Short reproductive 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, including how it varies across and within species. Here, we used autoregressive analyses on seed production data from 556 populations across 20 tree species, with an average time series length of 19 years (range: 10–62 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, effective mainly against specialized short-lived insect predators, with costs such as missed reproductive opportunities and resource losses. 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 reproductive periods in mast seeding, likely reflecting consistent evolutionary constraints on reproductive timing across diverse ecological conditions.

keywords: | masting | masting period | seed production | periodicity | 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). Consequently, understanding whether masting follows predictable periods has long interested ecologists and foresters (Elton, 1924), but 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 for defining 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 of 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 (Kelly *et al.*, 2001; Rapp *et al.*, 2013; Venner *et al.*, 2016). 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.*, 2024). 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). 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.*, 2024). 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, 2024). 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.*, 2024). These processes can stabilise the periodicity of masting, optimising intervals to maximise fitness benefits. However, environmental conditions influencing resource accumulation and weather cue frequency introduce stochastic variation into these intervals. Consequently, quantitative assessments of periodicity across multiple species are required to better understand how resource dynamics and cue frequency interact at broader ecological scales.

Here, 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. Additionally, we examine how local climate correlates with period length. To the extent that interaction between resource dynamics and weather cue frequency affects masting patterns, we expected period length to correlate with local climate and elevation. For example, within species, populations inhibiting harsher (e.g. drier and colder) climates or higher elevations may require more time to accumulate sufficient resource levels to trigger large reproductive events, prolonging the period length (Satake & Bjørnstad, 2008; Wion *et al.*, 2020; Foest *et al.*, 2025a) 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). 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) and mean annual precipitation (MAP) were calculated for each unique location, based on monthly values (1960 to 2020) from the corresponding 2.5 minute resolution in the WorldClim dataset (Harris *et al.*, 2020).

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 quantify the dependence of seed production in year t on seed production in the previous one and two years earlier, respectively. In this model, population dynamics are considered periodic if the combinations of $1 + a_1$ and a_2 fall within the parabola or to the left of the $1 + a_1 = 0$ line in the plot (see Fig. 1) (Bjørnstad *et al.*, 2008).

There are two primary ways to generate gradients in period length within the AR2 model (Bjørnstad *et al.*, 2008; Shibata *et al.*, 2020). First, increasing the $1 + a_1$ coefficient, provided the a_2 coefficient remains in the period region, elongates the period length. The period length is determined by the position of points in the parabola diagram (Fig. 1). 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). Secondly, increasing a_2, while $1 + a_1$ remains negative, shifts points leftward within

the periodic region of the parabola diagram (Fig. 1), typically shortening the estimated period length from 3–4 years to 2 years.

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).

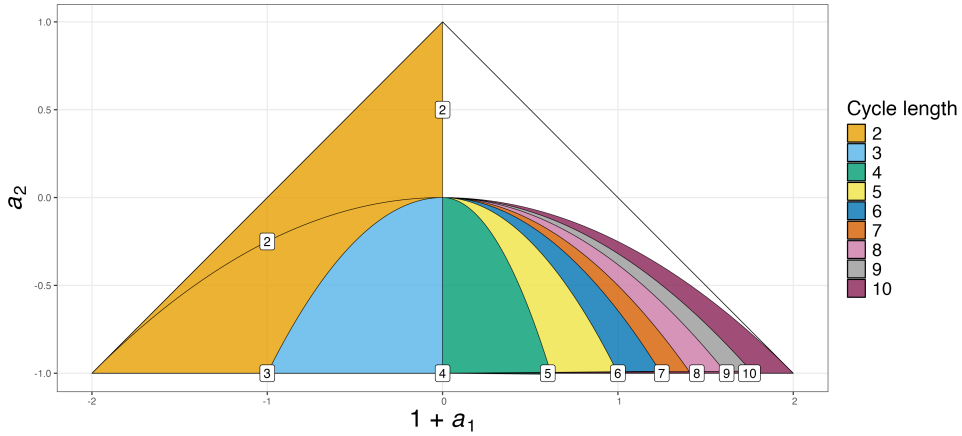

Figure 1: Parabola plot showing correspondence of combinations of $1 + a_1$ and a_2 coefficients values to period length. White space indicates a lack of period. See Bjørnstad *et al.* (1995, 2008).

We used Bayesian second-order autoregressive models to analyse the relationship between climate and $1 + a_1$ and a_2 coefficients for each species separately. Before modelling, we standardised MAT and MAP by centring and scaling (z-transformation), to place them on comparable scales. Given the correlation between these variables — evidenced by high VIF values in some species — we fitted separate models for MAT and MAP for each species. The model formulas were specified using the bf() function from the brms package (Bürkner, 2021), where the autoregressive coefficients $1 + a_1$ and a_2 were modelled as functions of standardised MAT and MAP. The models were fitted using the brm() function from the brms package (Bürkner, 2021), which supports multivariate response modelling and allowed both autoregressive terms to be estimated simultaneously. We used the default priors provided by the package. Each model was run with four MCMC chains, each consisting of 10,000 iterations, including 3,000 warm-up iterations. Model fitting was performed in parallel using 8 CPU cores. All data analysis was performed in R v. 4.2.3 (Team, 2020).

Results

Percentage of periodical 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*) (Fig. 2).

