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Masting is uncommon in trees that depend on mutualist dispersers in the context of global climate and fertility gradients

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The benefits of masting (volatile, quasi-synchronous seed production at lagged intervals) include satiation of seed predators, but these benefits come with a cost to mutualist pollen and seed dispersers. If the evolution of masting represents a balance between these benefits and costs, we expect mast avoidance in species that are heavily reliant on mutualist dispersers. These effects play out in the context of variable climate and site fertility among species that vary widely in nutrient demand. Meta-analyses of published data have focused on variation at the population scale, thus omitting periodicity within trees and synchronicity between trees. From raw data on 12 million tree-years worldwide, we quantified three components of masting that have not previously been analysed together: (i) volatility, defined as the frequency-weighted year-to-year variation; (ii) periodicity, representing the lag between high-seed years; and (iii) synchronicity, indicating the tree-to-tree correlation. Results show that mast avoidance (low volatility and low synchronicity) by species dependent on mutualist dispersers explains more variation than any other effect. Nutrient-demanding species have low volatility, and species that are most common on nutrient-rich and warm/wet sites exhibit short periods. The prevalence of masting in cold/dry sites coincides with climatic conditions where dependence on vertebrate dispersers is less common than in the wet tropics. Mutualist dispersers neutralize the benefits of masting for predator satiation, further balancing the effects of climate, site fertility and nutrient demands.

Unpredictable reproduction in trees ('masting') could be an evolved response to thwart seed consumers[1–3], but a conundrum arises: the volatility that limits seed predators could be just as deleterious to mutualist pollen and seed dispersers[2,4–6] while also concentrating competition within offspring[7,8]. For natural enemies and mutualists alike, masting effects depend on three elements (Fig. 1): (1) year-to-year 'volatility', or the time-dependent magnitude of variation, (2) 'quasi-periodicity', the lag between high seed-production years, and (3) 'quasi-synchronicity', the tendency for individuals to produce large seed crops in the same years[9]. Explanations for forest diversity invoke combinations of these three elements[10–12], but they operate together: the costs and benefits of masting depend on the interactions between them and the foraging ranges of consumers and dispersers[9,13]. Meta-analyses provide important insights at the aggregate population or species scale[14] but miss the volatility within and synchronicity between trees[15–17]. Efforts to generalize species- and site-specific results confront a diversity of methods, measurements and scales used in each study. In this paper, we integrate raw data at the individual-tree scale from all vegetated continents to allow formal inference on the joint distribution of masting components. We show that variation in

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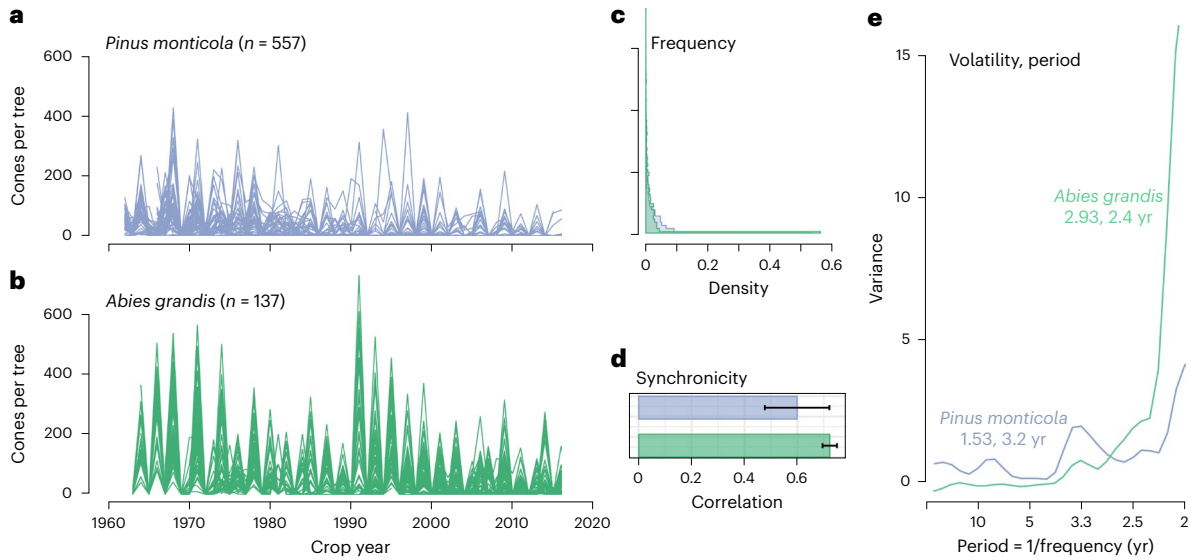

Fig. 1 | Illustration of three masting components for representative trees species from the central Cascades, USA. a,**b**, Crop counts for *P. monticola* and *A. grandis* vary between individual trees and drift over time. **c**, The frequency of counts in both species shows that zeros dominate, and there is no threshold that could be used to define masting events. **d**, Mean pairwise correlations between trees and their standard deviations are used to demonstrate quasi-synchronicity in both species. **e**, The volatility and period are shown beneath species name. *A. grandis* shows higher synchronicity between individuals (**d**) and higher volatility, especially concentrated at the 2 yr period in **e**. *P. monticola* also shows variance concentrated at 2 yr, with a secondary peak at 3.4 yr (**e**).

masting components across the diversity of tree species depends on how seeds and pollen are dispersed, indicating that mutualists may be just as important as consumers for the evolution of masting. Results show mediation of these effects by climate, soil fertility and nutrient demand.

We introduce specific definitions for volatility and periodicity that emphasize the contributions of low-frequency (long-period) variation. The masting phenomenon is remarkable (and important) because it does not simply reoccur each year; it is frequency-dependent, with low-frequency variation being especially important for its effects on animal dispersers and consumers. We define frequency-dependent variation as 'volatility' to avoid confusion with the term 'variance' (and its derivatives, 'variation' and 'variability'), which does not depend on time. Volatility emphasizes the contribution of variance that is concentrated at low frequency (long time lags). In the context of our analysis, 'periodicity' likewise emphasizes variance that is concentrated at low frequency. In both cases, variance is determined as a function of frequency, followed by transformation to frequency-weighted volatility and periodicity (see Methods).

The adaptive foundation for masting may involve escape from natural enemies that are satiated by large, quasi-synchronized crops and limited by intervening lean years[18,19], but this same variation can likewise negatively impact mutualists (Fig. 2a). Scatter-hoarding birds and rodents can be both seed predators and mutualists, consuming the entire seed crop in some years while also aiding reproduction through seed burial[20]. Predator satiation is most likely with high reproductive volatility, long periods between high-yield years and synchronicity between trees; this synchronicity reduces a consumer's capacity to simply average over interannual variation in one host tree by accessing others[9,13] (Fig. 2a). For example, erratic seed production by individual trees (volatile and quasi-periodic) may not deter natural enemies if high-production years are asynchronous between trees[9]. Any negative effects of quasi-periodic variation on a tree's consumers would be amplified by high year-to-year variation, especially when concentrated at long lags[2,21], again, defined here as 'volatility'. Weighing against the benefits of unreliable fruiting for its deleterious effects on enemies are the negative effects on mutualist dispersers[2,4,22]; the predator satiation hypothesis might not benefit species that are reliant on specialized pollinators and seed dispersers.

While volatility amplifies the effects of periodicity and synchronicity on enemies and benefactors alike, this same volatility could be mediated by resource availability and climate[21,23] (Fig. 2a). Limited resources might promote reproductive variation in trees[24–26] or not[27]. The mast interval could be prolonged where large crops deplete reserves that require years to replenish[21,28–30] or not[14,27]. In this global analysis, we use cation exchange capacity (CEC), a widely used index of soil fertility[31,32], and foliar nitrogen (N) and phosphorous (P) concentrations[27] to quantify the association between masting and resource supply (CEC) and resource demand: nutrient-demanding species tend to have high foliar N and P[33].

In addition to site differences in resources and climate norms, weather anomalies might contribute to large seed crops (for example, ref. 34), especially for species with limited dependence on stored reserves[1,23] (Fig. 2a). An 'anomaly' is defined here as the difference between a climate variable in a given year and the average of that variable for that site (the site 'norm'). At least for a few species at one or a few sites, warm and wet years may be associated with low seed production[35–39] and increased reproductive synchronicity[40,41] (Fig. 2a).

