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Manuscript title: Intraspecific variation in masting across climate gradients is inconsistent with the environmental stress hypothesis

Author names: Jessie J. Foest[1,2], Thomas Caignard[3], Ian S. Pearse[4], Michał Bogdziewicz[2], Andrew Hacket-Pain[1].

Affiliations: [1]University of Liverpool, Geography and Planning, School of Environmental Sciences, Roxby Building, L69 7ZT Liverpool, United Kingdom. [2]Forest Biology Center, Faculty of Biology, Adam Mickiewicz University, ul. Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland. [3]INRAE, BIOGECO, Université de Bordeaux, Pessac, 33615 France. [4]U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Ave #C, Ft Collins, CO, 80526 USA.

Corresponding author: *Jessie J. Foest* Email: j.j.foest@protonmail.com

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Abstract

Year-to-year variation in seed crop size (i.e. masting) varies strongly among populations of the same species. Understanding what causes this variation is vital, as masting affects the ability of tree species to regenerate and determines the population dynamics of a wide variety of animals. It is commonly thought that environmental stress is a key driver of masting variability. The environmental stress hypothesis posits that more marginal conditions increase the strength of masting. Using 437 time series from 19 tree species, we find that this hypothesis fails to fully explain how masting varies across marginality gradients. We expected higher interannual variation and less frequent masting events at species margins, but instead found that while mast years are indeed less frequent, the inter-annual variation was lower towards the margins. The observed patterns suggest that populations growing at the margins may invest more resources in low seed production years compared to their conspecifics, hedging their bets in these more challenging environments.

Introduction

For many long-lived plant species from diverse taxa and ecosystems, seed production is highly variable between years, and individuals within populations synchronise their reproductive effort (Pearse et al. 2016, Dale et al. 2021). The resulting population-level variability of seed production is known as masting (Kelly 1994, Pearse et al. 2016). A widely held hypothesis to explain masting variability is that plants growing in resource-poor, stressful or marginal environments show more pronounced masting (the ‘environmental stress’, or ‘productivity gradient’ hypothesis) (Kelly and Sork 2002, Satake and Bjørnstad 2008, Allen et al. 2012, Roland et al. 2014, Pearse et al. 2017, Wion et al. 2020, 2023). Here, we show that masting varies over environmental gradients, but that the environmental stress hypothesis does not explain this spatial variation.

We require a thorough understanding of what drives within-species variation in masting, given the important effects of masting on ecosystems. Masting increases reproductive efficiency through economies of scale that decrease seed predation rates and improve pollination efficiency (Kelly and Sork 2002, Pearse et al. 2016). Understanding these reproductive patterns in plants is increasingly important in the context of climate change, because plant reproduction is a critical component of forest dynamics following climate-driven disturbance and environmental change (Sharma et al. 2022). Climate-driven changes to mast seeding can severely limit the viability of seeds (Bogdziewicz et al. 2023). Moreover, seeds represent a foundational food source and masting affects animal populations throughout food webs (Clark et al. 2019).

The environmental stress hypothesis predicts that comparatively more stressful, lower productivity environments have less frequent large seed crops, resulting in higher inter-annual variability of seed production when compared to less limited populations (Kelly and Sork 2002, Satake and Bjørnstad 2008, Allen et al. 2012, Pearse et al. 2017). According to the hypothesis, such environments limit how quickly plants can accumulate sufficient resources to produce a bumper crop. With increasingly challenging growing conditions, we thus expect lower seed production in years following high seed crops (i.e. stronger resource depletion), causing the temporal autocorrelation at lag one year to become more negative (Sork et al. 1993, Koenig and Knops 2000).

Until now, the environmental stress hypothesis has not been tested at a large scale. Testing is complicated by the fact that many factors can reduce plant productivity, and the stresses experienced by plants vary by species and location. This may help explain why the few studies that have examined the effects of different climate and productivity gradients on masting find contradicting responses, i.e. positive, negative or neutral responses (Table 1). We propose a way to find commonalities between species in their responses to stress gradients by using the concept of ‘climate marginality’.

The limit of a species’ range is a manifestation of its ecological niche (Sexton et al. 2009). If the species range edges are near equilibrium (i.e. the species can be found throughout most of its potential distribution), climate marginality theory predicts that populations at the climatic periphery more frequently experience the effect of biotic and abiotic limiting factors compared to populations living in core conditions, and that demographic performance would consequently be impaired (Sexton et al. 2009, Pironon et al. 2017, Kunstler et al. 2021). Changes in reproduction patterns towards climatically marginal sites could result from the limited availability of resources, or from higher demands on these resources for maintenance or overcoming increased competition (Gaston 2009, Roland et al. 2014), or because of more frequent extreme climate events that affect reproduction such as late spring frosts and summer droughts (Nussbaumer et al. 2020, Journé et al. 2021, Willi and Van Buskirk 2022). All in all, we expect to observe changes in masting behaviour across climate marginality gradients, with masting becoming stronger with increasing climate marginality.