For the species that included both periodic and non-periodic time series, the proportion of periodic populations ranged from 81.8% (*Pinus palustris*) to 96.7% (*Quercus petraea*). Other species with relatively lower percentages of periodic populations included *Alnus incana*, *Quercus robur* (90%), *Pinus sylvestris* (88%), *Fagus crenata* (87%) and *Pinus palustris* (82%) (Fig. 2).

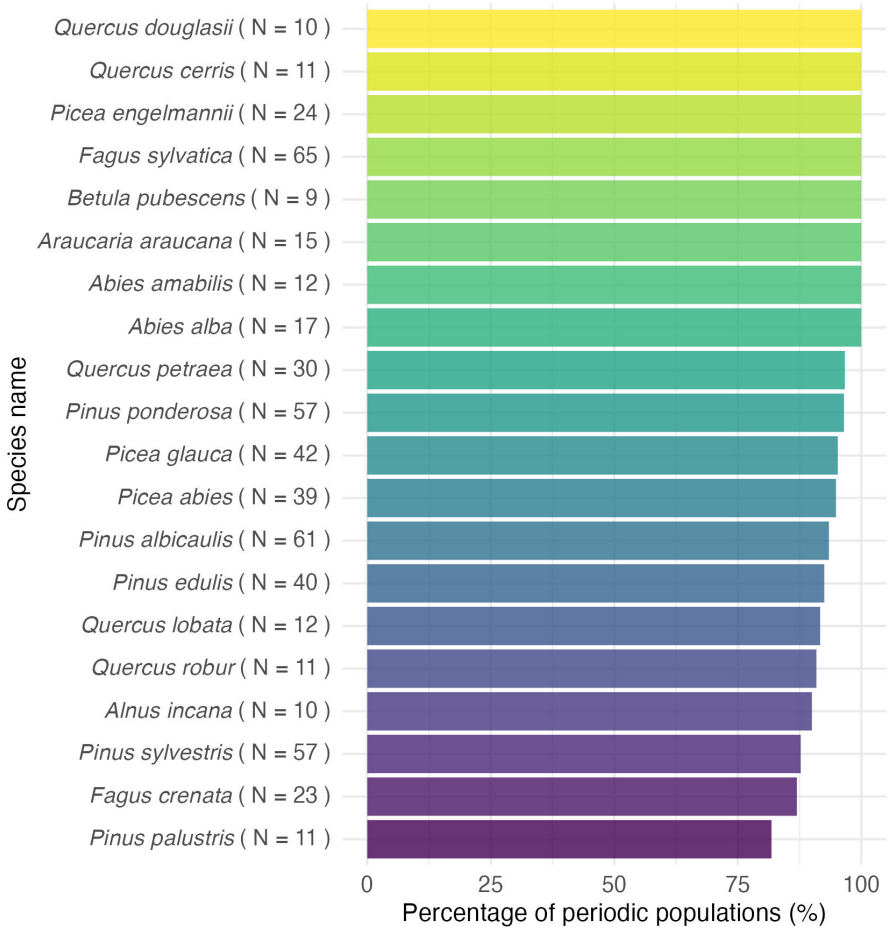

Figure 2: Percentage of periodic populations across species studied (N = 525 periodic populations, 20 species). The x-axis shows the percentage of periodic populations for each species. Whether a time series was categorised as periodic or not is based on whether a_1 and a_2 coefficients fell within the 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).

Period length The average period length across species was 2.65 (±0.49 SD) (Fig. 3), and was not correlated with the length of time series (Fig. S1). 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 (Figure S1). Among the species analysed, the shortest species-level average period length was observed in *Quercus lobata* (2 ± 0 SD), which displayed a highly consistent period length (all 11 populations had period = 2). In contrast, the longest average period length was recorded in *Quercus cerris* (3.27 ± 0.14 SD), also with relatively low variability. Most species exhibited average 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 10 time-series showing evidence of periods longer than 4 years, mainly associated with *Pinus species*, *Picea abies* and *Quercus petraea* (Fig. 3). *Quercus petraea* and *Picea abies* included outlier populations with 8-year and 7-year periods, respectively. Additionally, few populations with 5-year periods were observed in coniferous species from the *Pinus*, *Picea*, and *Alnus* genera (Fig. 3).

