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Vegetation Ecology

Reconstruction of *Araucaria araucana* cone production reveals warming intensifies regionally synchronized masting

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Abstract

The reproduction of many long-lived plants is highly variable and synchronized, known as masting. Masting is a key driver of plant regeneration dynamics and has cascading effects on food webs and carbon and nutrient fluxes through ecosystems. Masting patterns can respond to changes in climate, but natural long-term variability in masting behavior (i.e., baseline variability) is poorly understood. Here we use tree-rings to create a four-century reconstruction of annual cone production to uncover centennial-scale evolution in masting of *Araucaria araucana*, a dioecious masting species in South America. Over the last four decades, direct observations of annual cone production in this species revealed remarkable range-wide synchrony of masting. Our tree-ring-based reconstruction places this in a long-term context, revealing that intense regional masting is not a consistent feature of *A. araucana* reproduction. For extensive periods over the last four centuries, masting has been a site-specific phenomenon, with variability in cone production that was not regionally synchronized. Comparison with regional climate reconstructions indicates that regional synchrony of masting varies with regional temperature trends, including during recent decades. During warmer periods, synchrony is enhanced, and during cooler periods, regional synchrony breaks down. These dynamics have implications for understanding the reproduction of this iconic and endangered tree species and provide evidence of long-term linkages between climate change and masting behavior. Our study demonstrates the potential for novel tree-ring-based reconstructions of masting to reveal crucial insights into baseline variability and the response of masting to climate change.

KEYWORDS
climate change, dendrochronology, dendroecology, mast seeding, Patagonia, synchrony

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INTRODUCTION

Many long-lived plant species are characterized by variable reproduction that is synchronous within and among populations, commonly described as masting (Kelly, 1994). During years of peak reproductive effort (so-called mast years), seed crops synchronize from local to large scales (Figure 1) (Pesendorfer et al., 2021). Masting enhances pollination efficiency through the synchronization of large flowering efforts (Kelly et al., 2001) and reduces seed predation via starvation in poor reproductive years and subsequent satiation of predators in large reproductive events (Shepherd et al., 2008; Zwolak et al., 2022). The reproductive success of masting plants is therefore strongly linked to patterns in seed crop synchrony and variability (Martini et al., 2022; Sanguinetti & Kitzberger, 2010; Seget et al., 2022). Masting patterns have cascading effects on the dynamics of food webs (Clark et al., 2019; Liu et al., 2022; Touzot et al., 2020) and the behavior of seed-eating animals (Ascoli et al., 2021; Blanco et al., 2022; Strong et al., 2015; Szymkowiak & Thomson, 2019) and alter the allocation and fluxes of nutrients through ecosystems (Brumme et al., 2021).

Recent analysis of multi-decadal observations of masting suggests that masting patterns can shift in response to changes in climate (Hacket-Pain & Bogdziewicz, 2021). These long-term changes occur at local (Pearse et al., 2017; Shibata et al., 2020) and regional scales (Ascoli et al., 2020; Bogdziewicz et al., 2020; Meng et al., 2022) and have important consequences for plant reproductive success (Bogdziewicz, Kelly, et al., 2023) with wider cascading effects on ecosystems (Touzot et al., 2020). However, natural long-term variability in masting behavior (i.e., baseline variability) is poorly understood due to limited long-term observational records, which makes it challenging to place recent trends in context (Prebble et al., 2022; Shibata et al., 2020). Centennial-scale records of masting are limited to ordinal classification of seed crops (Ascoli et al., 2017; Hacket-Pain et al., 2022), or dendrochronological or palynological reconstructions that only distinguish mast and non-mast years, which unrealistically assumes that masting is bimodal (Drobyshev et al., 2014; Mundo et al., 2021; Prebble et al., 2022) (Figure 1C). Nevertheless, these reconstructions indicate long-term changes in masting behavior may be linked to changes in local and regional variation in climate (Ascoli et al., 2017; Mundo et al., 2021; Prebble et al., 2022).

Previous attempts tree-ring based masting reconstruction have illustrated the scale of the challenge (Drobyshev et al., 2014, for the monoecious *Fagus sylvatica*, Mundo et al., 2021, for the dioecious *Araucaria araucana*). Tree-ring based masting reconstructions have focused on detecting mast years via declines in radial growth associated with high investment in cones, fruit, and seed production, commonly interpreted as resource switching or a growth-reproduction trade-off. Major challenges have included weak or inconsistent masting signals in tree-rings (Koenig et al., 2020; Patterson et al., 2023; Speer, 2001) or the challenge separating masting signals from weather-induced variability (Hacket-Pain et al., 2017; Rodríguez-Ramírez et al., 2019). A promising approach is to use "non target" trees to remove the common climate signal from tree-ring chronologies while retaining the masting signal, similar to the widely used dendroecological approach for reconstructing insect outbreaks (Swetnam et al., 1985). In dioecious trees, a variant on this approach can be used to reconstruct masting, exploiting known sex-specific tree-ring signals associated with masting (Hadad, Roig, et al., 2021; Mundo et al., 2021; Rozas et al., 2019). If the costs of reproduction vary between males and females, either in the magnitude or timing, then masting is recorded as divergence between the growth of male and female trees.

Here, we develop a new and robust four-century reconstruction of annual cone production and uncover centennial-scale evolution in regional masting of *A. araucana*, a dioecious tree species in southern South America. We show remarkable range-wide synchrony of masting in recent decades is not a consistent feature. For extensive periods over the last four centuries, masting has been a site-specific phenomenon, with variability in cone production that was not synchronized regionally. Comparison with regional climate reconstructions indicates that regional synchrony is low during periods of cooler climate, but the mechanisms resulting in the variation in synchrony remain to be fully established.

METHODS

Masting data

We extracted data to reconstruct *A. araucana* masting from MASTREE+, a global compilation of population-level time series of reproductive effort (Hacket-Pain et al., 2022). MASTREE+ contains time series for annual *A. araucana* reproductive effort collected using three methods: female cone count per individual, cone counts per unit area, and annual seed harvests. Individual series range from 11 to 20 years (mean = 16.2, median = 17) and represent populations from across the species distribution, mainly on the leeward side of the Andes (Figure 1B). The time series show strong spatial synchrony of masting across the study region, consistent with Sanguinetti and Kitzberger (2008). To create a regional masting chronology, time series were standardized on a 0–100 scale. For the