Here, we present the first attempt to generalise, across 19 tree species, the effect of environmental stress on masting. While intraspecific variation in masting by populations is widely acknowledged (Herrera et al. 1998, Greene and Johnson 2004, Satake and Bjørnstad 2008, Crone et al. 2011), it has remained largely unclear how much intraspecific variation of masting exists within species across space, and what drives this variability. Thus far, studies designed to assess the effect of environmental stress on intraspecific masting variability have been constrained in terms of spatial and species coverage. Now, due to a recent synthesis of data on reproductive behaviour in plants (Hacket-Pain et al. 2022), we are able to test the long-standing environmental stress hypothesis across species and extensive environmental gradients.

We expect to observe parabolic relationships between climate variables and masting metrics. Specifically, we expect (1) seed production to be more variable, (2) more negatively autocorrelated through time (indicative of a stronger resource limitation; Koenig et al. 2003), and (3) have less frequent large seed crops in populations growing in marginal climates. In contrast, range centres should be characterised by less variable, less autocorrelated and more frequent large seed crops.

Materials and Methods

We describe the variability of masting for populations from 19 tree species occurring in mid-to-high-latitudes using three masting metrics. Subsequently, we test if these metrics vary along climate marginality gradients in the ways predicted by the environmental stress hypothesis. For the six best-represented species in terms of data coverage, we also fit models to gain insight into the species-specific responses behind the overall, across species, pattern. All models were fitted in R v. 4.3.1 (R Core Team 2023).

Intraspecific variation in reproductive patterns

Reproduction time series

We obtained time series of annual reproduction from the open-access MASTREE+ database (Hacket-Pain et al. 2022). This database collates geo-referenced reproductive time series from perennial plant species across the world. We subset MASTREE+ to seed, fruit and cone production time series of species which had extensive temporal (≥ 10 years of observation) and spatial (≥ 10 sites) replication. From here on, seeds, fruit and cones will be referred to as seeds, for simplicity. *Quercus robur* and *Quercus petraea* time series were grouped together, as the often sympatric species have high hybridisation rates (Abadie et al. 2012), and synchronise their seed production (Bogdziewicz et al. 2017). We only included series representing stand and patch scale populations (excluding (super-)regional scale records) with high-precision spatial references, to accurately link reproductive behaviour and climate. Moreover, to ensure the masting metrics could be meaningfully calculated and compared, we excluded series which lacked a unit (i.e. ordinal data, index data) or which had synchrony-based units (i.e. '% of individuals reproducing'). Comparable collection methods were grouped together before conducting the analyses, and classified as either seed trap data, seed counts, or harvest records. This approach resulted in a dataset of 8,082 annual records, forming 437 time series of the reproductive behaviour of 19 plant species in 357 locations (Appendix S1: Table S1). On average, time series were 18.5 years long (median: 14, range: 10-62).

Temporal reproductive patterns

Three metrics capturing temporal reproductive patterns were calculated for each time series to describe masting variability. Firstly, we calculated the coefficient of variation CVp, the standard deviation divided by the mean annual seed crop size (i.e. number of seeds). Temporal autocorrelation was calculated with the 1-year lagged autocorrelation, AR(1), and obtained with the Acf function in R (Hyndman et al. 2022). Lastly, we calculated the proportion of high seed crop years, Psd. High seed crop years (“mast years”) were defined as years when the standardised annual deviate of reproductive effort exceeded the absolute magnitude of the largest deviate below the mean, as proposed by LaMontagne and Boutin (2007). Additionally, we calculated the recently introduced kCVp, a bounded alternative to CVp, which was found to increase statistical power when compared with CVp when testing for latitudinal patterns in masting (Lobry et al. 2023). This metric can be calculated from the CVp by dividing the squared CVp by 1 + the squared CVp and subsequently taking the square root.