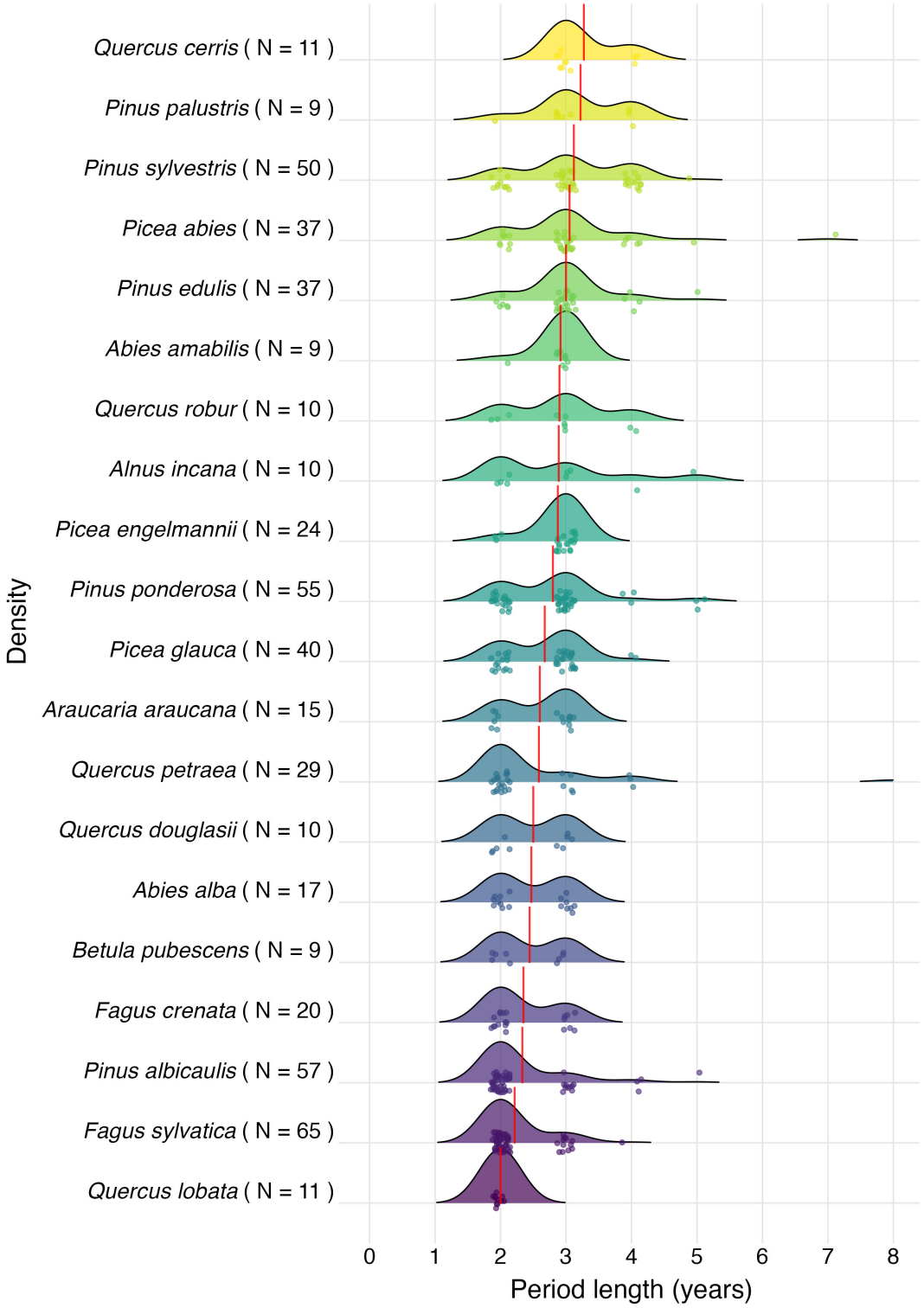

Figure 3: Inter- and intra-specific variation in period length (N = 525 periodic populations, 20 species). Each row represents the distribution of period lengths for populations of each species. Period length for each population was determined based on the position of the population $1 + a_1$ and a_2 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, the jitter was added to decrease overlap. Red vertical lines represent the species-level mean period length. Non-periodic populations are excluded from the graph. The $1 + a_1$ and a_2 coefficients for each population are given in Fig. S2.

Period length and climate While some species show an effect of local climate on their autoregressive coefficients ($1+a_1$ and a_2), many do not exhibit a strong or consistent relationship. The diversity of slope directions and significance levels indicate that the effect of climate on these autoregressive coefficients is species-specific. Higher mean annual temperatures (MAT) increased period length in two species, *A. araucana* and *P. abies*, as indicated by positive effect of MAT on $1 + a_1$. In turn, higher MAT reduced period length in three species, *Q. petraea*, *P. engelmannii*, and *A. incana*, as indicated by negative effects on $1 + a_1$ (Fig. 4A). Moreover, in five species— *Q. petraea*, *P. edulis*, *P. albicaulis*, *F. sylvatica*, and *B. pubescens*—the periods tended to be shorter, with species more likely to exhibit a two-year period in warmer locations, as indicated by positive effects on a_2. In contrast, in *P. engelmannii*, the period was longer in warmer climates (Fig. 4A, Fig.S2).

Period length increased with higher mean annual precipitation in four species - *P. albicaulis*, *F. sylvatica*, *F. crenata*, and *A. araucana*, as indicated by positive effects on $1 + a_1$. In turn, period length increased in drier locations in six species, *Q. petraea*, *Q. lobata*, *P. palustris*, *P. engelmannii*, *P. glauca*, and *A. incana*, as indicated by negative effects on $1+a_1$ (Fig. 4B). Periods became shorter and more likely to transition to a two-year period with increasing moisture in two species, *P. edulis* and *B. pubescens*, as indicated by positive effect on a_2. In contrast, in *F. sylvatica*, where precipitation has a negative effect on a_2, periods lengthened with higher moisture, increasing the likelihood of a shift to a three-year period (Fig. 4B, S2).

For the remaining species, *Q. cerris*, *P. sylvestris*, *A. amabilis*, *Q. robur*, *P. ponderosa*, *Q. douglasii*, and *A.alba*, climate variables had no significant effect on the length or strength of their periods.