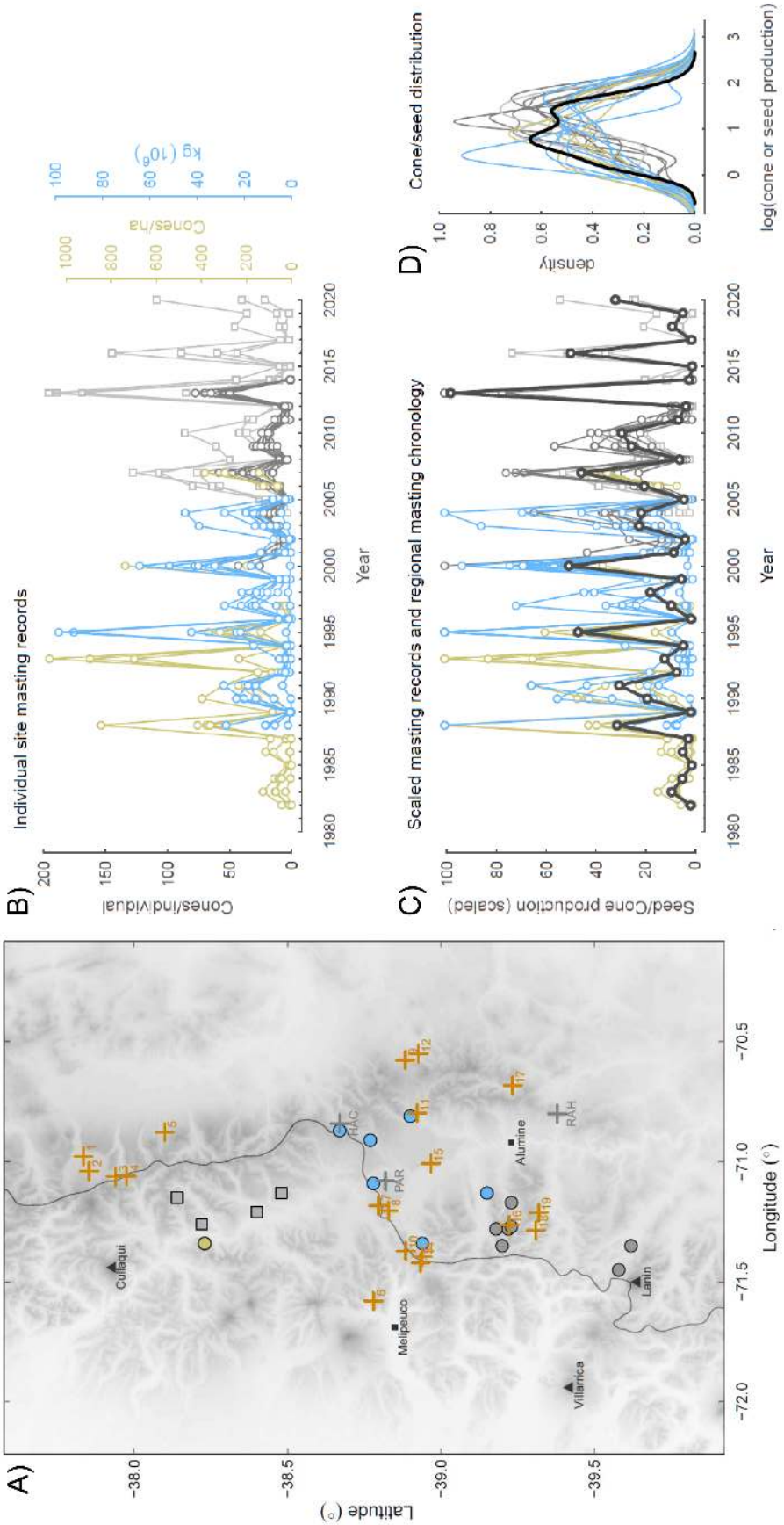


FIGURE 1 Study location and masting time series. (A) Map showing the location of *Araucaria araucana* masting time series (solid symbols, colors correspond to B–D) and tree-ring series (orange crosses; site numbers correspond to Appendix S1: Table S1). Gray crosses indicate the locations of the Mundo et al. (2021) sample sites. (B) *Araucaria* masting time series from MASTREE+ (Hacket-Pain et al., 2022), plotted according to the original units. (C) Scaled masting time series, with the mean regional Mast Index in black. (D) Distribution of scaled masting time series.

reconstruction, standardized masting time series were log transformed to improve normality, and then averaged to create a regional "Mast Index" (Figure 1C). When combined, these records provide a 39-year record of regional masting (1982–2020). However, the first 6 years are based exclusively on data from three directly adjacent plots from a single site in Chile (Figure 1A). All other years are represented by multiple sites, so the years 1982–1987 were excluded from analysis as we could not be confident that they represented regional masting. We used the resulting 1988–2020 regional Mast Index chronology for all subsequent analysis.

Tree-ring data

Tree-ring data were assembled from 19 sites distributed in a broad region overlapping with the regional mast record (Figure 1A). Ten to 60 dominant trees were sampled per site, and two or three increment cores were extracted per tree (Appendix S1: Table S1). *A. araucana* is a dioecious species, and the sex of each sampled trees was recorded based on the presence of male or female strobiles. Tree cores were polished in transverse section and individual tree-ring series were visually cross-dated. Ring widths were measured using a Velmex measuring device with a precision of 0.001 mm, and cross-dating was checked using COFECHA (Holmes, 2001). Raw ring width chronologies contain low-frequency signals associated with changes in tree size and age, canopy position and long-term changes in environmental conditions (Fritts, 1976). As we were focused on the masting signal contained in these chronologies, rather than long-term trends in absolute growth, we removed low-frequency variance using the dplR package in R (Bunn, 2008). Each series was fitted with a 32-year cubic smoothing spline with a 50% frequency cutoff, and dimensionless ring width indices (RWIs) were calculated by dividing measured ring width by the fitted spline. Multiple series from the same tree (i.e., multiple cores) were averaged at the tree level. As we predict that juvenile trees should not contain a masting signal (as they are not producing cones, Donoso et al., 2009; Hadad et al., 2020), we removed the first 50 years of ring width measurements from each individual tree. Finally, we averaged across trees to produce male and female mean RWI chronologies for each site. Each sex-specific site chronology was truncated when the number of trees dropped below three individuals. As our masting reconstruction method depends on a first-difference male–female chronology (see below for details), our analysis should be insensitive to detrending choices, and our results and conclusions were unchanged when we repeated analysis with less flexible 64- and 128-year smoothing splines (results not shown). Similarly, our analysis should be insensitive to temporal changes in growth variance, so long as any variance changes affect male and female trees similarly. Nevertheless, the variance of each male and female site RWI chronology was stabilized by dividing the RWI series by the SD of a moving 33-year window. Our results and conclusions were unchanged if this step was excluded or if the size of the moving window varied (results not shown).

In the Southern Hemisphere, tree-rings are conventionally dated to the calendar year at the start of the growing season (the Schulman convention). However, we re-dated all tree-ring records to be consistent with the masting record, which is dated according to the time of seed fall (i.e., Schulman year +1).

Model calibration and validation

Previous analyses have demonstrated that *A. araucana* tree-rings contain sex-specific masting signals (Hadad, Roig, et al., 2021; Mundo et al., 2021; Rozas et al., 2019). High cone production results in reduced growth in both male and female trees, but the main costs of reproduction are offset by 1 year between sexes (Hadad, Roig, et al., 2021). In female trees, the cones take 2 years to develop. In the first year, female cones develop and are fertilized by pollen originating from male trees. However, the female cones are not fully developed during this growing season, and only mature and eventually disperse seed at the end of the following growing season (Figure 2). Significant growth reductions in female trees are associated with the year of seed cone maturation (and dispersal). In male trees, the growth reduction occurs in the previous year, during male pollen cone development (Donoso et al., 2009; Hadad, Roig, et al., 2021) (Figure 2A). The magnitude of the growth reductions is similar in male and female trees (Figure 2B), albeit offset by 1 year. Consequently, while the main direct climate drivers of growth affect male and female trees similarly in the same year (e.g., drought years), high cone production is associated with a distinctive growth reduction which is offset in male and female trees by 1 year (Hadad, Roig, et al., 2021; Mundo et al., 2021). We used this signal as the basis for a reconstruction of annual cone production (masting). Our basic approach is similar to the host–non-host approach to reconstructing insect outbreak, where differences in growth between a host and non-host species are used to identify insect outbreaks in the host species (Swetnam et al., 1985; Swetnam & Lynch, 1989). In our case, we use the temporally offset masting signals in male and female chronologies to isolate a target masting signal