Environmental gradients

Climate data and species’ ranges

Climate data for each location were extracted from WorldClim v. 2.1 (Fick and Hijmans 2017). Temperature variables were adjusted (lapse rate: 0.65 °C/100 m) when the elevation of MASTREE+ time series was known and deviated from the SRTM data used for WorldClim (Fick and Hijmans 2017). To assess the climate gradients covered by our sampling, we extracted climate data for species distributions. Species distributions for all but two species were obtained from EUFORGEN (EUFORGEN 2022) and the Atlas of United States Trees (Petry 2021). The range of *Fagus crenata* was digitised from Kobashi et al. (2006), and a digitised range of *Araucaria araucana* was provided by CONICET-UNS (M. Hadad, CONICET-UNS, unpublished data, 2023). For most species in the dataset, wide spatial and elevational gradients were sampled (Appendix S1: Fig. S1, Appendix S1: Table S1), capturing a large part of the climatic envelope (Appendix S1: Fig. S2, Appendix S1: Section S2).

Linear models

Across-species patterns

We tested for intraspecific effects of climate gradients on temporal reproductive patterns (i.e. CVp, AR1, Psd) using the glmmTMB package (v. 1.1.7; Brooks et al. 2017). To allow for comparisons between CVp and kCVp, we also substituted kCVp in the final CVp models.

While the inclusion of the species as a predictor captures between-species differences in the dependent variable, this does not account for potential between-species differences in the other predictors (Van de Pol and Wright 2009; Pearse et al. 2020). We therefore subject-centred all dependent and independent numeric variables by subtracting the species' (i.e. 'subject') mean of each respective variable, except for climate variables (N.B. models using this data are referred to as 'subject-centred models'). For climate variables, we subtracted the median value observed in the species' range, which allowed for explicit testing of our hypotheses, as the centred value captures distance from the core climate.

For each metric, we ran two models, namely (1) an annual average model, including mean annual temperature (MAT), annual precipitation (AP), the interaction between MAT and AP, as well the second order polynomials of MAT and AP as predictors, and (2) a seasonal model, using the temperatures and precipitation of the coldest (cq) and hottest (hq) quarter of the year, the temperature-precipitation interactions for both quarters (i.e. $\mathrm{T}_{cq} \times \mathrm{P}_{cq}, \mathrm{T}_{hq} \times \mathrm{P}_{hq}$) and the second order polynomials of both temperature and precipitation variables. Since all sites are situated in mid-to-high latitudes, the hottest and coldest quarter correspond to summer and winter, respectively. We accounted for methodological differences and time series properties by including, as predictors (1) time series length, (2) a categorical classification of the measured reproductive variable (i.e. 'cone', 'fruit', 'seed'), and (3) the data collection method (i.e. 'harvest record', 'seed trap', 'count-based method'). Since centring removes the average effect of species, no random factor was used to capture between-species differences. The AR(1) models showed a statistically significant latitudinal trend in the model residuals, and we therefore included subject-centred 'Latitude' as a predictor in these models. All numeric predictor variables were scaled using the root mean square to ensure model convergence. We allowed the dispersion of residuals to vary as a function of species, collection method and reproductive variable. Models were examined and validated with DHARMa (v. 0.4.6), by simulating model residuals and plotting these against observations and predictors to check for misfits, as well as testing for correct distribution (KS test), dispersion and outliers (Hartig and Lohse 2022). Additionally, we tested for collinearity with car (v. 3.1.2; Fox and Weisberg 2019). To assess the significance of the linear terms in these across-species models, we conducted likelihood ratio tests. Standard p-values reflect conditional hypotheses and are not suitable for evaluating the independent contributions of predictors (x) due to the inclusion of quadratic terms ($I(x^2)$). Specifically, for each linear climate predictor, we compared a "full" model—i.e. the model described above but excluding the quadratic and interaction terms involving the focal predictor—to a "reduced" model in which the linear term itself was also removed (see Appendix S1: Table S2).

Species-specific patterns

Since mean trends may obscure ecologically relevant processes, we also fitted species-specific linear models with glmmTMB for CVp, AR(1) and Psd for six species with ≥ 30 observations. We used the same predictors as those used in the subject-centred models, but since only a single species was examined in each model, variables other than the climate variables were not species-centred. Variable scaling was not required for convergence. If there was no variation in reproductive variable or collection method for a species, the variable could not be included in the model. The collection method predictor was removed from the *Picea glauca* models because it exceeded the collinearity threshold ($GVIF^{\frac{1}{2\times df}} > \sqrt{10}$).

Results

Intraspecific variation

Reproductive patterns varied widely within species (Appendix S1: Table S1, Fig. 1, Fig. 2). Notably, for 14 out of 19 species, the observed intraspecific range of CVp values was greater than the interspecific variation in mean CVp (0.89-1.94, Appendix S1: Table S1, Fig. 1). Similarly, the intraspecific variation in AR(1) of 16 species exceeded the observed interspecific variation in mean AR(1) (-0.39-0.01, Appendix S1: Table S1, Fig. 1). The majority of time series, both within and across species, had negative AR(1) values. All intraspecific ranges in Psd exceeded the interspecific range in mean Psd (0.11-0.21, Appendix S1: Table S1, Fig. 1).

