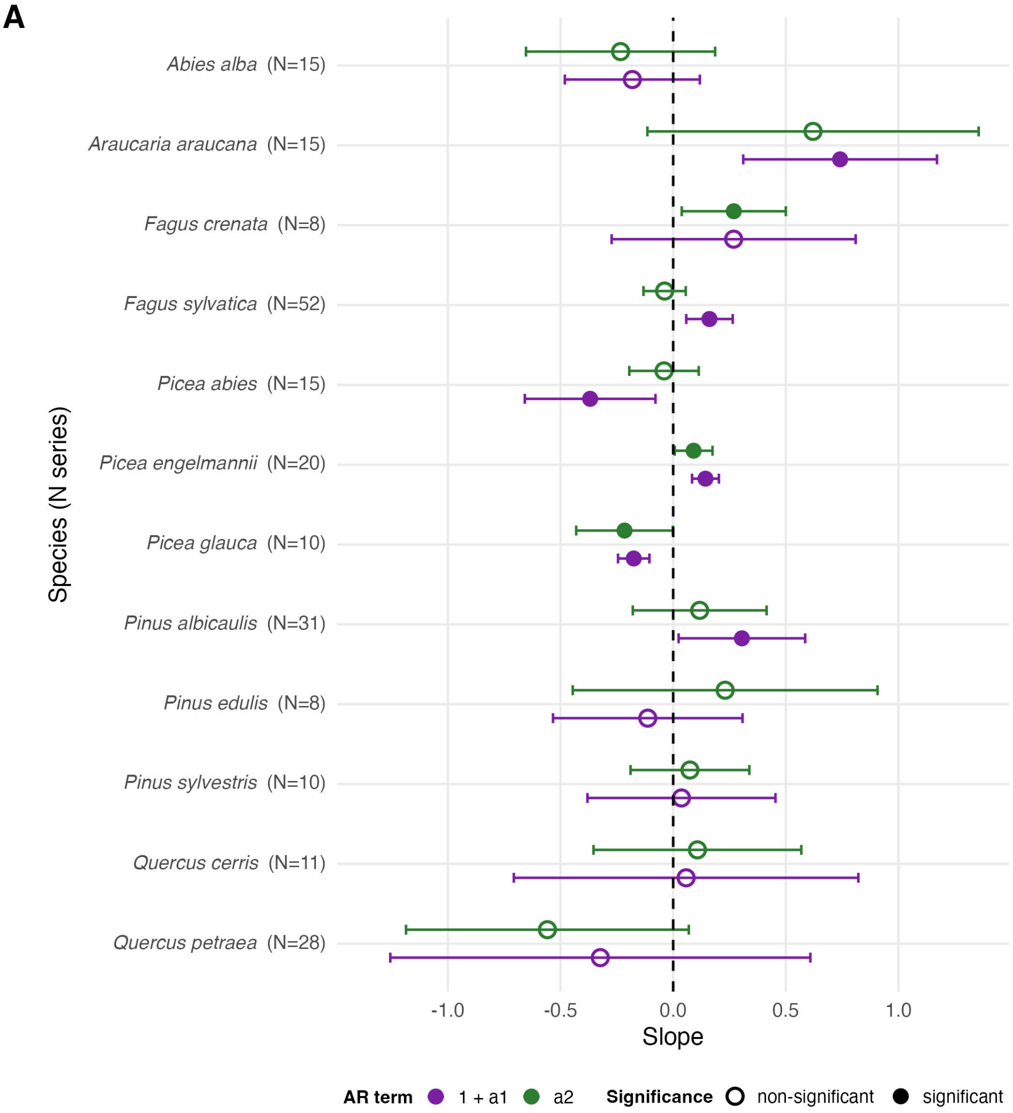

Figure S9: **Relationship between temporal autoregression coefficients $1 + a_1$ and a_2 and elevation (N = 223 populations, 10 species)**. Each row represents a separate species. Each point represents the coefficient of the linear regression of the relationship, with error bars indicating the 95% confidence intervals. Significant effects are shown as filled circles, while non-significant effects are shown as empty circles. Positive slopes of $1 + a_1$ are associated with longer period length, whereas negative slopes are associated with shorter period length. Positive slopes of a_2 indicate weaker or less regular periodicity, while negative slopes indicate stronger or more regular periodicity.