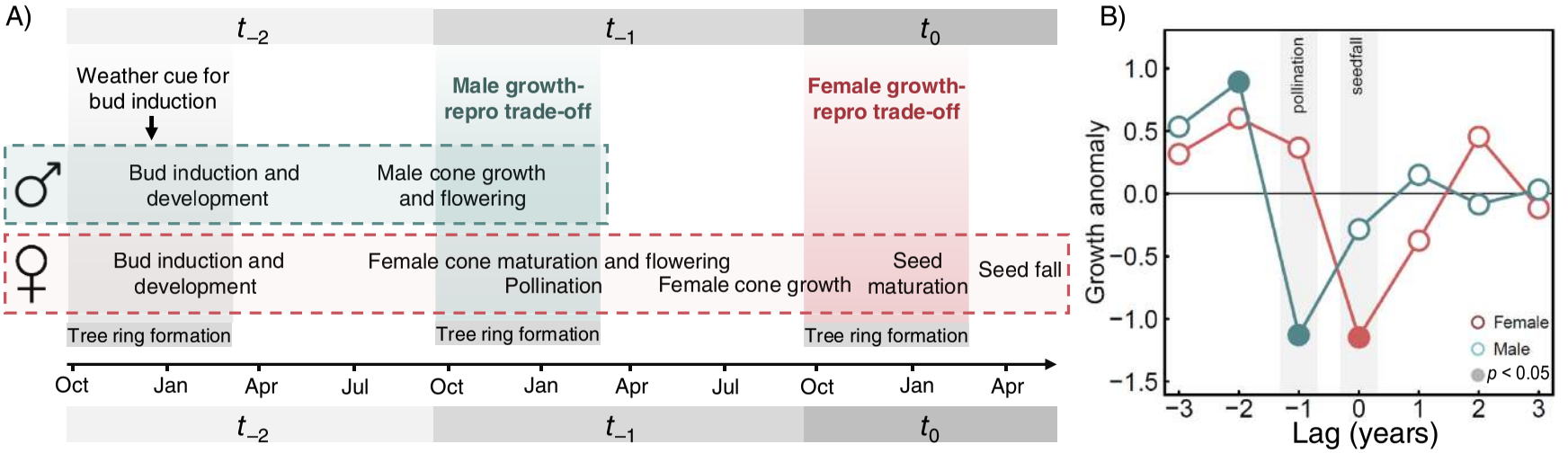


FIGURE 2 Schematic representation of the reproductive cycle of *Araucaria araucana* and the tree-ring-based reconstruction approach. (A) Cone development is a multi-year process (Donoso et al., 2009), and pollination occurs the year before (female) cone maturation and seed fall. The main costs of reproduction are offset by 1 year between male and female trees. Years are indicated according to the start of the annual growing season. (B) Due to the temporal offset in the main costs of reproduction, tree growth anomalies associated with masting in males and females occur in successive years, forming the basis of masting reconstruction (modified from Hadad, Roig, et al., 2021).

from non-target variability in growth (i.e., the variability related to varying weather conditions). Years of high seed production are associated with a distinct pattern in the tree-ring chronologies: first a year of low male growth relative to female growth, directly followed by a year of low female growth relative to male growth (Figure 2B). The sensitivity of male and female growth to monthly temperature and precipitation was very similar (Appendix S4), suggesting that varying growth responses to climate do not contribute to observed divergences between female and male growth (see Appendix S4).

In our case, the masting signal is expressed as the difference in growth between the two sexes, so we subtracted the female chronology from that of the male trees ($RWI_{male} - RWI_{female}$) for each site. This is not only positively correlated with female cone production but also displays a negative autocorrelation at a lag of 1 year, due to the opposite offset of growth responses of male and female trees in the previous year (Figure 2B). Consequently, in a final step we calculated a first difference chronology (i.e., year X_t − year X_{t-1}), which combines the masting signals present in the male trees ($t - 1$) and the female trees (t). This is positively correlated with female cone production. Differenced chronologies were normalized to ensure equal weighting, then averaged across sites to develop a regional chronology. We used this regional chronology as the basis of our masting reconstruction. The regional chronology was truncated where the number of individual sites represented dropped below five (1645 CE).

The relationship between the first difference chronology and Mast Index was quantified using a general linear model, which was used as the basis for our masting reconstruction. As we had only 33 years of overlapping tree-ring and masting observations (1988–2020), splitting our data into independent calibration and validation periods was not practical. Instead, we estimated model accuracy using a bootstrap resampling method, repeatedly fitting our calibration models to 500 resampled subsets of our data. Using this procedure, we estimated the SE of the coefficients in our reconstruction model and used this to estimate the uncertainty in our reconstruction. We also tested relationships at site level, and tested whether between-site differences were related to geography, elevation, climate, or the age and growth rate of sampled trees (see Appendix S2).

We quantified temporal change in our reconstruction of masting using the CV, a moving window approach, and wavelet analysis using the WaveletComp package (Roesch & Schmidbauer, 2018). As our site-level tree-ring chronologies did not correspond to the same locations as the site-level cone production data, we could not calibrate site-level masting reconstructions. Instead, we assumed that site-level first difference M–F chronologies were a proxy for site-level cone production. We use these site-level proxies to investigate individual-level changes in reproductive variability using CV, and we tested for changes in the synchrony of cone production among sites by calculating the mean pair-wise correlation using moving windows. Regional synchrony defined using this approach might be affected by changes in the mean distance between sites over time, as some sites have shorter chronologies and are consequently not included in the analysis of the earliest period (Appendix S1: Table S1). Consequently, we also tested for temporal changes in the distance-decay of synchrony using Mantel correlograms for different time periods. We used regional drought and temperature reconstructions to explore whether changes in masting were related to changes in regional climate (Ahmed et al., 2013; Hadad, Gonzalez-Reyes, et al., 2021; Morales et al., 2020; Mundo et al., 2012).

RESULTS

Our first difference M–F chronology was linearly and strongly positively correlated with Mast Index for the period 1988–2020. Overall, our model explained 64.4% of the observed variance in Mast Index during the calibration period (1988–2020) as estimated by the bootstrapping procedure (Appendix S1: Table S2). The model performed well in reproducing the observed magnitude of large regional mast events, and successfully reproduced the interannual variability of observed regional cone production. The model performed less well at reproducing the full magnitude of the reproductive failures that often follow large mast years, particularly in 1989, 1996, 2014, and 2017 (Figure 3B). However, as Mast Index represents log-transformed cone production, the overestimation in terms of cone production is small (Appendix S1: Figure S1).