The species-specific metric space plots in Fig. 2 highlight how intraspecific variation in CVp and AR(1) in some species cover large portions of the across-species metric space (e.g. *A. incana*: 49.5%, *P. abies*: 32.9%). In contrast, some species have high intraspecific variability in only one metric (e.g. CVp of *P. engelmannii*, AR(1) of *P. sylvestris*), or relatively low intraspecific variability in both CVp and AR(1) (e.g. *A. amabilis*: 2.9%, *Q. douglasii*: 3.7%).

Climate marginality

Across-species patterns

Large seeding years were less frequent towards more marginal climates, which is consistent with predictions of the environmental stress hypothesis. In the annual model, Psd responded to within-species change in MAT^2 (Fig. 3, climate effects: Table 2, full model: Appendix S1: Table S3). Sites with a climate closely matching the species' range median MAT displayed more frequent masting. It should be noted that while the concave relationship between Psd and AP best fitted the observations, this relationship was not statistically significant. Squared winter temperatures predicted Psd in the seasonal model, with the lowest masting frequencies occurring at cold and warm sites. Thus, annual climate patterns appear to be more closely related to climatic conditions in the winter rather than the summer.

Yet, these changes in the frequency of large seeding years did not result in a higher CVp towards the margins, as predicted by the environmental stress hypothesis. CVp varied significantly with temperature, with the annual model predicting lower CVp in the warmest sites, and no effect of precipitation was observed (Fig. 3, climate effects: Table 2, full model: Appendix S1: Table S3). The seasonal model shows that the effect of winter temperature depends on winter precipitation. For populations growing in sites close to the species' median winter precipitation level, the CVp declined with increasing winter temperatures. Combined, these findings show that the relationships between CVp and marginality gradients are more complex than anticipated under the environmental stress hypothesis. The simulated kCVp model residuals showed deviations from normality (Kolmogorov-Smirnov; annual model: $D = 0.08$, $p < 0.05$; seasonal model: $D = 0.09$, $p < 0.01$), but the model results are presented in Appendix S1: Fig. S3 and Appendix S1: Table S3 to allow for comparisons with the CVp models. The results from the annual average kCVp model imply that year-to-year variability in seed production decreases towards cold and warm margins, not just towards the warmer sites as in the CVp model. These findings directly contrast with the predictions under the environmental stress hypothesis. While the detected climate patterns differ from the annual average CVp model, the same methodological variables were found to have effects in both the annual average CVp and kCVp models (i.e. reproductive variable and data collection method). In the seasonal model, a similarly nuanced story emerges, and the observed relationships between climate and the temporal variability of seed production also differed. A concave relationship was found between squared winter temperatures and kCVp, rather than the significant interaction between winter temperature and precipitation detected in the CVp model. Both models show that kCVp is not simply a more powerful variant of CVp. Instead, different relationships may be detected.

Lastly, how AR(1) varies along climate marginality gradients is not well explained by the predictions under the environmental stress hypothesis. Intraspecific variation in AR(1) varied with MAT in the annual climate model, where sites with higher mean annual temperatures had lower AR(1) values (Fig. 3, climate effects: Table 2, full model: Appendix S1: Table S3). Similarly to the annual model, the seasonal model indicates AR(1) was lower when sites experienced warmer temperatures in winter. AR(1) decreased towards both winter precipitation margins, i.e. towards dry and wet sites. The effect of the summer temperatures depended on precipitation; lower AR(1) occurred in drier and colder sites, as well as in warmer and wetter sites. Summer precipitation also showed a parabolic relationship with AR(1), where AR(1) was lowest at the wettest and the driest sites. Thus, we only found limited evidence for concave relationships in the seasonal model.

Overall, we find that masting patterns vary across marginality gradients. However, this variation differs from predictions under the environmental stress hypothesis (Table 3). In addition to these diverging relationships, we also find that there is substantial, and potentially ecologically meaningful, variation around these predictions (see partial residuals, Fig. 3). This indicates that factors other than climate marginality or methodological differences play an important role in driving masting variability.

Species-specific patterns

There is always a risk that ecologically meaningful relationships go undetected if trends are only tested at a general level. Or, phrased differently, there is a chance that the hypothesis holds, but only for a subset of species. Consequently, we tested how masting metrics varied across annual climate marginality gradients for the six best-sampled species (Appendix S1: Table S4). Here, we reveal, where applicable, evidence of species-specific responses matching the predictions of the environmental stress hypothesis.