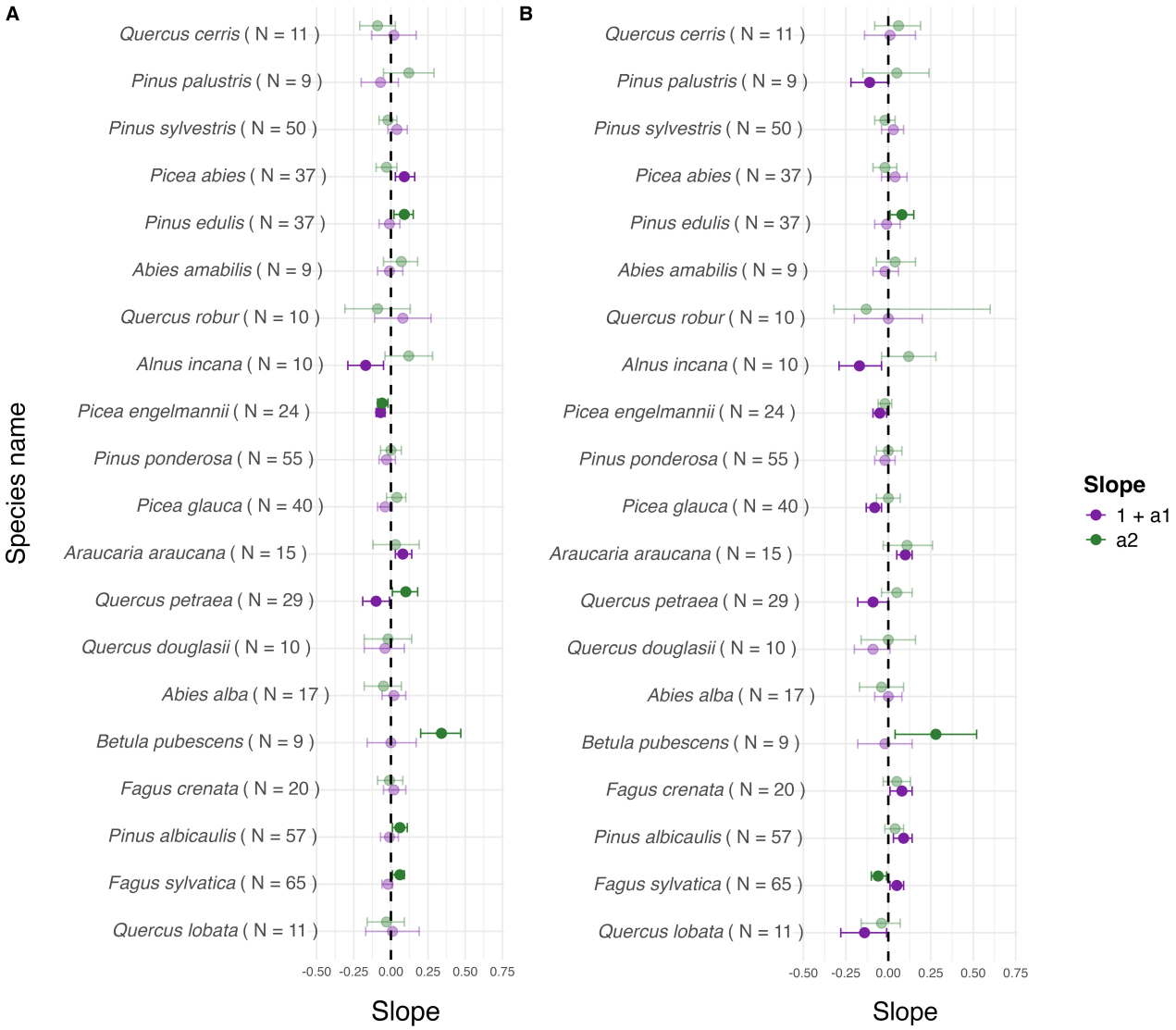

Figure 4: Relationship between autoregressive coefficients $1 + a_1$ and a_2 and local climate (MAT: mean annual temperature, and MAP: mean annual precipitation) (N = 525 populations, 20 species). Panel A shows effects of MAT, while panel B of MAP. Rows represent separate species. Each point represents the slope of the relationship, with error bars indicating the 95% confidence intervals. Coefficients $1 + a_1$ and a_2 reflect the relationship between MAT or MAP and period length. Non-significant effects are indicated by lower opacity.

Period length and elevation The correlations of elevation on autoregressive coefficients $1+a_1$ and a_2 were weak and largely not significant (Fig. S3). However, four species showed significant effects. In *P. glauca*, $1 + a_1$ and a_2 decreased with elevation, which, given the parameter space covered by this coefficient in that species, indicated a tendency of period length to increase at higher altitudes. Similarly, in *F. sylvatica* and *P. engelmannii*, $1 + a_1$ increased with elevation, suggesting a tendency for longer period length. In *A. alba*, a_2 decreased with elevation, suggesting that period length in that species tends to move from 2-year to 3 to 4-year period as elevation increases (Fig. S3). In other species, the effects of elevation on and $1 + a_1$ and a_2 were not significant (Fig. S3).