At the site level, the relationship between our male–female first difference chronology and Mast Index varied in strength but was positive at all sites (Appendix S2). The variation in site-specific masting signal was unrelated to geography or elevation. There was some evidence that the masting signal was stronger in tree-ring chronologies from sites with faster growing and younger trees (Appendix S2). As we only had 19 sites, and mean site age and growth rates were strongly correlated, we further investigated this at the individual-tree level. Comparing individual-level growth with the regional masting chronology, we found no evidence for age or growth-rate-related effects on the masting signal within sites. As we do not yet understand why some sites have stronger masting signals than

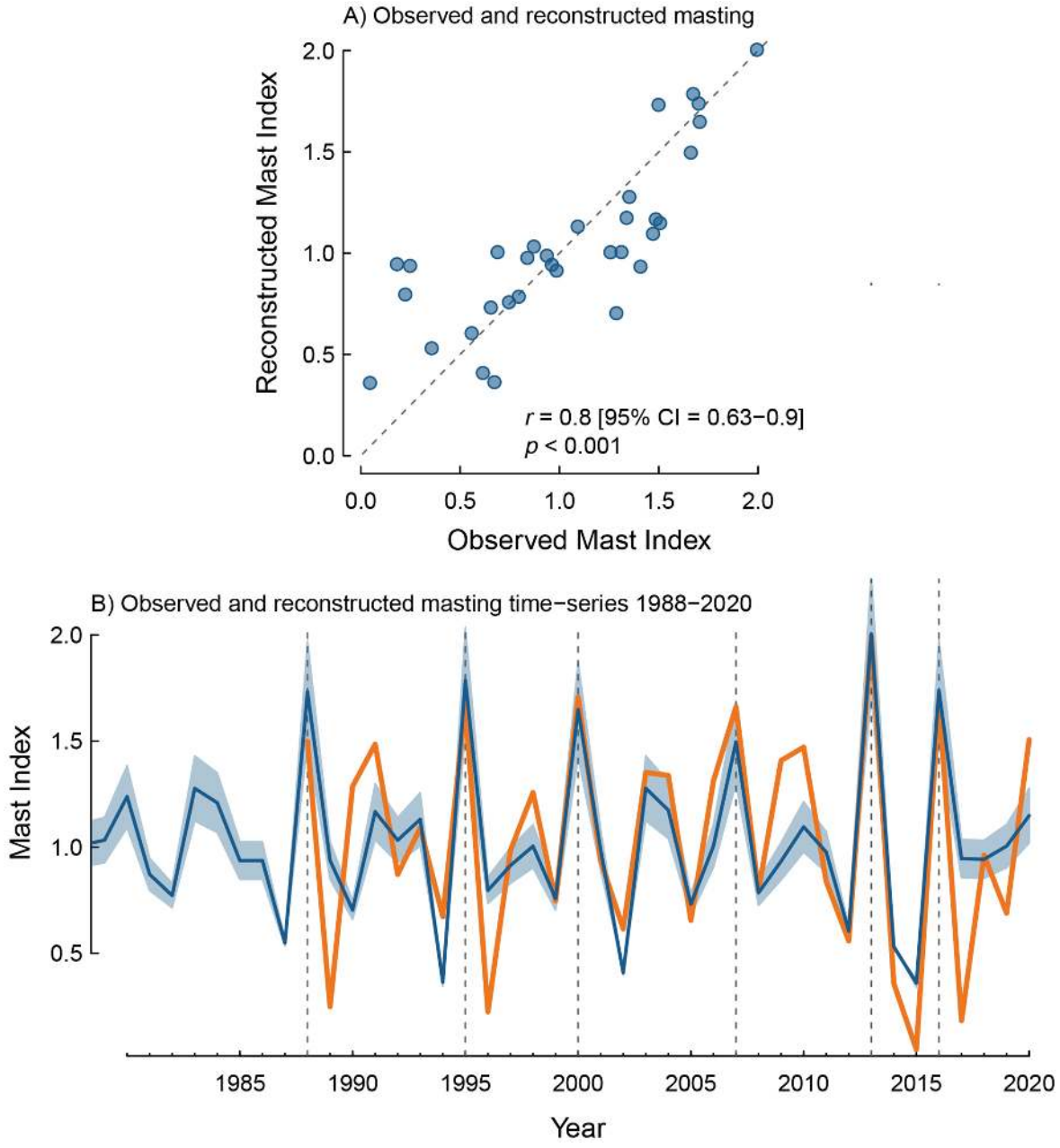


FIGURE 3 Regional *Araucaria araucana* masting reconstruction. (A) Observed and reconstructed Mast Index for the period 1988–2020. The dashed line shows the 1:1 line. (B) Comparison of observed (orange) and reconstructed Mast index (blue) time series. The shaded area around the reconstruction represents the uncertainty estimated using bootstrapping. Large observed regional mast events are indicated by the vertical dashed lines.

others, and this effect was not found at the individual tree level within sites, we conservatively retained all individual sites in the regional chronology used for the reconstruction. Restricting our regional chronology to sites with stronger masting signals had little effect on our reconstruction (Appendix S3).

The strong relationship between our first difference male–female chronology and Mast Index allowed us to reconstruct 376 years of regional masting in *A. araucana* (Figure 4). Our chronology extended to 1645 CE with representation from a minimum of five sites, and to 1748 CE with replication of 10 sites. Our reconstruction showed that masting characterized the reproductive behavior of *A. araucana* over multiple centuries, but that the intensity of regional masting varied substantially at decadal to centennial timescales. Recent decades were associated with more strongly synchronized regional masting than at any other period over the past four centuries, that is, higher values in regional synchrony and regional CV indexes (Figure 4B) and significant 4- to