Because the distribution of species across environments is uneven, species differences cannot be fully assessed from observational data, which dominate the masting literature. Climate anomalies in specific seasons are clearly important for many temperate species[38,40–42], but our analysis evaluates variation globally, spanning seasonal and aseasonal environments. The effect of a climate anomaly such as temperature or moisture must depend on the climate norm at each site, including seasonality. For example, the estimated effect of a spring-time temperature anomaly of 1 °C is not comparable between highly seasonal taiga and the aseasonal wet tropics where the notion of spring is not relevant. Including an interaction between anomalies and norms in data models cannot clarify their respective contributions because species are not observed across the same combinations of norms and anomalies in the data. For this reason, environmental anomalies are limited here to annual variation in temperature and moisture deficit, and comparisons between species in Fig. 2a include the caveat that we are not observing all of them in all of the same settings.

The three components of masting have not been analysed together, in part because a joint analysis requires substantial data

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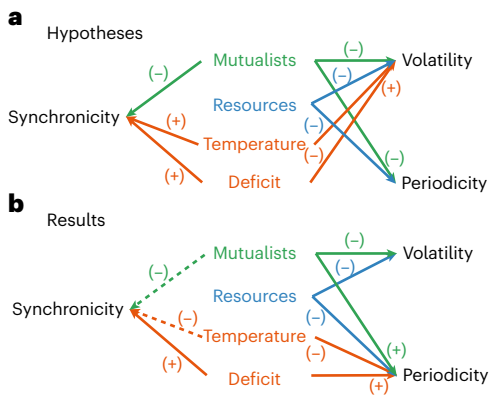

Fig. 2 | Hypothesized effects and summary of results in this study. a,**b**, We summarized the results (**b**) after testing the hypotheses (**a**) related to the effects of mutualists (green), resources (blue), and climate (red) on the three masting components. Arrows with (+) and (−) represent positive and negative effects, respectively. We expect that tree species with low volatility, short periodicity and low synchronicity benefit most from their mutualist pollinators and dispersers (**a**). Resources reduce volatility and periodicity (**a**). High temperature decreases volatility while promoting synchronicity (**a**). Dry sites (deficit) have higher volatility and synchronicity than wet sites (**a**). The summary of results in **b** comes from the joint model in Fig. 3. Dashed lines indicate that 90% credible intervals contain zero while 68% credible intervals do not.

at the individual (tree-year) scale. Unless individuals are perfectly synchronized, periodicity at the population scale underestimates periodicity at the individual scale; in fact, asynchronicity can entirely mask periodic reproduction where observed with population-scale data. Studies that examine both individual and population variation show that fecundity is typically quasi-synchronous at best[9,15,17,43,44]. Understanding spatial scales[45], allocation trade-offs[46,47], responses to climate[39,42,48–50], and effects on consumers[9,51] and dispersers[2,4] all require joint analysis of reproductive variance within and between individuals.

Synthesis is challenged not just by the incompatible reference used in literature studies (Supplementary information), but also by a need for measures of volatile, periodic and synchronous variability. All three elements vary between species and regions. The commonly used coefficient of variation (CV) omits time and frequency, two of the defining features of masting, and applications of CV to log values cannot properly incorporate zeros. This is important because zero is the most frequent observation in many data sets (for example, Fig. 1c) (Supplementary information). Estimating periodicity requires a definition of what constitutes a mast year[30,52–54], which is challenging because there is no identifiable threshold (for example, Fig. 1c) despite detectable indicators on trees (for example, twigs hanging from seed weights) and peaked seed numbers in Fig. 1a,b. The interval between mast years that would come from imposing an artificial threshold can range widely, in part due to variation within and between trees[55,56]. Using methods developed in this study, *Pinus monticola* (Fig. 1a) and *Abies grandis* (Fig. 1b) share biennial variation but differ in the secondary concentration of variance at 3–4 yr in *P. monticola*. The period-weighted variance spectrum (to emphasize low frequency) gives estimates of 2.4 and 3.2 yr in *P. monticola* and *A. grandis*, respectively (Fig. 1e). Not only are both species strongly biennial, they are also quasi-synchronous, with mean pairwise individual correlations being especially high for *A. grandis* (0.72 ± 0.12 compared with 0.60 ± 0.27 in *P. monticola*) (Fig. 1d). Quasi-synchronicity between trees within a species can extend over regions[40,41,45], but it is not global. In our case, regional variation is defined at the ecoregion scale and synchronicity is evaluated at the 1 km scale (Methods).

Our approach that leads to the summaries in Fig. 1 takes the perspective of each tree as a time series, with dependence between individuals from the same species, using a state–space representation for maturation and fecundity status[16,42]. A model that allows for dependent observations is especially important for masting, where synchronicity means that a single individual may offer almost the same information as an entire population. In our approach, dependent observations are taken up by the correlation structure contained in the posterior distribution of latent states, one for each tree-year. The approach can allow for either year effects or autoregressive [AR(p) with lag p] terms as alternative ways to incorporate variation over time. Zeros are accommodated by a hidden Markov process for maturation status and allowance for failed crops with censoring (see Methods). Year effects that are random by ecoregion have the advantage that they do not assume a fixed AR structure over time[9].

In three steps, we evaluated masting across species with contrasting reliance on mutualist dispersers at the global scale, and how the relationship between masting and mutualists varies with resources, climate and phylogeny. We hypothesized that mutualist pollinators and dispersers select for low volatility, short periods and low synchronicity[2,4,9] (Fig. 2a). We expected that nutrient-demanding species and species that commonly occur on fertile sites tend toward low volatility, rapid replenishment times following large crops and, thus, short periods[23,29] (Fig. 2a). We further hypothesized that warm climates favour low volatility and high synchronicity[2,14,40], while dry climates (high moisture deficit) favour high volatility and synchronicity[41,45] (Fig. 2a). To test these hypotheses, we begin by extracting the three components of masting (Fig. 1) from interannual and inter-tree variation[9] using methods that derive from signal processing for the time-series aspect of data and tree-to-tree correlation. Second, individual time series were aggregated by ecoregion–species, weighted by fecundity to emphasize large producers[57,58] (Methods). Finally, we evaluated the effects of pollen and seed dispersal modes, resources and climate on the joint response of masting components, both including and controlling for phylogeny.

Results

Across all species in the study, dependence on mutualist dispersers is linked to low masting volatility (Fig. 3a). Volatility for species that depend on animals for seed and/or pollen dispersal is substantially lower than that for wind-pollinated flowers and wind-dispersed seeds. The link between volatility and dispersal syndrome is mediated by resources and climate (Fig. 3a). In addition to wind dispersal (the positive mirror images of negative AD and AP in Fig. 3a), high volatility is associated with low nutrient demand (low foliar P and N:P) and with fertile soils (cation exchange capacity, CEC in Fig. 3a). Of course, there is within-species variation in response to fertility[58], which is distinct from the mean CEC on which species are located, as used in this study. There is a weak tendency for high volatility in cold, moist climates (credible intervals include zero for Temp and Def in Fig. 3a). High volatility is further associated with small seeds (SM < 0).

The volatility relationships are not isolated from the two other components of masting. High periodicity values in Fig. 3b mean that there are long periods between high-yield years. High synchronicity values in Fig. 3c mean that individuals produce large crops in the same years and vice versa. Because period and synchronicity are important only for trees with non-negligible seed production, both are weighted here by individual fecundity (see Methods). In the case of synchronicity, the distribution of pairwise correlations for trees of the same species within 1 km of one another (see Methods) has the mode near +1 but is broadly distributed over negative and positive values (Fig. 4a). When aggregated to the species level (averaged over pairwise correlations for the species), the distribution shifts to predominantly positive values (Fig. 4b, red). When weighted by fecundity, these averages increase further (Fig. 4b, blue) because large producers have the highest levels of synchronicity.

The long periods associated with animal seed dispersal (Fig. 3b) may not have meaningful effects on consumers or mutualists because

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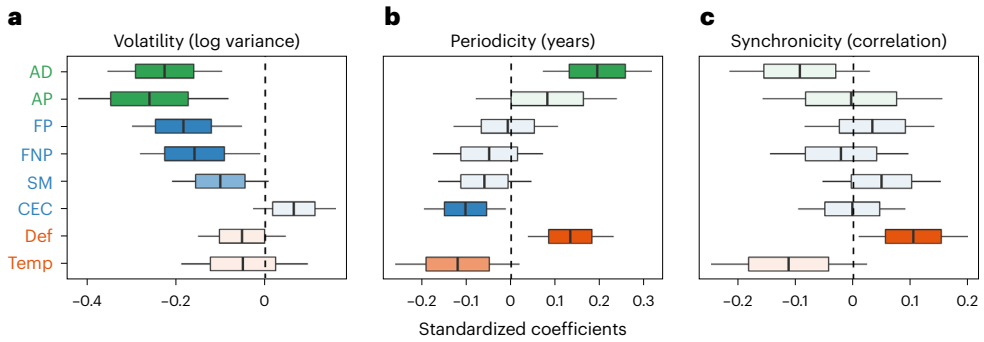

Fig. 3 | The joint response of masting components to mutualist dispersers, resources and climate. a–**c**, Three masting components include volatility (**a**), periodicity (**b**) and synchronicity (**c**) at ecoregion–species scales. Predictors include vertebrate dispersers (animal seed dispersal (AD) and animal pollination (AP)), resources (soil cation exchange capacity (CEC), foliar P (FP) and foliar N:P ratio (FNP)), seed mass (SM) and climate (accumulated moisture deficit (Def, ranging from wet to dry) and mean annual temperature (Temp, ranging from cold to warm)). Dispersal and pollination syndromes are included as two-level factors, so the negative coefficients for AD and AP have as mirror images the positive effects of wind dispersal and pollination. The analysis accounts for phylogeny as a random effect (Methods). Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Colours highlight different variable types, with opacity increasing from 90% to 95% of the distribution outside of zero. Variables included in the model were based on the lowest DIC. Coefficients are on the standard deviation scale for predictors and the correlation scale for responses (Methods). Results are summarized in Fig. 2b to compare with the hypotheses.