Evidence in line with our prediction that Psd would be lower in the climatic margins was found for *P. abies* and *P. sylvestris*. Specifically, we observed concave effects on Psd of MAT for *P. abies,* and of AP for *P. sylvestris,* although highest Psd values were found in sites with higher-than-median precipitation in this species.

The relationship between CVp and climate did not generally match the predicted convex pattern of highest variability in more marginal climates, with the exceptions of the effect of MAT on *F. sylvatica* and the effect of AP on *P. edulis (*although this later effect was not statistically significant ($p = 0.06$)).

For AR(1), the evidence in line with predictions is the concave relationship between AR(1) and annual precipitation in *Q. robur/petraea,* and between annual precipitation and temperature and AR(1) in *Picea abies*.

It is worth noting that these species-specific models have relatively small sample sizes (Appendix S1: Table S1), and therefore had lower power than the subject-centred models. Yet, these models reveal that species responses are diverse.

Discussion

The environmental stress hypothesis fails to explain intraspecific masting variation when evaluated across climate marginality gradients (Table 3). Under the environmental stress hypothesis, we would predict higher interannual variation and, simultaneously, less frequent large seeding events at species' margins (Kelly and Sork 2002, Satake and Bjørnstad 2008, Allen et al. 2012, Roland et al. 2014, Pearse et al. 2017, Wion et al. 2020, 2023). Instead, we found that while high seeding years indeed became less frequent towards the margins, the interannual variation becomes lower instead of higher towards the warm margin (or towards warm and cold margins for the alternative kCVp metric). Combined, these patterns signal more constant seed production towards the margins, not stronger masting. The patterns in the temporal autocorrelation are also indicative of more constant seed production. When there are few large seeding events (which happens towards the warm margins), this average relationship is determined mostly by pairs of subsequent low reproduction years. If populations shift from zero or extremely low seed output in low seed crop years to increased seed production in some of these years, the AR(1) would decrease, but the overall seed crop would become more constant. Overall, our results provide solid support that masting changes across climate gradients, but not in the way expected under the environmental stress hypothesis.

Our work helps to develop a clearer picture of how reproduction varies across climate space. Various studies have found that the number of flowers, fruits and seeds produced at the edge of the geographic distribution range were comparable to those produced at the geographic centre (Abeli et al. 2014, Pironon et al. 2017). However, in masting populations, reproductive outcomes depend not only on the number of seeds produced, but also on the temporal variability of these seed crops (Bogdziewicz et al. 2023). The more constant reproduction observed towards climate margins has many potential consequences for ecosystem dynamics. For example, less frequent mast years of large-seeded species like beech and oak lead to declines in seed consumer populations (Touzot et al. 2020). In addition to the general, across species, trends in masting variability across space, we find evidence that species-specific responses to climate gradients are diverse. This implies that the masting of some species is more responsive to climatic variation than others.

In this analysis, the spatial sampling was limited by the availability of long-term reproductive data. Future efforts which deliberately sample marginal populations over decades would be highly valuable, and would help to detect species-specific signals of stress on masting. However, such data are currently still limited. Regardless, our data were sampled across strong gradients, which, for the best-sampled species, cover the reported climatic envelope of the species (See Appendix S1: Section S2).

Our first large-scale assessment of within-species variation in masting shows that it can exceed the among-species variation. *Picea glauca*, for example, is a species that is typically associated with masting (i.e. high variability of seed production). Yet, we found that the CVp of populations of this species ranged from very high (3.34) to moderately low (0.93). This range is more than double the among-species range in mean CVp (0.89-1.94). Such high intraspecific variability provides further evidence of the pitfalls of classifying species as “masting” or “non-masting” (Kelly 2023), and illuminates the need for caution when working with species-level averages: such models implicitly assume that species means are meaningful, and that the intraspecific variation in the trait of interest is lower than the interspecific variation (Garamszegi 2014, Westerband et al. 2021). Moreover, the striking extent of intraspecific variation in masting suggests that the downstream consequences of masting may be more spatially variable than assumed. Given the important effects of masting on wider ecosystems, it is crucial that we develop a thorough understanding of what causes masting to vary so much between populations.