Discussion

Our findings reveal that periodicity in masting 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 incurs further risks, including losses of accumulated resources due to adverse events like insect outbreaks or drought. 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.*, 2024). 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. S4). 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 10 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 intervals (T Maki, 1952; Wagner *et al.*, 2010). Such discrepancies might arise from masting intervals 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. (S5), 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 reproductive 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.*, 2025a). 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, including those with weak or absent effects (Fig. S6), making this explanation unlikely. 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.*, 2024, 2025b). 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 intervals by inhibiting reproduction (Inouye, 2008; Éliane Schermer *et al.*, 2020). Similarly, precipitation variability affects reproductive dynamics; drought conditions may extend reproductive intervals 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 and MB co-wrote the first draft of the manuscript. All authors contributed to the interpretation of the analysis, revised the draft, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data availability statement

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

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Supporting Information

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Title: Short reproductive periods dominate mast seeding across diverse tree species

Table S1: Summary of per species sample size in our study.

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 engelmanii	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

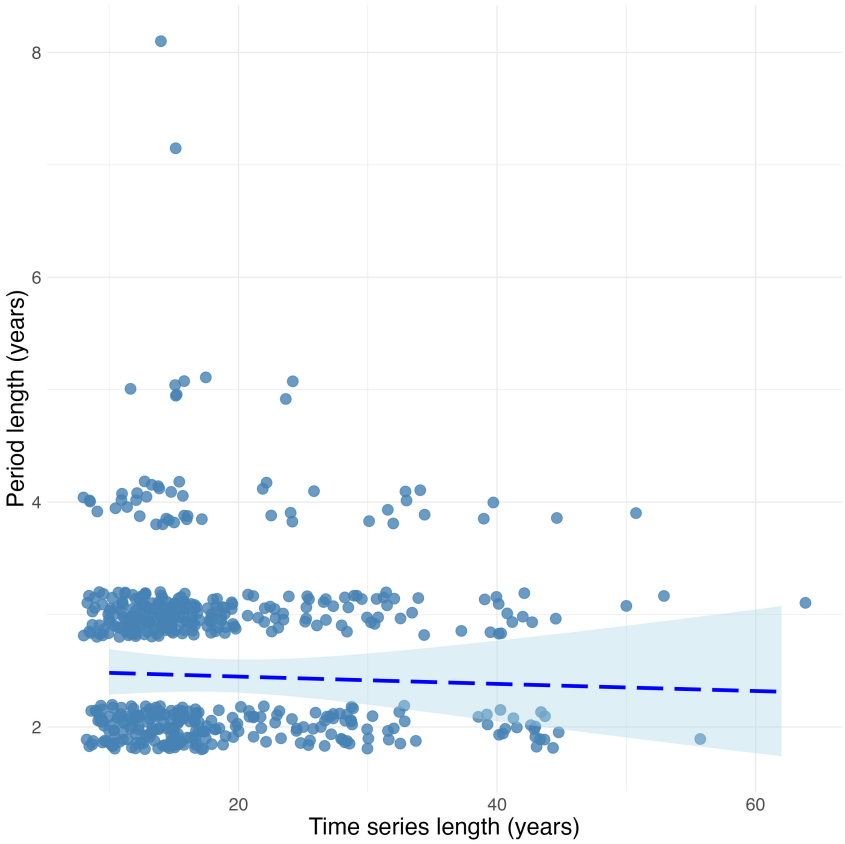

Figure S1: Relationship between period length and time series length. Each point represents an individual time series. A zero-truncated Poisson generalized linear model (GLM) was fitted to examine the relationship between period length as a response variable and time series length as an explanatory variable. 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.