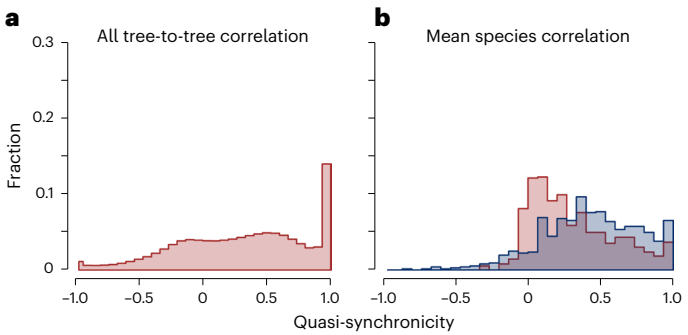

Fig. 4 | Quasi-synchronicity at individual and species level. a, Correlations between every pair of trees of the same species within 1 km show a mode near one, but a broad range. **b**, Species average correlations are concentrated near zero (red), but fecundity-weighted correlations are substantially higher (blue) (Methods).

these species are weakly synchronized (Fig. 3c). For consumers that can move between host trees, weak synchronicity means that there will be individuals producing seed in many years. Short periods are associated with warm, wet, fertile sites (negative Temp and CEC, positive Def in Fig. 3b). The quasi-synchronicity that is strongest for wind dispersal is amplified in cold, dry climates (negative AD and Temp, positive Def in Fig. 3c).

The most volatile species are not those having the highest sensitivity to climate anomalies. It is important to first note that climate anomalies make large contributions to variation in many species, both positive and negative (large coefficients in Fig. 5c,d). The absolute values of anomaly responses (Fig. 5a) summarize both positive and negative sensitivity to moisture deficit and temperature anomalies (Fig. 5a,b). The coefficients are less meaningful for low-volatility species because there is less total variation that could be driven by climate or intrinsic factors. Thus, the positive log volatility values in Fig. 5 are most telling and, at log volatility above zero, absolute sensitivity declines on average for both climate variables (Fig. 5a,b). Because few animal-dispersed species are highly volatile, the trends in these high values are driven more by wind-dispersed species (blue symbols) with low foliar N:P (small symbols). For animal-dispersed species, moisture-deficit sensitivities shift from negative to positive with increasing volatility (Fig. 5c, orange, green). For both dispersal modes (wind versus animals), temperature sensitivities trend from negative to near-zero with increasing volatility (Fig. 5d).

All elements of the three-part syndrome have phylogenetic dependence, which is especially strong for volatility and periodicity and less so for synchronicity (Fig. 6). Volatility is the highest in the temperate clades Pinales, Fagales and Sapindaceae (prominent exceptions include the shrub maples *Acer pensylvanicum* and *A. spicatum*). The wind-pollinated and (primarily) wind seed-dispersed genera *Abies* and *Betula* are near the highest volatility and the shortest period. Other volatile, wind-dispersed temperate groups include the Ulmaceae (*Ulmus*, *Zelkova*). Volatile animal-dispersed groups include the genera *Ficus*, *Swida* and *Nyssa*. Synchronicity is especially high in many of the Pinales and Fagales. Low volatility is common in the tropical groups Fabales, Malpighiales and Gentianales. For groups with mixed tropical/temperate affinities, volatility tends to be low in Magnoliids, Ericales and Cornales. Periodicity and synchronicity of most tropical species are not included in Fig. 6b,c because their low volatility values fall below the range where period and synchrony become meaningful (Methods).

Taken over all ecoregion–species combinations, volatile seed production is most common for species with short periods between productive years (correlation = −0.28, 95% CI = (−0.36, −0.21), Extended Data Fig. 2). This negative relationship between volatility and period holds within phylogenetic groups, where there are more negative than positive correlations between volatility and period (Extended Data Fig. 2). High volatility aligns with short periods in most temperate groups (*Abies*, *Quercus*, *Fagus*, residual Fagaceae, Pinaceae and Magnoliaceae), some tropical species (Meliaceae, Melastomataceae) and some with mixed tropical/temperate affinities (residual Sapindaceae). Correlations in other large temperate groups (*Pinus*, *Acer*, Cupressaceae, Betulaceae and Oleaceae), as well as in mixed tropical/temperate groups (Annonaceae, Araliaceae, Moraceae, Symplocaceae and Lauraceae) are negative but not significantly less than zero. Conversely, positive relationships are dominated by one mostly temperate group (Aquifoliaceae), others being non-significant but predominantly tropical.

Across species, the relationship between volatility and synchronicity is weak (correlation = −0.039, 95% CI = (−0.12, 0.043)), but strong correlations emerge within many phylogenetic groups (Extended Data Fig. 3). Volatile species have low synchronicity in many families of mixed temperate/tropical affinity (blue in Extended Data Fig. 3).

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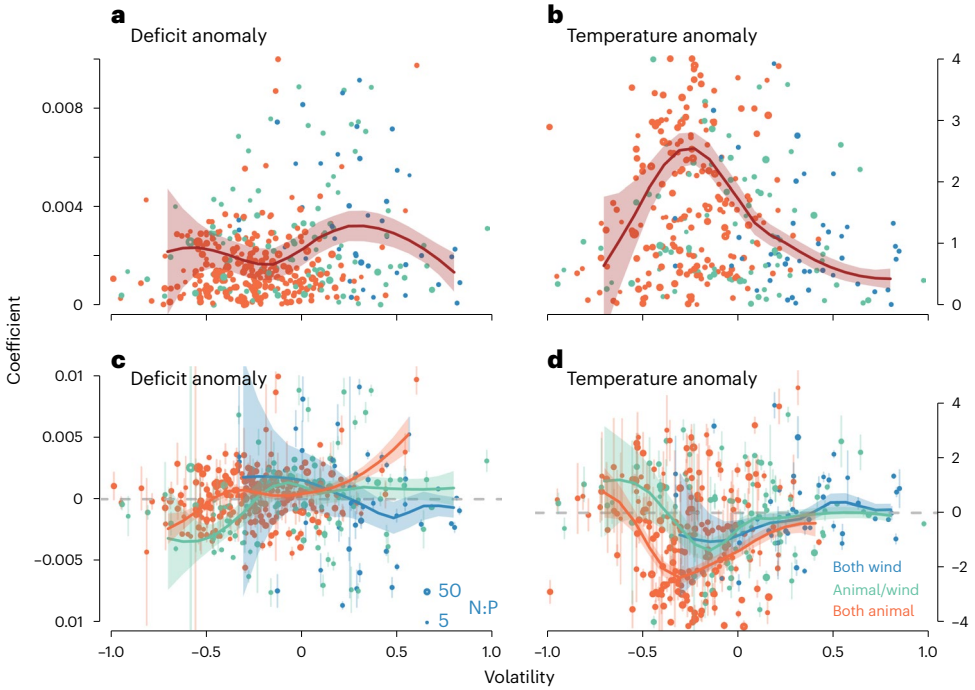

Fig. 5 | Volatility, dispersal mode, climate anomalies and foliar N:P. a–**d**, Each point locates species volatility (variability between years on log scales) with its coefficients to climatic anomalies in moisture deficit (**a**,**c**) and temperature (**b**,**d**). Coefficients were obtained from the fitted model (Methods). Overall sensitivity with no grouping by dispersal/pollination syndromes is shown as absolute values in **a** and **b**; and with their signs in **c** and **d**. The mean temperature from the previous year and accumulated moisture deficit from both the previous and current year were used to calculate anomalies. Symbol size scales with foliar N:P ratio. 'Both animal' species (orange) have both pollen and seeds dispersed by animals. 'Animal/wind' species (green) have either pollen or seeds dispersed by animals. High volatility is associated with positive responses to moisture deficit (**c**) and temperature (**d**) in animal-dispersed species, but generally declining absolute sensitivity to both variables (**a**,**b**). Loess regressions on parameter estimates (dots), weighted by the standard errors of the estimate (error bars), summarize trends with their confidence intervals (the coloured shades) in absolute sensitivity (**a**,**b**) and for the three dispersal groups (**c**,**d**).