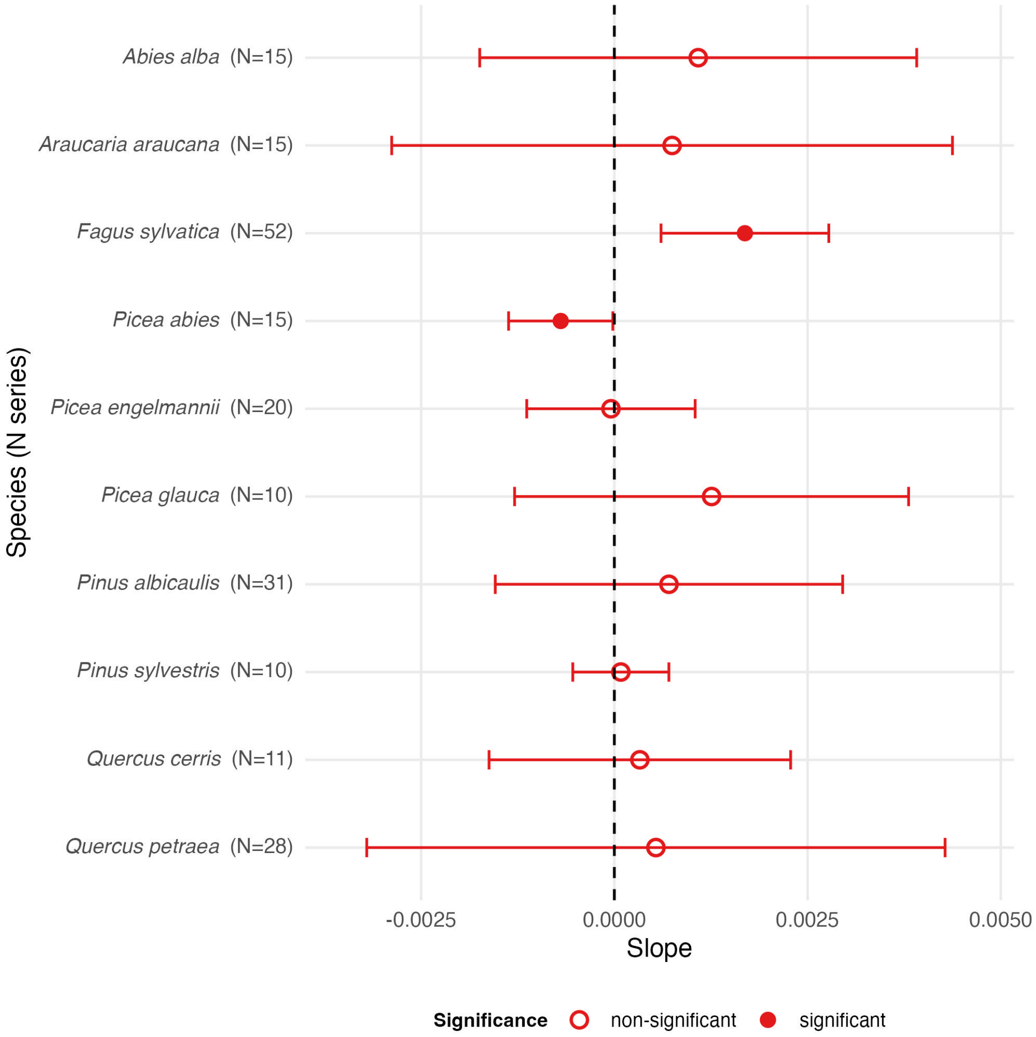

Figure S10: **Relationship between masting period length and elevation derived from per-species truncated Poisson models.** Each row represents a separate species. Points show model-estimated slopes with 95% confidence intervals. Positive values indicate a tendency toward longer masting periods with increasing elevation, while negative values indicate shorter periods. Significant effects are shown as filled circles, while non-significant effects are shown as empty circles.

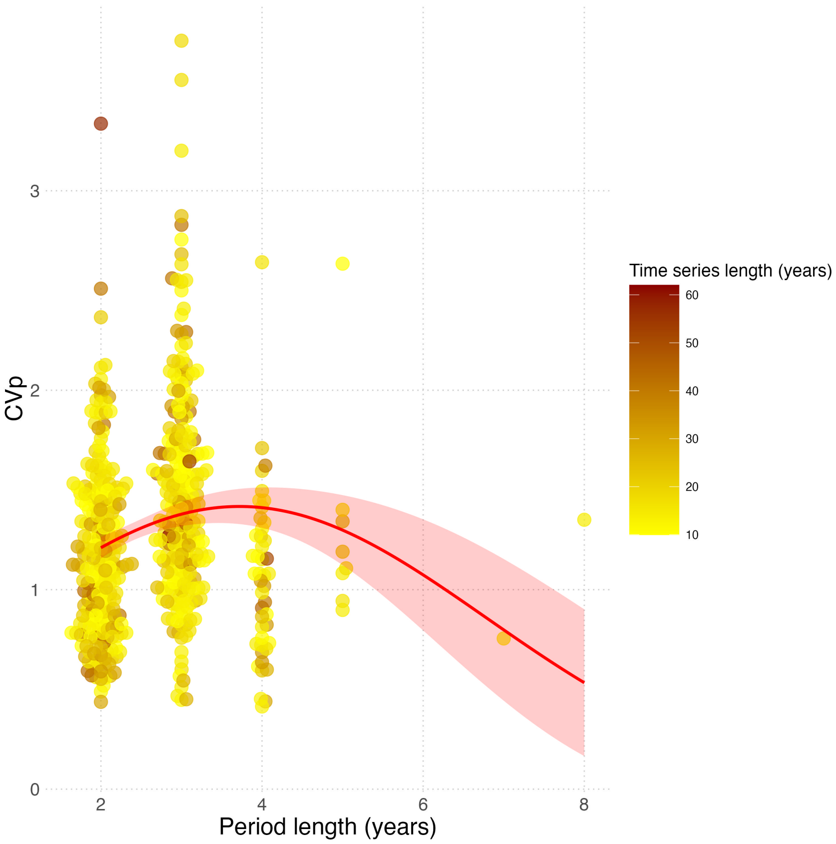

Figure S11: **Relationship between period length and CVp (coefficient of variation for each population).** Each point represents an individual time series, coloured by time series length. CVp is calculated as the standard deviation of seed production in a population divided by the mean seed production in that population. A Gamma generalized linear model (GLM) with a log link was fitted, including a quadratic term for period length and time series length as explanatory variables, with CVp as the response variable. Period length ($p < 0.001$) had a significant effect, while time series length was not significant ($p = 0.678$). The model had a marginal R^2 of 0.03, indicating that period length explained only a small proportion of the variation in CVp. The red line represents model predictions, with 95% confidence intervals.