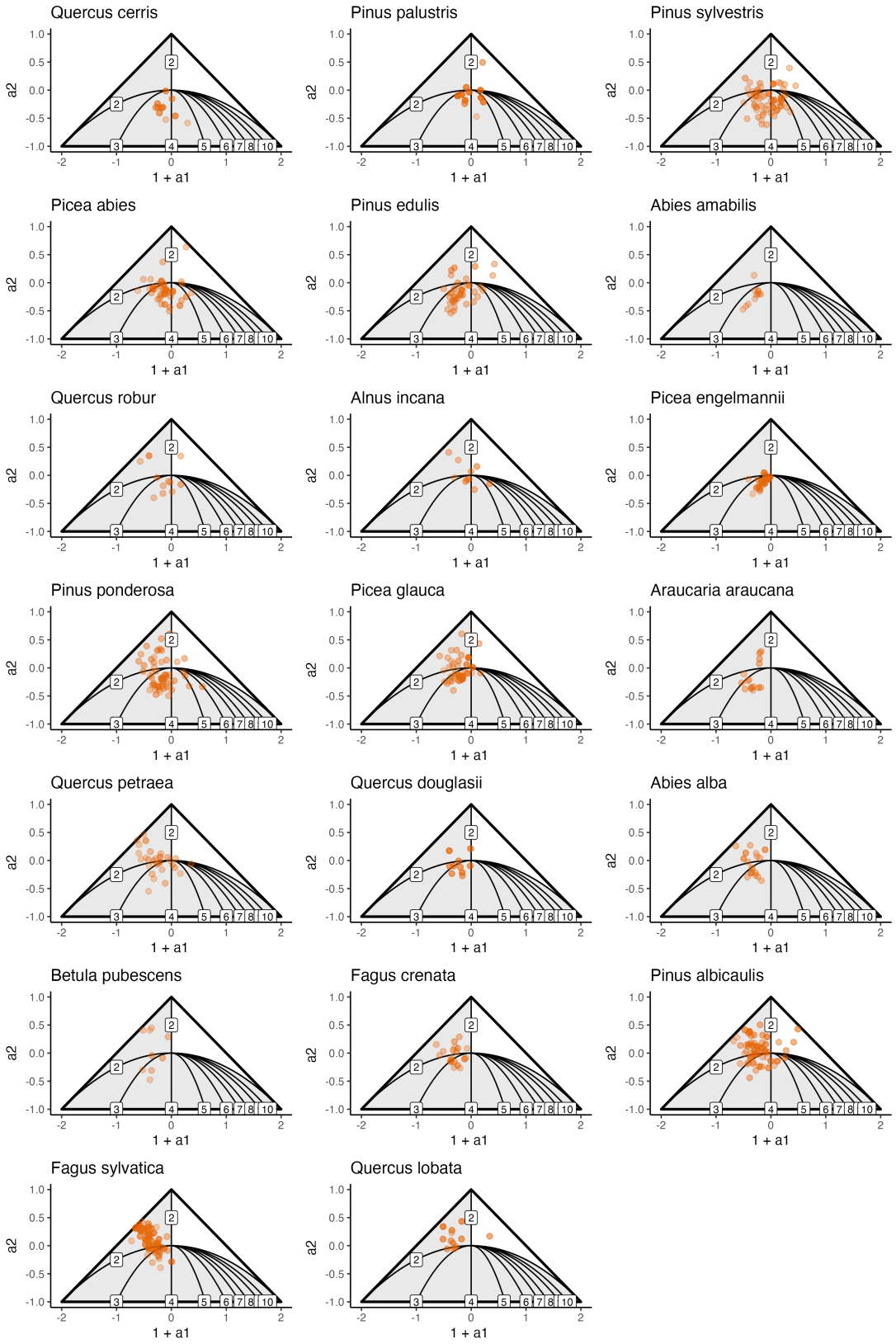

Figure S2: Temporal autoregression coefficients across studied species (N = 20). Each dot shows one population.

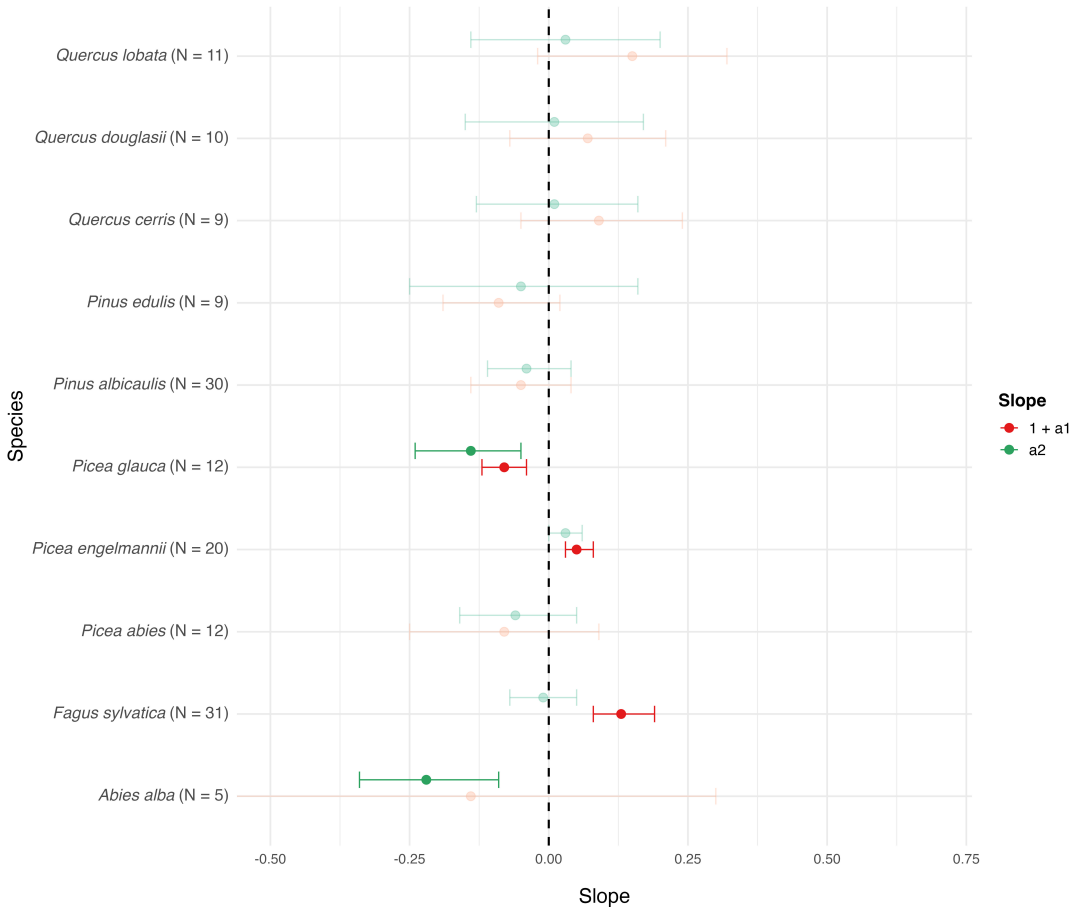

Figure S3: Relationship between temporal autoregression coefficients $1 + a_1$ and a_2 and elevation (N = 149 populations, 10 species). Each row represents a separate species. Each point represents the coefficient of the linear regression of the relationship, with error bars indicating the 95% confidence intervals. Non-significant coefficients are indicated by lighter colours.