High volatility combines with high synchronicity in the temperate genera *Fagus* and *Abies*, but only weakly in *Quercus* (brown in Extended Data Fig. 3). For the majority of species groups, high synchronicity is associated with low volatility.

Discussion

Seed and pollen dispersal syndromes emerge as the dominant trait associated with volatile seed production in trees; reliance on mutualist pollen and seed dispersal is among the strongest predictors of masting avoidance (Fig. 3a). The selective forces that have shaped associations between masting and animal dispersal include costs to mutualist dispersers and the benefits of reduced predation[2,4,14]. These selective forces are further complicated by the fact that at least some animal dispersers are also seed predators (for example, in *Quercus* and other species that are dispersed by scatter-hoarding vertebrates). While animal-dispersed species are overall less volatile (Fig. 3a), there are notable exceptions. For example, the volatile Fagaceae (Fig. 6a) have primarily wind-dispersed pollen but depend on scatter-hoarding seed dispersers–mutualists that suffer in low-yield years and disperse and satiate in high-yield years[59,60]. Perhaps as an exception that supports the rule, within Fagaceae the lowest volatility is estimated for *Castanea* with primarily insect-dispersed pollen[61]. The strong connection between mast volatility and wind dispersal (Fig. 3a) supports the hypothesis that animal pollination may suffer from volatile masting[2,4,6,23,62].

Insights from this study could not have come from a traditional treatment of variation. Traditional comparisons based on the coefficient of variation and its derivatives omit the basic attribute of frequency (Fig. 1). Extracting mean intervals between events becomes highly subjective because there is no threshold value that distinguishes an event from background (Fig. 1c). All three components of mast variation require individual-scale data. Analysis of raw data, with dependence between individuals and over time, allowed quantification of the contributions of volatility, quasi-periodicity and quasi-synchronicity.

Volatile species have low reliance on animal dispersal, low nutrient demands and generally low sensitivity to climate anomalies (Fig. 5a,b). The classic masting response—volatile, synchronized reproduction at lagged intervals—is associated with species traits and conditions that lead to low seed production. Cold, dry climates at high latitudes, where reproductive output is two orders of magnitude lower than in the wet tropics[63], are dominated by small seeds, wind-dispersed pollen and seeds, and volatile reproduction (Fig. 3a). Synchronized reproduction at long periods is a feature of dry climates (Fig. 3b,c) where pollination efficiency is expected to be high[45]. Even the increased volatility with soil fertility fits this negative relationship between fecundity and volatility: mean fecundity declines with foliar P[58] as volatility increases (soil CEC in Fig. 3a). Despite the limitations of comparing environmental responses across species that differ in their distribution of exposures to the environment, results are not consistent with the expectation that volatility at the species level increases with higher variations in climate anomalies[34].

Synchronicity has the tendency to be associated with wind dispersal (Fig. 3c), consistent with costs to mutualist dispersers that include not only satiated frugivores, but also competition for animal pollinators[64]. Synchronized flowering may increase pollinator visitation rates[65,66]; however, if unreliable flowering limits specialized pollen dispersers, then benefits of synchronicity could be mixed (Fig. 3c). A tendency for long intervals between mast years in mast-avoiding tree species has a muted effect on their animal seed dispersers because it is associated with low volatility and asynchronicity (Fig. 3b,c).

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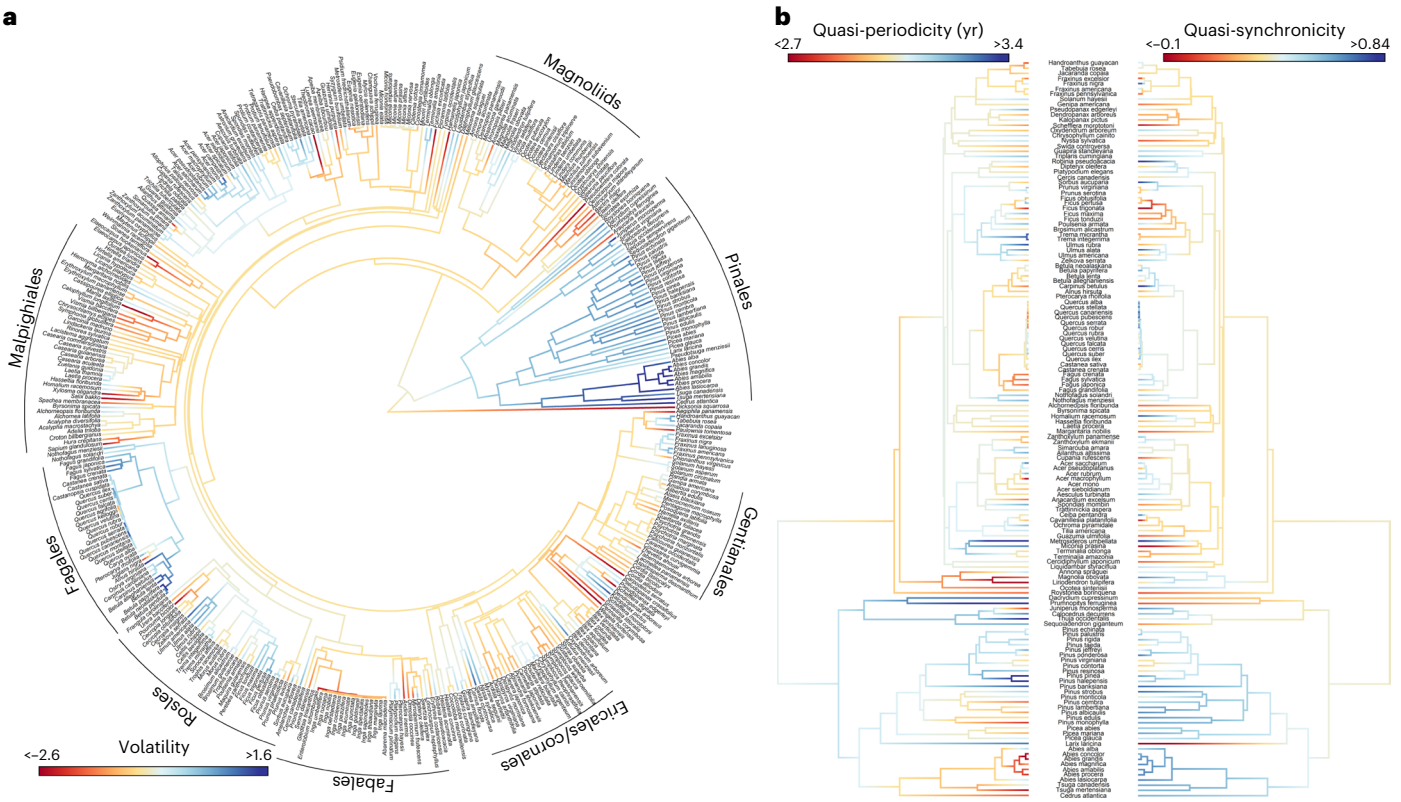

Fig. 6 | Phylogenetic coherence in the three masting components. a, Volatility (on log scale) has a phylogeny component (Pagel's $\lambda = 0.83$, $P < 10^{-9}$, $n = 394$). **b**, Quasi-periodicity (left) exhibits a weaker phylogenetic coherence compared with volatility (*Pagel*'s $\lambda = 0.52$, $P = 0.0023$, $n = 142$). Quasi-synchronicity (right) shows the weakest signal (Pagel's $\lambda = 0.21$, $P = 0.0064$, $n = 142$). Species with volatility of at least 0.94 (62.5% quantile) are shown in **b** because periodicity becomes noisy and less meaningful at low levels of volatility.

The association of wind pollination with high volatility but not with long periods agrees with the largely untested notion that quasi-synchronous flowering effort increases pollination efficiency while long intervals between mast years have no additional benefits[1].

The synchronicity that is typically emphasized for masting populations belies the overall weak tree-to-tree correlation. The distribution of inter-tree correlations weighted by fecundity (Fig. 4b) could resolve the paradox of low synchronicity in species traditionally identified as iconic mast producers[15–17]. Low and even negative correlations characterize populations as a whole (Fig. 4a), but strong producers are dominated by positive correlations (Fig. 4b). The production of some non-synchronized offspring is an expected bet-hedging maternal strategy even where quasi-synchronicity is generally beneficial. The advantages of predator satiation must balance the potential costs of concentrated intraspecific competition between sibling seedlings and of satiating mutualist pollinators and dispersers. Indeed, heterogeneous volatility–synchronicity relationships between lineages (Extended Data Fig. 2) suggest the potential for region/species-scale adaptation in response to variable predation pressure[22,67].