Masting at species climate margins was characterised by less frequent large-seeding years and lower interannual variation in seed production. The observed patterns might be explained by larger reproductive investment in small seed production years towards species margins, as has been observed for European beech (Müller-Haubold et al. 2015). Theory predicts that the costs of masting, such as the risk of dying before producing bumper cops, increases with decreased adult survivorship, and that longer periods between large seeding years elevate these costs (Waller 1979, Journé et al. 2023). Therefore, lower survival rates at marginal populations together with lower frequencies of producing large seeding years may translate into higher reproductive investment in low seed production years, a form of bet hedging in these more challenging environments. Moreover, lower benefits to masting may also occur in these sites if seed predator pressures are lower (Alexander et al. 2007, Vaupel and Matthies 2012). Future work considering masting variability alongside factors determining the cost - balance equation of masting benefits is therefore required.

The observed variance of masting patterns around the effects of climate marginality suggests that factors beyond climate contribute to intraspecific masting variability. The importance of local environmental effects was demonstrated in *Pinus ponderosa*, where intraspecific variation in masting was associated with stand characteristics including strand density, tree size and age (Wion et al. 2023). Plant ontogeny was also found to be an important determinant of masting in some temperate forest trees (Pesendorfer et al. 2020). If these stand characteristics explain a large proportion of variability in masting, then the effects of climate change on masting and the availability of viable seeds at the climatic margins might be alleviated through appropriate management strategies (Bogdziewicz et al. 2023). A limited number of studies indicate that additional reproductive variability is explained by provenance (Mark 1965, Caignard et al. 2021), but data from reciprocal transplant or common gardens established along climate gradients are still needed.

Due to the rapid accumulation of data on reproductive behaviours (Pearse et al. 2020, Hacket-Pain et al. 2022), we have been able to test the long-standing environmental stress hypothesis and unveil the remarkable within-species variation in masting. We find masting variation across climate space is inconsistent with the environmental stress hypothesis. High seed crop years are less frequent at the climatic periphery, but, importantly, the year-to-year variability of seed crops is lower towards the warm margin (or warm and cold margins for the alternative kCVp metric). As climate change may drive more populations to the climatic periphery, it is urgent that we establish if the spatial patterns observed here translate into temporal patterns. Recent work shows that this is not the case in European beech (Foest et al. 2024). Moreover, more work is required to establish if changes in masting result in lower reproductive efficiency. Lower interannual variation at marginal populations may translate into less effective predator satiation, higher losses to seed predators, and lower reproductive efficiency (Zwolak et al. 2022). The large unexplained variation around the effects of climate not only sets important challenges, but also offers management potential (e.g. managing stand age and structure). If the source of this variability results from stand characteristics, we may be able to develop appropriate management strategies to optimise reproductive efficiency.

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Author Contributions

JJF, AH-P and TC conceptualised the study, and JJF led the development of the methodology, with support from AH-P, IP and TC. Investigation, formal analysis and data visualisation were performed by JJF. JJF wrote the original draft, and all authors contributed critical feedback on the manuscript. AH-P provided supervision.

Conflict of interest statement

The authors declare to have no competing interests.

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Table section

Table 1: Relationships between environmental gradients and metrics capturing temporal reproductive patterns per tree species reported in the literature.

			Direction of effect		
Metric	**Gradient**	**Decrease**	**Neutral**	**Increase**	**Species**
CVp	Elevation	Masaki *et al.* (2020); Roland *et al.* (2014)			*Fagus crenata, Swida controversa; Picea glauca*
			Lázaro *et al.* (2006); Masaki *et al.* (2020); Mencuccini *et al.* (1995); Mooney *et al.* (2011)		*Buxus balearica; Quercus serrata, Castanea crenata, Prunus grayana; Picea abies; Pinus ponderosa*
				Buechling *et al.* (2016); Kelly *et al.* (2001); Kelly *et al.* (2008); Masaki *et al.* (2020); Sullivan and Kelly (2000); Webb and Kelly (1993)	*Picea engelmannii; Nothofagus solandri; Chionochloa pallens, Chionochloa macra; Quercus crispula; Chionochloa rubra; Subalpine plants*
	Elevation & latitude		LaMontagne *et al.* (2021)		*Abies, Picea, Pinus, Tsuga*
	Latitude		Pearse *et al.* (2020)		Global scale
	Nitrogen	Tanentzap *et al.* (2012); Smaill *et al.* (2011)			*Chionochloa spp.; Nothofagus solandri*
	Water availability	Espelta *et al.* (2008); Wion *et al.* (2020)			*Quercus humilis; Pinus edulis*
			Bogdziewicz *et al.* (2020); Espelta *et al.* (2008); Fernández-Martínez *et al.* (2012); Le Roncé (2021)		*Quercus ilex, Phillyrea latifolia, Arbutus unedo; Quercus ilex; Quercus ilex, Quercus pubescens; Quercus ilex*
CVi & S	Water availability		Wion *et al.* (2023)		*Pinus ponderosa*