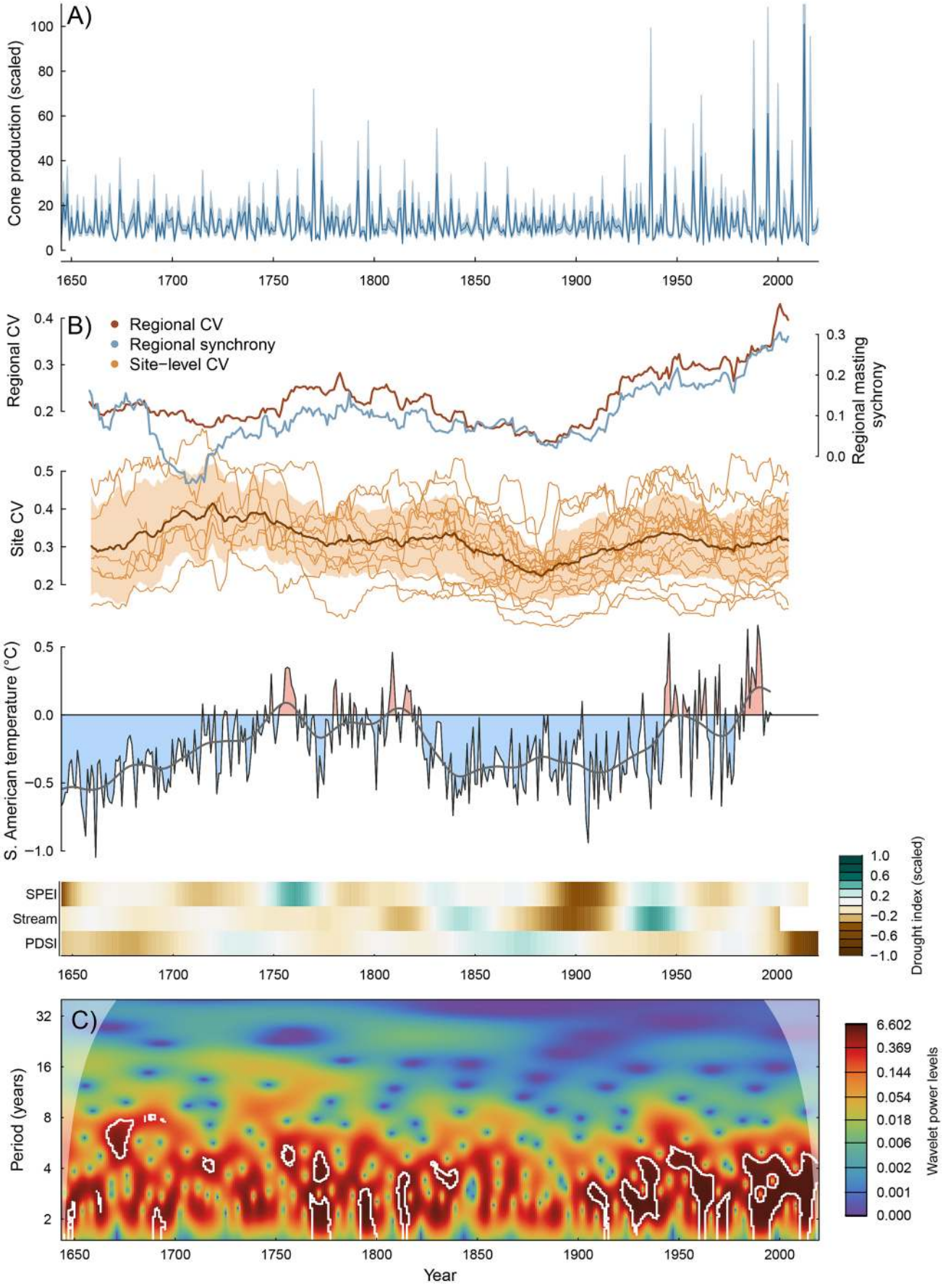


FIGURE 4 Legend on next page.

5-year periodicity (Figure 4C). The reconstruction revealed 12 exceptionally large regional masting events with reconstructed regional cone production more than two SD above the mean, and nine of these occurred during the last century (1937, 1944, 1958, 1962, 1988, 1995, 2000, 2013, 2016), including the largest event in the last four centuries (2013). A smaller increase in regional masting also occurred during the late 18th and early 19th century, which included three further large regional mast events (1770, 1780, and 1831). The reconstruction revealed that between these episodes, long periods occurred without large synchronized regional mast events (Figure 4A). For example, the periods 1645–1769 and 1861–1931 were associated with very low intensity regional masting (30-year moving window CV_r of Mast Index <0.25). The latter of these periods includes an exceptional 57-year period (1867–1923) without a single large regional mast event.

The changes in regional masting over multiple decades could reflect at least two contributing processes. It may reflect synchronized changes in population-level masting (i.e., CV_p) (Bogdziewicz et al., 2020) or changes in the regional synchrony of masting (Ascoli et al., 2017). To test which of these two processes might be responsible for the observed changes in regional masting, we compared long-term changes in individual-site first-difference chronologies. As these site-level chronologies could not be calibrated to observed site-level cone production data (see *Methods*), we assumed that they represent a proxy of site-level cone production. Individual site chronologies showed some long-term variation in CV_p that after 1850 matched the regional CV_r pattern, with a decline in CV around 1900 and a positive trend over the last century (Figure 4B). Nevertheless, this was insufficient to explain the large trends in regional CV_r, which were instead explained by temporal variation in the degree of among-site synchrony (Figure 4). The recent period, characterized by the occurrence of large regional masting events, was also characterized by higher regional synchrony of reproduction than at any period over the previous four centuries (Figure 4; Appendix S1: Figure S2). Together, these results demonstrate the rarity of large regional mast events in the past appeared to be mainly due to lower spatial synchrony. Large magnitude masting events still occurred in individual populations, but they did not occur synchronously across populations; the period 1670–1770 exemplified this, with higher CV_p indicating strong masting at the population level, but low regional synchrony preventing this local-level strengthening of masting from scaling to stronger regional masting.

The recent changes in cone production variability and spatial synchrony are not matched by a parallel change in radial growth variability or synchrony, as indicators of physiologically relevant environmental variability and its spatial synchrony (Appendix S1: Figure S3). Peaks in synchrony and variability of radial growth occurred in the early 19th century, and at the start of the 20th and 21st centuries, but these did not consistently correspond with the reconstructed temporal changes in masting.

Notably, long-term variations in cone production variability and spatial synchrony corresponded to long-term changes in regional temperature, but not to regional drought (Figure 4). Peaks in the strength of regional masting (CV_r) corresponded to periods of increased regional temperature around 1800 CE and during recent decades, while regional masting was weaker during cooler regional temperatures around 1900 CE. In contrast, the dip in site-level CV_p and regional masting synchrony around 1900 corresponded to a major regional drought phase (Figure 4), and a similar correspondence was absent in the earlier part of the reconstruction.

DISCUSSION

Our reconstruction of four centuries of regional masting of *A. araucana* shows that the reproduction of this species has been characterized by remarkably synchronized variation in cone production during the last

FIGURE 4 Long-term change in regional cone production variability and synchrony. (A) 376 years of reconstructed cone production (i.e., back-transformed from Mast Index). (B) Long-term evolution of cone production variability and synchrony, and regional climate change. Solid lines show the 30-year moving window of regional CV_r (red) and regional synchrony (blue). Orange lines show individual site CV_p, and the dark orange line the mean site CV_p with the shaded area representing ±1SD. All moving window values are plotted according to the mid-point of the 30-year window. Regional summer temperature change from PAGES2K reconstruction (Ahmed et al., 2013) (gray line, with anomalies colored according to the 1961–1990 mean), and regional drought trends for three reconstructions, plotted as the 64-year smoothed spline to emphasize low-frequency variability. SPEI is a NW Patagonian reconstruction of $SPEI_{Nov–Dec}$ from Hadad, Gonzalez-Reyes, et al. (2021), Stream is an October–June mean streamflow reconstruction for the Neuquén River from Mundo et al. (2012), and PDSI is a regional $PDSI_{Dec–Feb}$ reconstruction from the South American Drought Atlas (Morales et al., 2020). Note that only the PDSI reconstruction extends to 2020, but the most recent two decades are characterized by ongoing regional drought (González-Reyes et al., 2017). (C) Wavelet analysis of Mast Index. White contours designate significant wavelet power ($p < 0.1$), and the lighter shading shows the cone of influence where edge effects become important.

century—that is, large-scale synchronized masting across populations separated by more than 100 km and across strong environmental gradients. Combined with high variability in cone production at individual sites, which our results indicate was generally maintained throughout the past four centuries, this has resulted in a recent phase of exceptionally intense regional masting. This phase of intense masting is observed in direct observations since the 1980s, and our reconstruction shows it started in the first half of the 20th century. Similar large-scale spatial synchrony of reproduction was observed between the mid-18th and mid-19th centuries (albeit not as pronounced), but at other times, the regional synchrony of masting of *A. araucana* is lost. This is consistent with the analysis of an independent reconstruction of *A. araucana* masting at three locations within our study region, which also showed high synchrony in recent decades but lower synchrony in the past (Mundo et al., 2021).