The finding that volatile species tend to have short periods (Fig. 6), including within multiple phylogenetic groups (Extended Data Fig. 2), is not consistent with the view that resource depletion followed by delayed replenishment is a dominant source of variation between species. This lack of association 'between' species does not preclude a need for extended replenishment following high yields 'within individuals' in ways that differ between species. Although less studied, it is also important to understand how local adaptation (that is, genetic differences among populations[68]) and gene × environment interactions that affect seed enemies and dispersers[5,69] may contribute to the evolution of volatility, periodicity and synchronicity.

If consistently high nutrient concentrations obviate the need for prolonged nutrient recovery, then we expect the observed negative association between foliar nutrients and volatility (Fig. 3a). By allowing for the effects of both foliar nutrient concentrations and site fertility, our results diverge from previous studies suggesting low volatility on fertile sites. However, comparisons must consider that previous studies include few species[24–26]. The effects of nutrient demand versus supply can be confounded by the fact that nutrient-demanding species are most abundant on fertile sites. By including differences in foliar nutrients as a species-level trait with the CEC where trees occur, this global analysis finds that low volatility is associated with nutrient-demanding species, not low-fertility sites. The association of high volatility and short periods with nutrient-rich habitats (CEC in Fig. 3) could result from accelerated nutrient replenishment on fertile soils. However, as noted above, volatile species are not those with short periods in general. Not only do nutrient-demanding species (as reflected in foliar nutrient content) have lower species seed production (SSP, defined as seed number × seed size)[58], but they are also less volatile (Fig. 3a). Limited effects of resources on synchronicity can be related to the weak effects of soil CEC on seed production[58] and intense competition on nutrient-rich sites[42].

The expectation that large seeds might demand long recovery intervals was not supported by comparisons between species. Using data published previously[70], Sork et al.[30] found a positive relationship between acorn size and mast period for 18 temperate *Quercus* species. We find a negative relationship at the global scale: species with large seeds are less volatile and have short periods in Fig. 3a,b. In the limited dataset[70], the negative correlation is driven by a longer interval for *Q. alba* than for *Q. falcata*. In general, we find that red oaks (*Q. falcata*, *Q. rubra*, *Q. velutina* and *Q. coccinea*) have longer periods than white oaks

(*Q. alba*, *Q. montana*, *Q. pubescens*, *Q. robur*, *Q. stellata* and *Q. serrata*), Cerris oaks (*Q. cerris*, *Q. ilex* and *Q. suber*) and *Fagus* (Fig. 6b), perhaps related to the 2 yr development time for red oak seeds.

The wide variation in seed production[57,58] emphasizes the importance of large data sets to estimate effects, represented here by 12 million tree-years at a global scale. As is common in observational studies, the geographic coverage of raw observations is not uniform across different regions (Extended Data Fig. 1). Expanding the MASTIF network with additional sites in South America and Africa would contribute to a more balanced global coverage.

The negative association between masting intensity and fecundity suggests the view of masting as desperation: an evolutionary option most common in species and settings where seed production is limited primarily by climate and habitat, and where animal dispersal is less common. There is no question that predator satiation occurs and seedling escape can result[71–73]. Although it is not uncommon for a given tree species to have multiple pollinators and seed dispersers[74], the diet breadth of seed consumers (for example, specialist and generalist) clearly affects masting[9]. Quantifying different degrees of specialization between seed predators, pollinators and dispersers is an important future research avenue. Still, at the global scale, species differences in masting depend on their reliance on animal dispersers.

The emergence of dispersal syndrome as a dominant link to species differences in masting intensity (Fig. 3) supports the view that mutualist relationships could be just as important as predator satiation—the cold, dry settings where masting is intense coincides with low reliance on mutualist dispersers. The conundrum faced by species that depend on animal dispersal while also suffering from seed predation makes for conflicting selection pressures that are evident when viewed across the diversity of tree species.

Methods

MASTIF summary

The MASTIF model allowed us to jointly model individual trees, with their dependence on one another and over time. This hierarchical, state–space model and the Gibbs sampling used for posterior simulation are detailed in ref. 9, with only key elements that relate to mast syndromes summarized here. Model fitting included approximately 12 million tree-years from 898 species (Extended Data Fig. 1). The MASTIF model is open-access in the R package MASTIF on CRAN.

The core quantity of interest is the tree-year fecundity $f_{ijr,t}$ for tree i on stand j, in ecoregion–species r and year t. Fecundity varies individually with tree size[75] and crowding, locally with interannual climate anomalies, geographically with climate norms, soil and drainage and regionally through shared year effects. The shared variation between trees in year effects are random between ecoregion–species combinations, allowing for covariation that is broader than local climate but still regionally variable. Because the model includes interannual anomalies at the local scale, year effects quantify shared variation beyond that explained by climate anomalies and at a coarse (ecoregion) scale.

The MASTIF model incorporates two data types including crop counts and seed traps. Crop counts $c_{ijr,t}$ are conditionally beta-binomial, which allows for uncertainty in the fraction of the crop that is observed,

$$\begin{aligned}&\text{betaBinom}(c_{ijr,t}|f_{ijr,t}, a_{ijr,t}, b_{ijr,t})\\&= \int_0^1 \text{binom}(c_{ijr,t}|f_{ijr,t}, q_{ijr,t})\text{beta}(q_{ijr,t}|a_{ijr,t}, b_{ijr,t})dq_{ijr,t}\end{aligned} \quad (1)$$

where $q_{ijr,t}$ is an estimate of the fraction of the crop observed, $a_{ijr,t}$ and $b_{ijr,t}$ are parameters selected that have mean fraction $q_{ijr,t}$ (that is, the fraction reported), but error that increases with small $q_{ijr,t}$. This approach allows for the fact that the lower the reported crop fraction, the less certain it is.

Seed trap counts are conditionally Poisson,

$$\text{Poi}\left(\mathbf{y}_{jr,t}|A_{j,t}\mathbf{S}\mathbf{f}_{jr,t}\right) \quad (2)$$

where trap area $A_{j,t}$ can vary by study and year t, $\mathbf{y}_{jr,t}$ is a vector of seed counts for S_j traps, $\mathbf{S}$ is the $S_j \times n_j$ kernel matrix that determines dispersal from each of $i = 1, \ldots, n_j$ trees to S_j traps, depending tree-to-trap distances and $\mathbf{f}_{jr,t}$ is the length-n_j vector of tree fecundities. The dispersal kernel follows that of ref. 76.

Fecundity is the product of latent states for maturation status and conditional fecundity, $f_{ijr,t} = \psi_{ij,t}\rho_{ijr,t}$ having the joint distribution $[\psi_{ijr,t}, \rho_{ijr,t}] = [\psi_{ijr,t}|\rho_{ijr,t}][\rho_{ijr,t}]$. (We use bracket notation $[x]$ to indicate a distribution or density of x). Maturation is a one-way process, modelled as a probit hidden Markov model. The maturation status $\rho_{ijr,t} \in (0, 1)$ is known to be 1 (that is, mature) for trees that have been observed to produce seed in the past (that is, $[\rho_{ijr,t} = 1|\rho_{ij,t-1} = 1] = 1$) and 0 if known to be immature subsequently (that is, $[\rho_{ijr,t} = 1|\rho_{ij,t+1} = 0] = 0$). For tree-years of unobserved maturation status, the probability of being mature in year t, given past and future status is the probit,

$$\begin{aligned}&\rho_{ijr,t}|\rho_{ijr,t-1}, \rho_{ijr,t+1} \sim \text{Bernoulli}(p_{ijr,t})\\&p_{ijr,t} = \rho_{ijr,t-1} + (1 - \rho_{ijr,t-1})\rho_{ijr,t+1}\Phi(\mathbf{v}'_{ijr,t}\boldsymbol{\beta}^{v})\end{aligned} \quad (3)$$

where $\Phi(\cdot)$ is the standard cumulative normal distribution, $\mathbf{v}_{ijr,t}$ are predictors and $\boldsymbol{\beta}^{v}$ are fitted coefficients. All unknown statuses must be imputed, so that ρ coefficients in equation (3) are the currently imputed values in Gibbs sampling.