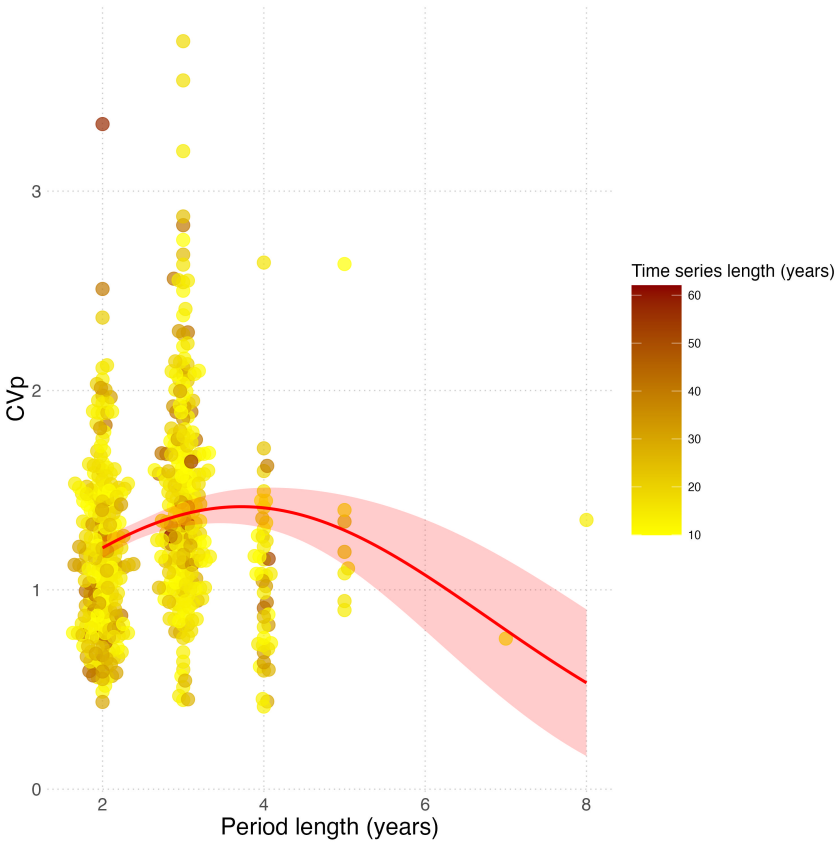

Figure S4: Relationship between period length and CVp (coefficient of variation for each population). Each point represents an individual time series, coloured by time series length. CVp is calculated as the standard deviation of seed production in a population divided by the mean seed production in 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.