High spatial synchrony of masting is associated with shared weather cues and the Moran effect (Bogdziewicz, Journe, et al., 2023). This implies that the elevated regional synchrony and subsequent strengthening of regional masting during warm phases reflected changes in sensitivity to dominant weather cues or changes in the spatial synchrony of these cues. Years of high cone production in *A. araucana* are linked to drought conditions during cone bud induction 2 years prior to seed dispersal (Mundo et al., 2021; Sanguinetti & Kitzberger, 2008; see also Figure 2), in association with the behavior of Pacific sea surface temperature (SST) and land surface temperature (Hadad, Roig, et al., 2021). Insufficient local meteorological records prevent direct testing of long-term changes in regional climate synchrony. However, changes in the variability and spatial synchrony of tree growth did not covary with changes in masting, which is relevant as radial growth varies according to physiologically relevant summer climate (Hadad & Roig, 2016). Therefore, we infer that changes in climate synchrony are unlikely to fully explain changes in masting synchrony. Instead, we suggest that the temporal alignment of cues may explain changes in regional synchrony (Ascoli et al., 2021) similar to the drivers of decadal variability in large-scale synchrony of *F. sylvatica* masting in Europe (Ascoli et al., 2017). For example, in addition to the main summer drought cue for cone development (Mundo et al., 2021; Sanguinetti & Kitzberger, 2008), we hypothesize that severe frost events might damage and kill developing cones, and regional frost frequency increased around 1700 and 1900 (Hadad et al., 2019), coincident with periods of low regional masting synchrony. Regional drought could also influence synchrony by affecting the rate at which trees can replenish reserves depleted during masting events, determining their ability to respond to the drought cue for cone induction (Bogdziewicz, 2021). The effects of frost vetoes or drought-influenced resource recovery would vary between sites depending on local site conditions, which vary markedly across strong local environmental gradients (Allevato et al., 2019; Hadad et al., 2019; Piraino et al., 2022). Changes in the regional climate circulation due to the nonstationary interaction between large-scale modes of climate variability could also lead to different spatial synchronization of weather cues in different time periods (Ascoli et al., 2021). Mundo et al. (2021) provide evidence for a regional synchronizing mechanism of masting which is induced by strong cold La Niña phases of El Niño/Southern Oscillation (ENSO) amplified by the positive phases of the Southern Annular Mode (SAM). Long-term changes in both modes of climate variability (Abram et al., 2014) might have affected the synchronization of masting weather cues in the region. Nevertheless, while it appears that regional synchrony is enhanced during warm phases, including during the remarkable and unprecedented increase in regional masting synchrony over the last century, the mechanism linking regional synchrony and temperature remains unclear. Establishing this mechanism is a major priority, especially given recent reports consistent with a masting breakdown in *A. araucana*, which imply a nonlinear or threshold response of masting to climate change (Mundo et al., 2021). While the warm phases around 1800 CE and in recent decades are both associated with stronger regional masting in our reconstruction, future reconstructions taking advantage of the exceptionally long maximum lifespan of *A. araucana* present an opportunity to test the response of masting during an earlier—and much longer—warm phase lasting from the mid-12th to mid-14th centuries CE (Ahmed et al., 2013).

Methods to reconstruct masting over centennial timescales are revealing hitherto unknown long-term variability in masting behavior. Reconstructions that enable the extension of observation masting records provide a unique opportunity to improve understanding of baseline variability (Prebble et al., 2022) and place recent reports of changes in masting in a long-term context (Hacket-Pain & Bogdziewicz, 2021). For example, pollen concentrations in annually laminated sediments (Prebble et al., 2022) or tree-ring proxies (Drobyshev et al., 2014; Mundo et al., 2021) have been used to identify decadal- to centennial-scale changes in the frequency of mast years. In our reconstruction, we also show changes in the frequency of exceptionally large regional cone production events, including an unprecedented concentration of such events in the last century, associated with a warming regional climate (Figure 4). However, the approach of previous studies, focusing on the identification of mast

events (Drobyshev et al., 2014; Mundo et al., 2021), simplifies masting to a binary mast-non-mast characterization, hiding important components of masting (Kelly, 1994), especially where reproductive effort is not bimodally distributed. Importantly, our reconstruction approach demonstrates the potential to reconstruct cone production on a continuous scale, containing substantially more information on past changes in masting behavior. Nevertheless, further work is still required to address remaining uncertainties. Understanding the underlying cause of the variability in masting signals among trees and sites is a priority (Hadad, Roig, et al., 2021). We initially explored that variability, but we were not able explain why some sites (and trees) have stronger masting signals than others. Analysis that uses tree-ring chronologies sampled from the same stands where long-term cone production data have been collected offers potential to address this uncertainty, and analyses pairing individual-level records of masting and growth will prove particularly valuable. Similarly, in our analysis we rely on records of female cone production, but records of male cone production (or pollen concentration, as a proxy) (Díaz et al., 2012) will increase further confidence in our interpretation of masting signal found in tree-ring chronologies, which underpins our approach to reconstruction.

Tree-ring-based reconstructions of masting depend not only on the presence of strong signals in tree-ring chronologies (Hadad, Roig, et al., 2021; Mundo et al., 2021; Patterson et al., 2023; Speer, 2001) but also on the ability to distinguish growth responses related to masting from other drivers of growth (Drobyshev et al., 2014; Hacket-Pain et al., 2019). In dioecious *A. araucana*, this is possible due to temporal offset in growth reductions associated with masting. In monoecious species, a similar approach may utilize tree-ring parameters with contrasting sensitivity to masting. Masting in *F. sylvatica* is also associated with reduced ring width but this signal is difficult to distinguish from growth reductions caused directly by summer drought (Drobyshev et al., 2014; Hacket-Pain et al., 2017). Instead, reconstructions may leverage contrasting sensitivity of radial growth and other tree-ring parameters such as wood density, anatomy, or stable isotopes (Olano et al., 2022; Tumajer & Lehejcek, 2019).

CONCLUSIONS

The recent masting behavior of *A. araucana* is characterized by high spatial synchrony, resulting in intense regional masting with high and low seed production years occurring simultaneously across most of the species' range. However, our reconstruction of cone production indicates that such large-scale regional synchrony of cone production is unusual over the past four centuries and that regional masting synchrony varies with regional temperature trends. Masting in this species is more typically associated with population-level masting, but less extensive spatial synchrony. These results highlight the value of renewed efforts to reconstruct masting using tree-rings and other proxies to provide understanding of baseline variability in masting behavior and drivers of long-term changes in masting. Such efforts are increasingly urgent given the accumulating evidence of climate-driven changes in masting and their consequences on ecological systems.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Hacket-Pain, 2024) are available from Figshare: https://doi.org/10.6084/m9.figshare.27678336.

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REFERENCES

Abram, N. J., R. Mulvaney, F. Vimeux, S. J. Phipps, J. Turner, and M. H. England. 2014. "Evolution of the Southern Annular Mode during the Past Millennium." *Nature Climate Change* 4: 564–69.

Ahmed, M., K. J. Anchukaitis, A. Asrat, H. P. Borgaonkar, M. Braida, B. M. Buckley, U. Büntgen, et al. 2013. "Continental-Scale Temperature Variability during the Past Two Millennia." *Nature Geoscience* 6: 339–346.

Allevato, E., L. Saulino, G. Cesarano, G. B. Chirico, G. D'urso, S. F. Bolognesi, A. Rita, S. Rossi, A. Saracino, and G. Bonanomi. 2019. "Canopy Damage by Spring Frost in European Beech along the Apennines: Effect of Latitude, Altitude and Aspect." *Remote Sensing of Environment* 225: 431–440.

Ascoli, D., A. Hacket-Pain, J. M. Lamontagne, A. Cardil, M. Conedera, J. Maringer, R. Motta, I. S. Pearse, and G. Vacchiano. 2020. "Climate Teleconnections Synchronize Picea Glauca Masting and Fire Disturbance: Evidence for a Fire-Related Form of Environmental Prediction." *Journal of Ecology* 108: 1186–98.

Ascoli, D., A. Hacket-Pain, I. S. Pearse, G. Vacchiano, S. Corti, and P. Davini. 2021. "Modes of Climate Variability Bridge Proximate and Evolutionary Mechanisms of Masting." *Philosophical Transactions of the Royal Society B-Biological Sciences* 376: 12.