The process model for fecundity is log-normal and dynamic,

$$\log \psi_{ijr,t}|\rho_{ijt,t} \sim N\left(\mathbf{x}'_{ij,t-1}\boldsymbol{\beta} + \alpha_{ij} + \gamma_{r,t}, \sigma^2\right) I(\psi_{ijt,t} \le 1)^{1-\rho_{ijr,t}} I(\psi_{ijt,t} > 1)^{\rho_{ijr,t}} \quad (4)$$

where $\mathbf{x}_{ij,t}$ are predictors in the model with coefficients $\boldsymbol{\beta}$, α_{ij} is the random effect for tree ij, $\gamma_{r,t}$ is the year effect for ecoregion–species r, and σ^2 is the residual variance. The factors containing the indicator function (I) specify that mature individuals have latent conditional fecundity sufficient to generate at least one seed. Importantly, the approach allows for observed zero fecundity for both seed traps and crop counts while latent fecundity remains finite. This approach follows the approach used in Tobit models for discrete zeros in otherwise continuous data[77,78]. Predictors in the design vector $\mathbf{x}_{ijr,t}$ include known climate and habitat variables combined with variable selection by Deviance Information Criterion (DIC).

Masting syndromes

The analysis of masting components at individual level is based on the estimate of the fecundity, $f_{ijr,t}$, on the log (proportionate) scale. The mast syndrome consists of three elements $M = (M_v, M_p, M_c)$, the volatility M_v having units of variance in $\log f$, period M_p in years and the dimensionless synchronicity M_c. The first two elements emerge from the spectral density $S_f(\omega)$, evaluated in the frequency ω domain. Technically, $S_f(\omega)$ is obtained by transforming the auto-covariance function $C(t)$ from the time domain to the frequency domain or, alternatively, by taking the Fourier transform of the autocorrelation function $C(t)/C(0)$. There is an associated spectral 'variance', obtained by integrating the spectral density over frequency

$$\text{Var}_{\omega}(f) = \frac{1}{\pi}\sum_{k=0}^{\omega^*} S_f(\omega_k) \quad (5)$$

where ω^* is the last frequency term. Period (years) is the reciprocal of frequency, ω^{-1}. To capture the defining feature of masting, that of variance concentrated at low frequency, we define 'volatility' as the period-weighted spectral variance,

$$E_\omega(M_v) = \frac{1}{\pi T}\sum_{k=0}^{T-1}\omega_k^{-1}S_f(\omega_k) \quad (6)$$

where T is the number of terms included in the summation. The subscripts of tree i, stand j and ecoregion–species r are omitted to reduce clutter. Because short time series could be dominated by noise, we focused on mature individuals that include at least 10 yr of observations (139,785 trees and 2,841,238 tree-years from 468 species). Detailed data distribution can be found in the Supplementary Data. We set T to be half of the threshold, that is, $T = 5$ yr. Likewise, 'periodicity' emphasizes variance at low frequency,

$$E_\omega(M_p) = \frac{1}{\pi \mathrm{Var}_\omega[f]}\sum_{k=0}^{T-1}\omega_k^{-1}S_f(\omega_k) \quad (7)$$

with variance

$$Var_\omega(M_p) = \frac{1}{\pi \mathrm{Var}_\omega(f)}\sum_{k=0}^{T-1}\omega_k^{-2}S_f(\omega_k) - E_\omega^2(M_p) \quad (8)$$

The span of variance captures the quasi-periodic nature of masting, being broad where period is unpredictable (Fig. 1d). The notation E_x indicates the expectation of the variable x. We obtained the spectral density $S_f(\omega_k)$ for each tree ($\log f_{ijr}$) using the R package 'spectrum'. Volatility and periodicity complement currently used metrics for masting. Volatility measures variance in the frequency domain, capturing the out-sized importance of variation at the multiyear scale, moving beyond lag-0 (CV) or lag-1 approaches. Periodicity side-steps the need to define a threshold productivity for mast years or the fact that a simple mean interval may not represent quasi-periodic variation.

The ecoregion–species masting syndromes, $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$, are the expectations of individual-level estimates M_{ijr}. Because individual volatility $M_{v,ijr}$ and quasi-periodicity $M_{p,ijr}$ could be dominated by large numbers of small and thus low-fecundity trees, we evaluated the $M_{v,r}$ and $M_{p,r}$ in a weighted way to increase signal-to-noise ratio and to emphasize the large seed producers:

$$M_{v,r} = \frac{\sum_{ij}\mathrm{ISP}_{ij}M_{v,ijr}}{\sum_{ij}\mathrm{ISP}_{ij}} \quad (9)$$

$$M_{p,r} = \frac{\sum_{ij}\mathrm{ISP}_{ij}M_{p,ijr}}{\sum_{ij}\mathrm{ISP}_{ij}} \quad (10)$$

where ISP is individual standardized productivity[58,63]. It is defined as seeds per tree times mass per seed divided by tree basal area and averaged across multiple years.

We evaluated the weighted synchronicity at ecoregion–species level following a similar procedure as that for volatility and periodicity. Tree-to-tree correlation coefficients were calculated between all conspecific individuals within 1 km of one another. We included correlations $M_{c,k}$ over years for which both trees of a pair k are estimated to be in the mature state (3,539,315 tree-years and 274,024 trees from 468 species). For the tree-to-tree correlations, both the correlation and the product of fecundity were calculated for each pair, the latter having large values for trees with high production. A weighted synchronicity over all trees of a species within 1 km was evaluated as

$$M_{c,r} = \frac{\sum_k M_{c,kr}C_k}{\sum_k C_k} \quad (11)$$

for all pairwise correlations $M_{c,kr}$ at ecoregion–species r, with weight C_k being the absolute value of the pairwise covariance, that is, the product of fecundities for each pair of trees k.

Analyses at ecoregion–species level

We evaluated variations in $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$ jointly at ecoregion–species level ($n = 583$) by incorporating phylogeny, species traits, soil and climate covariates in a generalized joint attribute model (GJAM). Our analyses were implemented at ecoregion–species level because 15% of the total species ($n = 468$) have within-species variations across ecoregions (Supplementary Data). The remaining (85%) species that were sampled at one ecoregion are primarily tropical species. As of now, MASTIF coverage could be improved with the addition of more sites in South America, Africa and Asia. One of the masting families, Dipterocarpaceae, is not included in the network. However, the MASTIF network is continuously expanding to achieve a more balanced global coverage. Ecoregions in this study follow the same definition as World Wildlife Fund (WWF) terrestrial ecoregions[79].

Phylogeny. We quantified the phylogenetic signal in volatility and quasi-periodicity using Pagel's λ. Species differences in masting syndromes were averaged across ecoregion–species combinations. Phylogeny was obtained for 394 species (84% of the total 468 species) from ref. 80. We used the continuous character mapping method from the R package 'phytools'[81] to visualize the phylogenetic coherence in volatility, periodicity, and synchronicity.

To account for phylogeny in the joint model of the three masting syndromes, we departed from traditional assumptions concerning residual covariance, turning instead to direct inference on the effects of phylogenetic groups. The aim to control for phylogenetic association in comparative studies[82,83] suggests a capacity to take up variation that might be linked to relatedness in a general sense. Instead, current methods impose a highly specific assumption that residual variance between species traits results from a random walk that proceeds at a fixed rate across species pairs. However, natural selection would not operate in this way, not for a given species pair and certainly not across a large number of species. Residual variance constitutes all sources of variation that are not taken up by the mean structure of the model. Just as there could be massive phylogenetically constrained traits between specific species pairs that have diverged under differing intensities of selection, there could be minimally constrained pairs within the same comparative study where others are strong. The important modelling concern for valid inference on coefficients is a covariance matrix that can take up relationships that remain after accounting for the mean, regardless of their source and without imposing specific assumptions about rates of divergence.

Our joint analyses of masting syndromes explored phylogenetic contributions, with species groups treated as random effects and covariance that is unconstrained by assumptions on divergence rates. Rather than assume a fixed relationship between residual covariances, our approach provides a transparent estimate for differences between species groups, allowing that they need not be anchored to pairwise divergence times. For genera having at least 10 species in the MASTIF data, species were grouped at the genus level. All remaining species in families having at least 5 species were grouped at the family level. Remaining species were aggregated into an 'other' group for purposes of model fitting, but they are displayed separately in the correlation plots (for example, Extended Data Fig. 3). Relationships between masting syndromes within each phylogenetic group were evaluated using Pearson's correlation coefficient.

Joint modelling of masting syndromes. To evaluate masting as a syndrome and the variables associated with it, we conducted joint analyses of mast attributes against predictors that include species traits, environment and phylogeny. Species traits included dispersal mode (anemochory vs zoochory), pollination mode (animal vs wind-pollinated syndromes), mean foliar N and P (percentage of dry mass) and seed size (g per seed). Traits information were obtained from collections in our labs and supplemented with the TRY database[84].