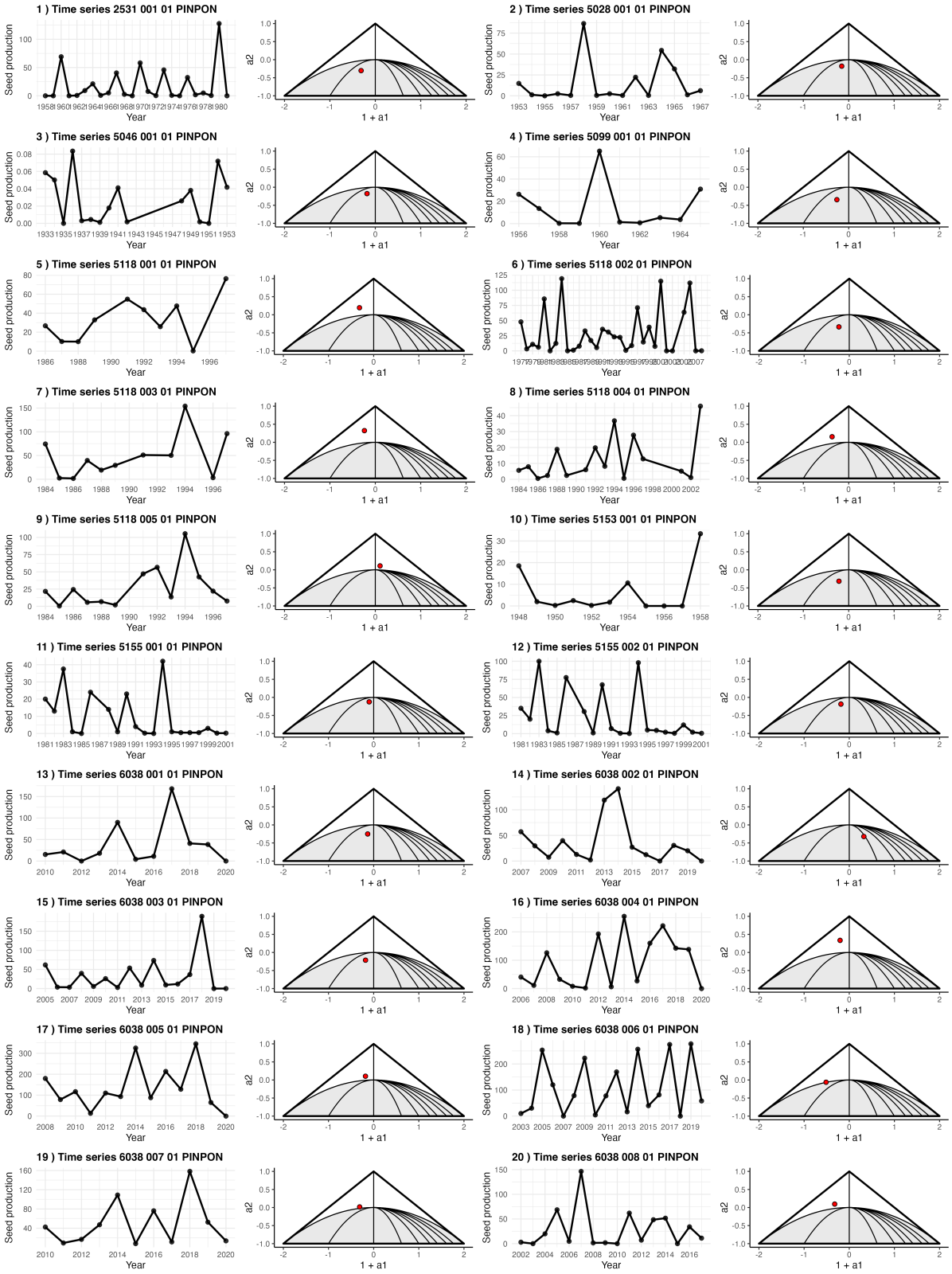

Figure S5: Time series of seed production and respective parabola plots for 20 populations of *Pinus ponderosa* Each row contains two populations, with time series graphs (first and third columns) showing interannual variation in seed production and parabola plots (second and fourth columns) showing the period length of given time series based on $1 + a_1$ and a_2 coefficients from AR2 model.

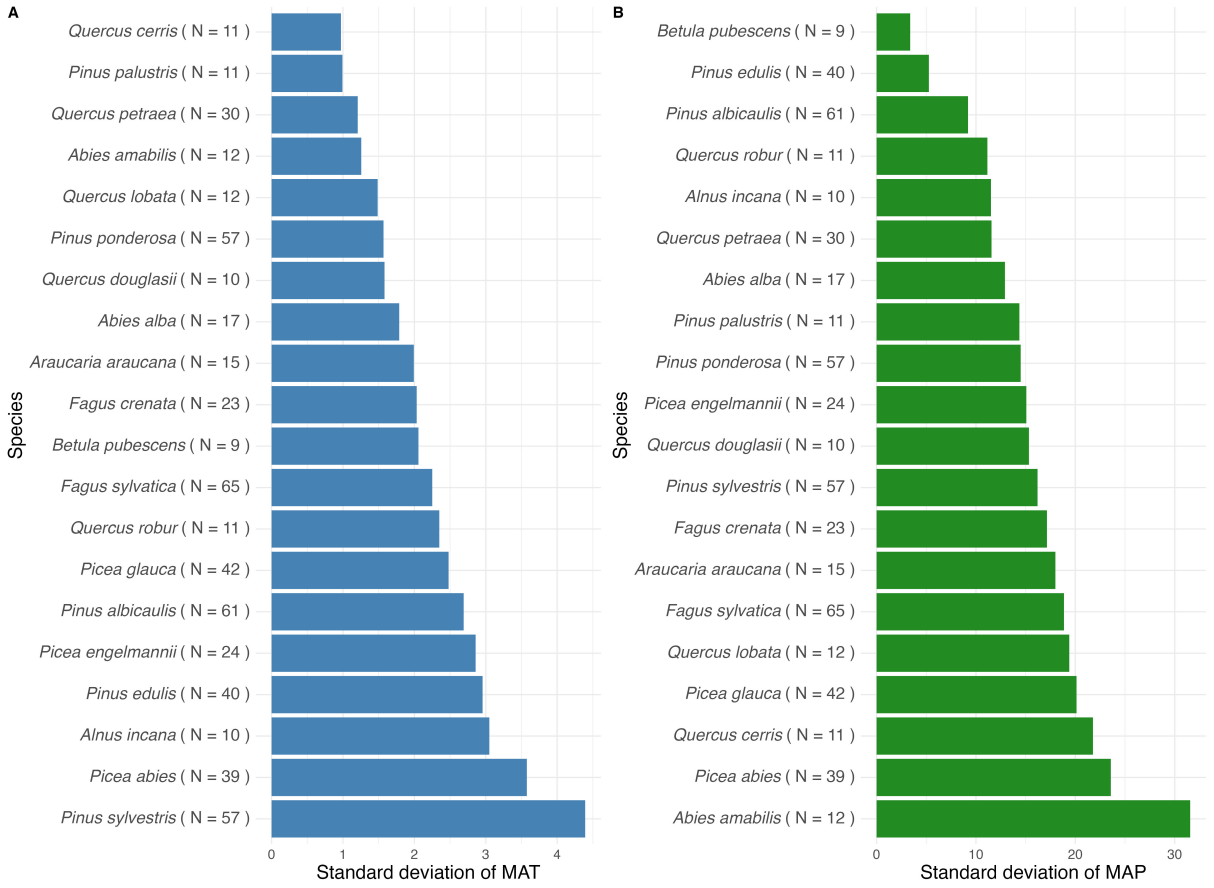

Figure S6: Variation in mean annual temperature (MAT) and mean annual precipitation (MAP) across populations within species. Each bar represents the standard deviation of MAT and MAP values across sites for each species, with species ordered from lowest to highest variation.