Ascoli, D., G. Vacchiano, M. Turco, M. Conedera, I. Drobyshev, J. Maringer, R. Motta, and A. Hacket-Pain. 2017. "Inter-Annual and Decadal Changes in Teleconnections Drive Continental-Scale Synchronization of Tree Reproduction." *Nature Communications* 8: 2205.

Blanco, G., P. Romero-Vidal, J. L. Tella, and F. Hiraldo. 2022. "Novel Food Resources and Conservation of Ecological Interactions between the Andean Araucaria and the Austral Parakeet." *Ecology and Evolution* 12: 15.

Bogdziewicz, M. 2021. "How Will Global Change Affect Plant Reproduction? A Framework for Mast Seeding Trends." *New Phytologist* 234: 14–20.

Bogdziewicz, M., V. Journe, A. Hacket-Pain, and J. Szymkowiak. 2023. "Mechanisms Driving Interspecific Variation in Regional Synchrony of Trees Reproduction." *Ecology Letters* 26: 754–764.

Bogdziewicz, M., D. Kelly, A. J. Tanentzap, P. Thomas, J. Foest, J. Lageard, and A. Hacket-Pain. 2023. "Reproductive Collapse in European Beech Results from Declining Pollination Efficiency in Large Trees." *Global Change Biology* 29: 4595–4604.

Bogdziewicz, M., D. Kelly, P. A. Thomas, J. G. A. Lageard, and A. Hacket-Pain. 2020. "Climate Warming Disrupts Mast Seeding and Its Fitness Benefits in European Beech." *Nature Plants* 6: 88–94.

Brumme, R., B. Ahrends, J. Block, C. Schulz, H. Meesenburg, U. Klinck, M. Wagner, and P. K. Khanna. 2021. "Cycling and Retention of Nitrogen in European Beech (*Fagus sylvatica* L.) Ecosystems under Elevated Fructification Frequency." *Biogeosciences* 18: 3763–79.

Bunn, A. G. 2008. "A Dendrochronology Program Library in R (dplR)." *Dendrochronologia* 26: 115–124.

Clark, J. S., C. Nunez, and B. Tomasek. 2019. "Foodwebs Based on Unreliable Foundations: Spatiotemporal Masting Merged with Consumer Movement, Storage, and Diet." *Ecological Monographs* 89: e01381.

Díaz, S., T. Kitzberger, and S. Peris. 2012. "Food Resources and Reproductive Output of the Austral Parakeet (*Enicognathus ferrugineus*) in Forests of Northern Patagonia." *EMU-AUSTRAL Ornithology* 112: 234–243.

Donoso, S., H. Schmidt, and K. Pena. 2009. "Bosques de Araucanía, producción de Piñones y Sustentabilidad." In *Araucaria araucana (Mol.) K. Koch: Un Recurso Promisorio*, edited by A. Lizana, 5–27. Santiago: Universidad de Chile.

Drobyshev, I., M. Niklasson, M. J. Mazerolle, and Y. Bergeron. 2014. "Reconstruction of a 253-Year Long Mast Record of European Beech Reveals Its Association with Large Scale Temperature Variability and no Long-Term Trend in Mast Frequencies." *Agricultural and Forest Meteorology* 192: 9–17.

Fritts, H. 1976. *Tree Rings and Climate*. New York: Academic Publishers.

González-Reyes, A., J. Mcphee, D. A. Christie, C. Le Quesne, P. Szejner, M. H. Masiokas, R. Villalba, A. A. Muñoz, and S. Crespo. 2017. "Spatiotemporal Variations in Hydroclimate across the Mediterranean Andes (30°-37° S) since the Early Twentieth Century." *Journal of Hydrometeorology* 18: 1929–42.

Hacket-Pain, A. 2024. "Reconstruction of *Araucaria araucana* Cone Production Reveals Warming Intensifies Regionally Synchronised Masting." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.27678336.v1.

Hacket-Pain, A., D. Ascoli, R. Berretti, M. Mencuccini, R. Motta, P. Nola, P. Piussi, F. Ruffinatto, and G. Vacchiano. 2019. "Temperature and Masting Control Norway Spruce Growth, but with High Individual Tree Variability." *Forest Ecology and Management* 438: 142–150.

Hacket-Pain, A., and M. Bogdziewicz. 2021. "Climate Change and Plant Reproduction: Trends and Drivers of Mast Seeding Change." *Philosophical Transactions of the Royal Society B-Biological Sciences* 376: 20200379.

Hacket-Pain, A., J. J. Foest, I. S. Pearse, J. M. Lamontagne, W. D. Koenig, G. Vacchiano, M. Bogdziewicz, et al. 2022. "MASTREE Plus: Time-Series of Plant Reproductive Effort from Six Continents." *Global Change Biology* 28: 3066–82.

Hacket-Pain, A. J., J. G. A. Lageard, and P. A. Thomas. 2017. "Drought and Reproductive Effort Interact to Control Growth of a Temperate Broadleaved Tree Species (*Fagus sylvatica*)." *Tree Physiology* 37: 744–754.

Hadad, M. A., J. G. Arco Molina, and F. A. Roig. 2020. "Dendrochronological Study of the Xeric and Mesic *Araucaria araucana* Forests of Northern Patagonia: Implications for Ecology and Conservation." In *Latin American Dendroecology: Combining Tree-Ring Sciences and Ecology in a Megadiverse Territory*, edited by M. Pompa-García and J. Camarero. Cham: Springer International Publishing.

Hadad, M. A., A. Gonzalez-Reyes, F. A. Roig, V. Matskovsky, and P. Cherubini. 2021. "Tree-Ring-Based Hydroclimatic Reconstruction for the Northwest Argentine Patagonia since 1055 CE and its Teleconnection to Large-Scale Atmospheric Circulation." *Global and Planetary Change* 202: 103496.

Hadad, M. A., J. A. Molina, F. A. R. Junent, M. M. Amoroso, G. Muller, D. Araneo, and J. C. Tardif. 2019. "Frost Record in Tree Rings Linked to Atmospheric Circulation in Northern Check Tor Patagonia." *Palaeogeography Palaeoclimatology Palaeoecology* 524: 201–211.

Hadad, M. A., F. A. Roig, J. G. A. Molina, and A. Hacket-Pain. 2021. "Growth of Male and Female *Araucaria araucana* Trees Respond Differently to Regional Mast Events, Creating Sex-Specific Patterns in Their Tree-Ring Chronologies." *Ecological Indicators* 122: 14.

Hadad, M. A., and F. A. J. Roig. 2016. "Sex-Related Climate Sensitivity of *Araucaria araucana* Patagonian Forest-Steppe Ecotone." *Forest Ecology and Management* 362: 130–141.

Holmes, R. L. 2001. *Dendrochronology Program Library*. Tuscon, AZ: Laboratory of Tree Ring Research, Univrsity of Arizona. http://ltrr.arizona.edu/software.html.

Kelly, D. 1994. "The Evolutionary Ecology of Mast Seeding." *Trends in Ecology & Evolution* 9: 465–470.

Kelly, D., D. E. Hart, and R. B. Allen. 2001. "Evaluating the Wind Pollination Benefits of Mast Seeding." *Ecology* 82: 117–126.

Koenig, W. D., J. M. H. Knops, and W. J. Carmen. 2020. "Can Mast History Be Inferred from Radial Growth? A Test Using Five Species of California Oaks." *Forest Ecology and Management* 472: 118233.