Genus or family-level means were used where seed size and foliar nutrients were missing at the species level. Similarly, genus or family-level modes were used for dispersal and pollination syndromes. Foliar N:P was calculated as the ratio between the two nutrients. Foliar N:P measures the nutrient limitations[33] and could affect the masting syndrome[29]. Environmental covariates included soil fertility (CEC), mean annual temperature (ranging from cold to warm) and accumulated annual moisture deficit (differences between potential evapotranspiration and precipitation, ranging from wet to dry) averaged at ecoregion–species level. We used GJAM[78] to allow for the dependence between mast components and the fact that masting components are non-negative (they are non-Gaussian),

$$\mathbf{w}_r \sim MVN(\mathbf{x}_r'\boldsymbol{\beta}, \Sigma) \times \prod_{l=1}^{S} I(w_{r,l} \le 0)^{I(M_{r,l}=0)} I(w_{r,l} > 0)^{I(M_{r,l}=w_{r,l})} \quad (12)$$

where $\mathbf{w}_r$ is the length-S vector holding the latent (and uncensored) mast response for ecoregion–species r and $\mathbf{M}_r$ is the length-S observation vector ($S = 3$ for the three components). Covariates occupy the length-Q vector $\mathbf{x}_r'$, including species traits and environmental conditions. Responses to covariates are included in the $Q \times S$ matrix of coefficients $\boldsymbol{\beta}$. The latent variable has the mean vector $\mathbf{x}_r'\boldsymbol{\beta}$ and $S \times S$ covariance matrix Σ. The product including indicator functions $I(\cdot)$ allows for negative values on the latent scale, essentially a multivariate Tobit[78].

Model fitting with GJAM included phylogeny as random groups (previous section). Variable selection was done using DIC as the criterion for additional predictors in the model. Volatility (response) and seed mass (covariates) were modelled on the log (proportionate) scale. Dispersal and pollination modes were included as factors. Standardized coefficients $\boldsymbol{\beta}$ were summarized using the posterior median, 90% and 95% credible intervals from the Markov chain Monte Carlo (MCMC) chains. GJAM fitting is open-access in the R package GJAM on CRAN.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Seed production data are available at the Duke Data Repository https://doi.org/10.7924/r4348ph5t. Species traits are downloaded from TRY Plant Trait database at https://www.try-db.org/TryWeb/Home.php. Cation exchange capacity data were obtained at https://soilgrids.org/. Climate data were extracted from Terraclimate at http://www.climatologylab.org/ and CHELSA at https://chelsa-climate.org/.

Code availability

R statistical software v.4.0.2 was used in this work. All analyses used published R packages, with details stated in Methods. MASTIF includes code in R and C++, which is published on CRAN at https://cran.r-project.org/web/packages/mastif/index.html.

References

1. Janzen, D. H. Seed predation by animals. *Annu. Rev. Ecol. Syst.* **2**, 465–492 (1971).
2. Kelly, D. & Sork, V. L. Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* **33**, 427–447 (2002).
3. Jansen, P. A., Bongers, F. & Hemerik, L. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol. Monogr.* **74**, 569–589 (2004).
4. Herrera, C. M., Jordano, P., Guitian, J. & Traveset, A. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *Am. Nat.* **152**, 576–594 (1998).
5. Siepielski, A. M. & Benkman, C. W. Conflicting selection from an antagonist and a mutualist enhances phenotypic variation in a plant. *Evolution* **64**, 1120–1128 (2010).
6. Wang, Y. Y. et al. Variation and synchrony of tree species mast seeding in an old-growth temperate forest. *J. Veg. Sci.* **28**, 413–423 (2017).
7. Huang, L. et al. Benefit versus cost trade-offs of masting across seed-to-seedling transition for a dominant subtropical forest species. *J. Ecol.* **109**, 3087–3098 (2021).
8. Seget, B. et al. Costs and benefits of masting: economies of scale are not reduced by negative density-dependence in seedling survival in *Sorbus aucuparia*. *New Phytol.* **233**, 1931–1938 (2022).
9. Clark, J. S., Nunez, C. & Tomasek, B. Foodwebs based on unreliable foundations: spatiotemporal masting merged with consumer movement, storage, and diet. *Ecol. Monogr.* **89**, e01381 (2019).
10. Janzen, D. Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528 (1970).
11. Clotfelter, E. D. et al. Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* **154**, 493–503 (2007).
12. Chen, W. et al. Proximity to roads disrupts rodents' contributions to seed dispersal services and subsequent recruitment dynamics. *J. Ecol.* **107**, 2623–2634 (2019).
13. Curran, L. M. & Leighton, M. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting dipterocarpaceae. *Ecol. Monogr.* **70**, 101–128 (2000).
14. Pearse, I. S., LaMontagne, J. M., Lordon, M., Hipp, A. L. & Koenig, W. D. Biogeography and phylogeny of masting: do global patterns fit functional hypotheses? *New Phytol.* **227**, 1557–1567 (2020).
15. Greenberg, C. H. Individual variation in acorn production by five species of southern Appalachian oaks. *For. Ecol. Manage.* **132**, 199–210 (2000).
16. Clark, J. S., LaDeau, S. & Ibanez, I. Fecundity of trees and the colonization-competition hypothesis. *Ecol. Monogr.* **74**, 415–442 (2004).
17. Chen, X., Brockway, D. G. & Guo, Q. Characterizing the dynamics of cone production for longleaf pine forests in the southeastern United States. *For. Ecol. Manage.* **429**, 1–6 (2018).
18. Pucek, Z., Jedrzejewski, W., Jedrzejewska, B. & Pucek, M. Rodent population-dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. *Acta Theriol.* **38**, 199–232 (1993).
19. Bogdziewicz, M., Zwolak, R. & Crone, E. E. How do vertebrates respond to mast seeding? *Oikos* **125**, 300–307 (2016).
20. Christensen, K. M. & Whitham, T. G. Impact of insect herbivores on competition between birds and mammals for pinyon pine seeds. *Ecology* **74**, 2270–2278 (1993).
21. Crone, E. E. & Rapp, J. M. Resource depletion, pollen coupling, and the ecology of mast seeding. *Ann. N. Y. Acad. Sci.* **1322**, 21–34 (2014).
22. Steele, M. A. & Yi, X. Squirrel-seed interactions: the evolutionary strategies and impact of squirrels as both seed predators and seed dispersers. *Front. Ecol. Evol.* https://doi.org/10.3389/fevo.2020.00259 (2020).
23. Pearse, I. S., Koenig, W. D. & Kelly, D. Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytol.* **212**, 546–562 (2016).
24. Janzen, D. H. Tropical blackwater rivers, animals, and mast fruiting by the dipterocarpaceae. *Biotropica* **6**, 69–103 (1974).
25. Smaill, S. J., Clinton, P. W., Allen, R. B. & Davis, M. R. Climate cues and resources interact to determine seed production by a masting species. *J. Ecol.* **99**, 870–877 (2011).
26. Tanentzap, A. J., Lee, W. G. & Coomes, D. A. Soil nutrient supply modulates temperature-induction cues in mast-seeding grasses. *Ecology* **93**, 462–469 (2012).