AR(1)	Water availability	Barringer *et al.* (2013)			*Quercus lobata, Quercus agrifolia*
Periodicity	Elevation	Allen *et al.* (2012)			*Nothofagus solandri*
Mast frequency	Elevation	Mencuccini *et al.* (1995)			*Picea abies*
	Nitrogen			Tanentzap *et al.* (2012)	*Chionochloa spp.*

Reference details in Appendix S1: Section S1. CVp: coefficient of variation of population-level seed crop size; CVi: coefficient of variation of tree-level seed crop size; S = between-tree synchrony; AR(1): 1-year lagged autocorrelation.

Table 2: Relationships between climate variables and masting metrics CVp, AR(1) and Psd found using subject-centred annual average and seasonal models.

	CVp			**AR(1)**			**Psd**		
Term	**Estimate**	**z**	***P-value***	**Estimate**	**z**	***P-value***	**Estimate**	**z**	***P-value***
Annual									
AP	9.73×10^{-3} (3.07×10^{-2})	0.32	0.75	1.49×10^{-3} (1.29×10^{-2})	0.12	0.91	**9.67×10^{-3}** **(4.51×10^{-3})**	**2.14**	**0.03**
AP^2	-1.40×10^{-3} (1.38×10^{-2})	-0.10	0.92	-2.86×10^{-3} (5.32×10^{-3})	-0.54	0.59	-3.75×10^{-3} (2.03×10^{-3})	-1.84	0.07
MAT	**-6.21×10^{-2}** **(2.69×10^{-2})**	**-2.31**	**0.02**	**-3.45×10^{-2}** **(1.10×10^{-2})**	**-3.13**	**<0.01**	-1.31×10^{-3} (4.08×10^{-3})	-0.32	0.75
MAT × AP	1.43×10^{-2} (1.95×10^{-2})	0.73	0.47	-1.51×10^{-2} (9.75×10^{-3})	-1.55	0.12	2.37×10^{-3} (3.55×10^{-3})	0.67	0.50
MAT^2	-8.66×10^{-3} (8.77×10^{-3})	-0.99	0.32	9.95×10^{-3} (5.95×10^{-3})	1.67	0.09	**-4.23×10^{-3}** **(2.06×10^{-3})**	**-2.05**	**0.04**
Seasonal									
hq P	-4.08×10^{-3} (2.77×10^{-2})	-0.15	0.88	2.29×10^{-3} (1.09×10^{-2})	0.21	0.83	-1.74×10^{-3} (3.81×10^{-3})	-0.46	0.65
hq P^2	6.14×10^{-3} (1.22×10^{-2})	0.50	0.61	**-1.14×10^{-2}** **(3.98×10^{-3})**	**-2.87**	**<0.01**	1.35×10^{-3} (1.60×10^{-3})	0.84	0.40
hq T	5.15×10^{-3} (2.44×10^{-2})	0.21	0.83	2.32×10^{-4} (8.66×10^{-3})	0.03	0.98	-1.07×10^{-3} (3.21×10^{-3})	-0.33	0.74
hq T × hq P	-4.49×10^{-3} (1.83×10^{-2})	-0.25	0.81	**-2.18×10^{-2}** **(7.17×10^{-3})**	**-3.05**	**<0.01**	-2.91×10^{-3} (2.70×10^{-3})	-1.08	0.28
hq T^2	-5.03×10^{-3} (1.33×10^{-2})	-0.38	0.70	-1.79×10^{-3} (5.07×10^{-3})	-0.35	0.72	1.07×10^{-3} (1.91×10^{-3})	0.56	0.58
cq P	1.96×10^{-2} (3.15×10^{-2})	0.62	0.54	1.78×10^{-2} (1.25×10^{-2})	1.43	0.15	6.74×10^{-3} (4.87×10^{-3})	1.39	0.17
cq P^2	-1.36×10^{-2} (1.01×10^{-2})	-1.35	0.18	**-8.32×10^{-3}** **(3.79×10^{-3})**	**-2.20**	**0.03**	-2.23×10^{-3} (1.53×10^{-3})	-1.46	0.14
cq T	**-1.02×10^{-1}** **(4.45×10^{-2})**	**-2.30**	**0.02**	**-5.96×10^{-2}** **(1.92×10^{-2})**	**-3.10**	**<0.01**	8.26×10^{-3} (5.98×10^{-3})	1.38	0.17
cq T × cq P	**4.46×10^{-2}** **(2.11×10^{-2})**	**2.11**	**0.03**	8.31×10^{-3} (1.40×10^{-2})	0.59	0.55	3.42×10^{-3} (4.53×10^{-3})	0.75	0.45
cq T^2	-4.68×10^{-3} (1.45×10^{-2})	-0.32	0.75	7.67×10^{-3} (8.76×10^{-3})	0.88	0.38	**-8.13×10^{-3}** **(2.53×10^{-3})**	**-3.21**	**<0.01**