Liu, R., Y. Zhang, H. Zhang, L. Cao, and C. Yan. 2022. "A Global Evaluation of the Associations between Long-Term Dynamics of Seed Falls and Rodents." *Integrative Zoology* 12: 831–842.

Martini, F., C. H. Chang-Yang, and I. F. Sun. 2022. "Variation in Biotic Interactions Mediates the Effects of Masting and Rainfall Fluctuations on Seedling Demography in a Subtropical Rainforest." *Journal of Ecology* 110: 762–771.

Meng, F., Y. Yuan, S. Jung, B. Stimm, N. Estrella, and A. Menzel. 2022. "Long-Term Flowering Intensity of European Tree Species under the Influence of Climatic and Resource Dynamic Variables." *Agricultural and Forest Meteorology* 323: 109074.

Morales, M. S., E. R. Cook, J. Barichivich, D. A. Christie, R. Villalba, C. Lequesne, A. M. Srur, et al. 2020. "Six Hundred Years of South American Tree Rings Reveal an Increase in Severe Hydroclimatic Events since Mid-20th Century." *Proceedings of the National Academy of Sciences of the United States of America* 117: 16816–23.

Mundo, I. A., M. H. Masiokas, R. Villalba, M. S. Morales, R. Neukom, C. Le Quesne, R. B. Urrutia, and A. Lara. 2012. "Multi-Century Tree-Ring Based Reconstruction of the Neuquén River Streamflow, Northern Patagonia, Argentina." *Climate of the Past* 8: 815–829.

Mundo, I. A., J. Sanguinetti, and T. Kitzberger. 2021. "Multi-Centennial Phase-Locking between Reproduction of a South American Conifer and Large-Scale Drivers of Climate." *Nature Plants* 7: 1560.

Olano, J. M., H. Hernandez-Alonso, G. Sangueesa-Barreda, V. Rozas, A. I. Garcia-Cervigon, and M. Garcia-Hidalgo. 2022. "Disparate Response to Water Limitation for Vessel Area and Secondary Growth along *Fagus sylvatica* Southwestern Distribution Range." *Agricultural and Forest Meteorology* 323: 109082.

Patterson, T. W., C. H. Greenberg, and A. Hacket-Pain. 2023. "Acorn Production, Climate, and Tree-Ring Growth of Five Oak Species in Southern Appalachian Forests." *Forest Ecology and Management* 546: 121310.

Pearse, I. S., J. M. Lamontagne, and W. D. Koenig. 2017. "Inter-Annual Variation in Seed Production Has Increased over Time (1900-2014)." *Proceedings of the Royal Society B-Biological Sciences* 284: 20171666.

Pesendorfer, M. B., D. Ascoli, M. Bogdziewicz, A. Hacket-Pain, I. S. Pearse, and G. Vacchiano. 2021. "The Ecology and Evolution of Synchronized Reproduction in Long-Lived Plants." *Philosophical Transactions of the Royal Society B* 376: 20200369.

Piraino, S., J. A. Molina, M. A. Hadad, and F. A. R. Juñent. 2022. "Resilience Capacity of *Araucaria araucana* to Extreme Drought Events." *Dendrochronologia* 75: 125996.

Prebble, J. G., G. Dunbar, V. van den Bos, X. Li, M. Vandergoes, S. Richardson, H. Horgan, K. A. Holt, J. Howarth, and R. Levy. 2022. "Toward a Novel Multi-Century Archive of Tree Mast Using Pollen from Lake Sediments." *Holocene* 32: 1184–92.

Rodríguez-Ramírez, E. C., T. Terrazas, and I. Luna-Vega. 2019. "The Influence of Climate on the Masting Behavior of Mexican Beech: Growth Rings and Xylem Anatomy." *Trees* 33: 23–35.

Roesch, A., and H. Schmidbauer. 2018. "WaveletComp: Computational Wavelet Analysis. R Package Version 1.1."

Rozas, V., C. Le Quesne, M. Rojas-Badilla, A. Gonzalez-Reyes, S. Donoso, and J. M. Olano. 2019. "Climatic Cues for Secondary Growth and Cone Production Are Sex-Dependent in the Long-Lived Dioecious Conifer *Araucaria araucana*." *Agricultural and Forest Meteorology* 274: 132–143. https://cran.r-project.org/web/packages/WaveletComp

Sanguinetti, J., and T. Kitzberger. 2008. "Patterns and Mechanisms of Masting in the Large-Seeded Southern Hemisphere Conifer *Araucaria araucana*." *Austral Ecology* 33: 78–87.

Sanguinetti, J., and T. Kitzberger. 2010. "Factors Controlling Seed Predation by Rodents and Non-Native *Sus scrofa* in *Araucaria araucana* Forests: Potential Effects on Seedling Establishment." *Biological Invasions* 12: 689–706.

Seget, B., M. Bogdziewicz, J. Holeksa, M. Ledwon, F. Milne-Rostkowska, L. Piechnik, A. Rzepczak, and M. Zywiec. 2022. "Costs and Benefits of Masting: Economies of Scale Are Not Reduced by Negative Density-Dependence in Seedling Survival in *Sorbus aucuparia*." *New Phytologist* 233: 1931–38.

Shepherd, J. D., R. S. Ditgen, and J. Sanguinetti. 2008. "*Araucaria araucana* and the Austral Parakeet: Predispersal Seed Predation on a Masting Species." *Revista Chilena de Historia Natural* 81: 395–401.

Shibata, M., T. Masaki, T. Yagihashi, T. Shimada, and T. Saitoh. 2020. "Decadal Changes in Masting Behaviour of Oak Trees with Rising Temperature." *Journal of Ecology* 108: 1088–1100.

Speer, J. H. 2001. *Oak Mast History from Dendrochronology: A New Technique Demonstrated in the Southern Appalachian Region*. Knoxville, TN: University of Tennessee.

Strong, C., B. Zuckerberg, J. L. Betancourt, and W. D. Koenig. 2015. "Climatic Dipoles Drive Two Principal Modes of North American Boreal Bird Irruption." *Proceedings of the National Academy of Sciences of the United States of America* 112: E2795–E2802.

Swetnam, T., and A. Lynch. 1989. "A Tree-Ring Reconstruction of Western Spruce Budworm History in the Southern Rocky Mountains." *Forest Science* 35: 962–986.

Swetnam, T. W., M. A. Thompson, and E. K. Sutherland. 1985. *Using Dendrochronology to Measure Radial Growth of Defoliated Trees*. U.S. Department of Agriculture, Forest Service, Cooperative State Research Service.

Szymkowiak, J., and R. L. Thomson. 2019. "Nest Predator Avoidance during Habitat Selection of a Songbird Varies with Mast Peaks and Troughs." *Behavioral Ecology and Sociobiology* 73: 91.

Touzot, L., E. Schermer, S. Venner, S. Delzon, C. Rousset, E. Baubet, J.-M. Gaillard, and M. Gamelon. 2020. "How Does Increasing Mast Seeding Frequency Affect Population Dynamics of Seed Consumers? Wild Boar as a Case Study." *Ecological Applications* 30: e02134.

Tumajer, J., and J. Lehejcek. 2019. "Boreal Tree-Rings Are Influenced by Temperature up to Two Years Prior to Their Formation: A Trade-Off between Growth and Reproduction?" *Environmental Research Letters* 14: 124024.

Zwolak, R., P. Celebias, and M. Bogdziewicz. 2022. "Global Patterns in the Predator Satiation Effect of Masting: A Meta-Analysis." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2105655119.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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