Standard errors within parentheses. P-values were calculated with Wald tests via the summary() function. For linear predictors, these p-values reflect conditional hypotheses and should not be interpreted as evidence of independent contributions due to the inclusion of quadratic terms as I(x^2). Significant effects are in bold, and underlined values indicate that the independent linear predictor was also significant in likelihood ratio tests comparing a model with the predictor (excluding interactions and quadratic terms) to one without it, to test the independent contributions. These likelihood ratio results can be found in Appendix S1:

Table S2. Abbreviations = CVp: coefficient of variation of population-level seed crop size; AR(1): 1-year lagged autocorrelation; Psd: the proportion of large seed production years; AP: annual precipitation; MAT: mean annual temperature; hq: hottest quarter; cq: coldest quarter; T: temperature; P: precipitation.

Table 3: Summary of main findings, showing if the relationship between climate and masting metrics matched predictions under the environmental stress hypothesis.

	Environmental stress hypothesis			
Metric	Prediction	Climate variable	Supported	Results
Psd	Less frequent masting in more marginal climates	MAT	Yes	Less frequent masting in cool & warm sites
		AP	Partially	Less frequent masting in dry & wet sites, but not significant
AR(1)	More negative autocorrelation in more marginal climates	MAT	No	More negative autocorrelation in warm sites
		AP	No	No significant effects
CVp	Higher variability in more marginal climates	MAT	No	Lower variability in warm sites
		AP	No	No significant effects
kCVp	Higher variability in more marginal climates	MAT	No	Lower variability in cold & warm sites
		AP	No	No significant effects

Psd: the proportion of large seed production years; AR(1): 1-year lagged autocorrelation; CVp: coefficient of variation of population-level seed crop size; AP: annual precipitation; MAT: mean annual temperature.

Figure caption section

Figure 1: Intraspecific variation in masting metrics often exceeds interspecific variation. The shaded grey rectangle indicates the interspecific range in metric values. The colours of the violin plots indicate plant families, with blue-greens reserved for gymnosperms and orange-reds for angiosperms. CVp: coefficient of variation of population-level seed crop size; AR(1): 1-year lagged autocorrelation; Psd: the proportion of large seed production years. See Fig. 2 for genus names.

Figure 2: Within-species variation in masting metrics covers a large part of across-species masting metric space for some, but not all tree species. The top-left plot shows how three metrics co-vary (CVp: coefficient of variation of population-level seed crop size; AR(1): 1-year lagged autocorrelation; Psd: the proportion of large seed production years). Dashed-line convex hull: variation of CVp and AR(1) across all analysed species. Solid-line convex hull: the CVp and AR(1) metric space of all 378 species (1,018 time series) in MASTREE+ with time series matching subsetting criteria, irrespective of whether they had adequate spatial replication for inclusion in our analyses. Species-specific metric space is shown in surrounding plots. Percentages in the top-right corner of plots show the ratio of the solid to dashed convex hull area. Outlined time series in the top-left plot are plotted in the 'Subsample' plots (3 random time series [1960-2020] per region; regions marked with 1-3 and A-C) to illustrate example time series. Example time series are scaled by their maximum value.

Figure 3: Climate marginality explains variation in masting, but patterns diverge from predictions under the environmental stress hypothesis. The three columns on the left show response surfaces for the subject-centred models of masting metrics CVp, AR(1) and Psd (CVp: coefficient of variation of population-level seed crop size; AR(1): 1-year lagged autocorrelation;

Psd: the proportion of large seed production years) at baseline levels of the centred and scaled predictor variables. The annual average model is found in the first column, and the results of the seasonal model (hq: hottest quarter; cq coldest quarter; T: temperature, P: precipitation) are found in columns 2-3. The boundaries of the response surfaces in columns 1-3 were determined by a convex hull of climate data of the time series (open circles). The right-most column shows an alternative representation of the annual model found in the first column. Specifically, it shows the marginal effects (and associated 95% confidence intervals, shaded) for mean annual temperature (MAT) at different levels of annual precipitation (AP; blue colours) in the annual CVp, AR(1) and Psd models, alongside partial residuals. Spp.: species.