27. Fernández-Martínez, M. et al. Nutrient scarcity as a selective pressure for mast seeding. *Nat. Plants* **5**, 1222–1228 (2019).
28. Rosecrance, R. C., Weinbaum, S. A. & Brown, P. H. Alternate bearing affects nitrogen, phosphorus, potassium and starch storage pools in mature pistachio trees. *Ann. Bot.* **82**, 463–470 (1998).
29. Sala, A., Hopping, K., McIntire, E. J. B., Delzon, S. & Crone, E. E. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytol.* **196**, 189–199 (2012).
30. Sork, V. L. Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.). *Vegetatio* **107**, 133–147 (1993).
31. Sharma, A., Weindorf, D. C., Wang, D. D. & Chakraborty, S. Characterizing soils via portable X-ray fluorescence spectrometer: 4. Cation exchange capacity (cec). *Geoderma* **239**, 130–134 (2015).
32. Hazelton, P. & Murphy, B. *Interpreting Soil Test Results: What Do All the Numbers Mean?* (CSIRO Publishing, 2016).
33. Elser, J. J. et al. Growth rate-stoichiometry couplings in diverse biota. *Ecol. Lett.* **6**, 936–943 (2003).
34. Kelly, D. et al. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecol. Lett.* **16**, 90–98 (2013).
35. Schauber, E. M. et al. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* **83**, 1214–1225 (2002).
36. Espelta, J. M., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B. & Retana, J. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. *Ecology* **89**, 805–817 (2008).
37. Pérez-Ramos, I. M., Ourcival, J. M., Limousin, J. M. & Rambal, S. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology* **91**, 3057–3068 (2010).
38. Koenig, W. D., Knops, J. M. H., Carmen, W. J. & Pearse, I. S. What drives masting? The phenological synchrony hypothesis. *Ecology* **96**, 184–192 (2015).
39. Wion, A. P., Weisberg, P. J., Pearse, I. S. & Redmond, M. D. Aridity drives spatiotemporal patterns of masting across the latitudinal range of a dryland conifer. *Ecography* **43**, 569–580 (2020).
40. LaMontagne, J. M., Pearse, I. S., Greene, D. F. & Koenig, W. D. Mast seeding patterns are asynchronous at a continental scale. *Nat. Plants* **6**, 460–465 (2020).
41. Vacchiano, G. et al. Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytol.* **215**, 595–608 (2017).
42. Clark, J. S., Bell, D. M., Kwit, M. C. & Zhu, K. Competition-interaction landscapes for the joint response of forests to climate change. *Glob. Change Biol.* **20**, 1979–1991 (2014).
43. Lamontagne, J. M. & Boutin, S. Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. *J. Ecol.* **95**, 991–1000 (2007).
44. Straub, J. N., Leach, A. G., Kaminski, R. M., Ezell, A. W. & Leininger, T. D. Red oak acorn yields in green-tree reservoirs and non-impounded forests in Mississippi. *Wildl. Soc. Bull.* **43**, 491–499 (2019).
45. Ascoli, D. et al. Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nat. Commun.* **8**, 2205 (2017).
46. Hacket-Pain, A. J., Friend, A. D., Lageard, J. G. & Thomas, P. A. The influence of masting phenomenon on growth-climate relationships in trees: explaining the influence of previous summers' climate on ring width. *Tree Physiol.* **35**, 319–330 (2015).
47. Berdanier, A. B. & Clark, J. S. Divergent reproductive allocation trade-offs with canopy exposure across tree species in temperate forests. *Ecosphere* **7**, e01313 (2016).
48. Redmond, M. D., Forcella, F. & Barger, N. N. Declines in pinyon pine cone production associated with regional warming. *Ecosphere* **3**, 120 (2012).
49. Whipple, A. V. et al. Long-term studies reveal differential responses to climate change for trees under soil- or herbivore-related stress. *Front. Plant Sci.* **10**, 132 (2019).
50. Bogdziewicz, M., Kelly, D., Thomas, P. A., Lageard, J. G. A. & Hacket-Pain, A. Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nat. Plants* **6**, 88–94 (2020).
51. Espelta, J. M., Bonal, R. & Sanchez-Humanes, B. Pre-dispersal acorn predation in mixed oak forests: interspecific differences are driven by the interplay among seed phenology, seed size and predator size. *J. Ecol.* **97**, 1416–1423 (2009).
52. Yamauchi, A. Theory of mast reproduction in plants: storage-size dependent strategy. *Evolution* **50**, 1795–1807 (1996).
53. Koenig, W. D. & Knops, J. M. H. The mystery of masting in trees: some trees reproduce synchronously over large areas, with widespread ecological effects, but how and why? *Am. Sci.* **93**, 340–347 (2005).
54. LaMontagne, J. M. & Boutin, S. Quantitative methods for defining mast-seeding years across species and studies. *J. Vege. Sci.* **20**, 745–753 (2009).
55. Clark, J. S. Individuals and the variation needed for high species diversity in forest trees. *Science* **327**, 1129–1132 (2010).
56. Shibata, M., Masaki, T., Yagihashi, T., Shimada, T. & Saitoh, T. Decadal changes in masting behaviour of oak trees with rising temperature. *J. Ecol.* **108**, 1088–1100 (2020).
57. Clark, J. S. et al. Continent-wide tree fecundity driven by indirect climate effects. *Nat. Commun.* **12**, 1242 (2021).
58. Qiu, T. et al. Limits to reproduction and seed size-number trade-offs that shape forest dominance and future recovery. *Nat. Commun.* **13**, 2381 (2022).
59. Vander Wall, S. B. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Phil. Trans. R. Soc. B* **365**, 989–997 (2010).
60. Zwolak, R., Bogdziewicz, M., Wrobel, A. & Crone, E. E. Advantages of masting in European beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia* **180**, 749–758 (2016).
61. Larue, C., Austruy, E., Basset, G. & Petit, R. J. Revisiting pollination mode in chestnut (*Castanea* spp.): an integrated approach. *Bot. Lett.* **168**, 348–372 (2021).
62. Garcia, G., Re, B., Orians, C. & Crone, E. By wind or wing: pollination syndromes and alternate bearing in horticultural systems. *Phil. Trans. R. Soc. B* **376**, 20200371 (2021).
63. Journe, V. et al. Globally, tree fecundity exceeds productivity gradients. *Ecol. Lett.* **25**, 1471–1482 (2022).
64. Smith, C. C., Hamrick, J. L. & Kramer, C. L. The advantage of mast years for wind pollination. *Am. Nat.* **136**, 154–166 (1990).
65. Augspurger, C. K. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators in *Hybanthus prunifolius* (Violaceae). *Ecology* **62**, 775–788 (1981).
66. Crone, E. E. Responses of social and solitary bees to pulsed floral resources. *Am. Nat.* **182**, 465–473 (2013).
67. Koenig, W. D. et al. Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* **102**, 581–591 (2003).
68. Satake, A. & Kelly, D. Studying the genetic basis of masting. *Phil. Trans. R. Soc. B* **376**, 20210116 (2021).
69. Mueller, R. C., Wade, B. D., Gehring, C. A. & Whitham, T. G. Chronic herbivory negatively impacts cone and seed production, seed quality and seedling growth of susceptible pinyon pines. *Oecologia* **143**, 558–565 (2005).
70. Schopmeyer, C. S. et al. *Seeds of Woody Plants in the United States* (US Department of Agriculture, 1974).

71. Crawley, M. J. & Long, C. R. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *J. Ecol.* **83**, 683–696 (1995).
72. Manson, R. H., Ostfeld, R. S. & Canham, C. D. The effects of tree seed and seedling density on predation rates by rodents in old fields. *Écoscience* **5**, 183–190 (1998).
73. Zwolak, R., Celebias, P. & Bogdziewicz, M. Global patterns in the predator satiation effect of masting: a meta-analysis. *Proc. Natl Acad. Sci. USA* **119**, e2105655119 (2022).
74. Bascompte, J. Mutualistic networks. *Front. Ecol. Environ.* **7**, 429–436 (2009).
75. Qui, T. et al. Is there tree senescence? The fecundity evidence. *Proc. Natl Acad. Sci USA* **118**, e2106130118 (2021).
76. Clark, J. S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* **80**, 1475–1494 (1999).
77. Tobin, J. Estimation of relationships for limited dependent variables. *Econometrica* **26**, 24–36 (1958).
78. Clark, J. S., Nemergut, D., Seyednasrollah, B., Turner, P. J. & Zhang, S. Generalized joint attribute modeling for biodiversity analysis: median-zero, multivariate, multifarious data. *Ecol. Monogr.* **87**, 34–56 (2017).
79. Olson, D. M. et al. Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933–938 (2001).
80. Zanne, A. E. et al. Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**, 89–92 (2014).
81. Revell, L. J. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223 (2012).
82. Freckleton, R. P., Harvey, P. H. & Pagel, M. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726 (2002).
83. Hadfield, J. D. & Nakagawa, S. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J. Evol. Biol.* **23**, 494–508 (2010).
84. Kattge, J. et al. TRY plant trait database – enhanced coverage and open access. *Glob. Change Biol.* **26**, 119–188 (2020).

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Author contributions

J.S.C. and T.Q. designed the study, performed analyses and wrote the paper. J.S.C. compiled the MASTIF data and wrote the MASTIF model and software. M.B., B.C., V.J. and G.K. co-wrote the paper. T.Q., M.-C.A., D.A., Y.B., M.B., T.B., R.B., T.C., M.C., R.C., S.D.C., J.J.C., C.-H.C-Y., J.C., F.C., B.C., A.C., A.J.D., N.D., S.D., M.D., L.D., J.M.E., T.J.F., W.F.-R., J.F.F., C.A.G., G.S.G., G.G., C.H.G., A.G., Q.G., A.H.-P., A.H., Q.H., J.H., K.H., I.I., J.F.J., V.J., T.K., J.M.H.K., G.K., H.K., J.G.A.L., J.M.L., F.L., T.L., J.-M.L., J.A.L., D.M., A.M., E.J.B.M., C.M.M., E.M., R.M., J.A.M., T.A.N., S.N., M.N., M.O., R.P., I.S.P., I.M.P.-R., L.P., T.P., J.P., M.D.R., C.D.R., K.C.R., F.R.-S., P.S., J.D.S., C.L.S., B.S., S. Sharma, M. Shibata, M. Silman, M.A.S., N.L.S., J.N.S., S. Sutton, J.J.S., M. Swift, P.A.T., M.U., G.V., A.V.W., T.G.W., A.P.W., S.J.W., K.Z., J.K.Z., M.Z. and J.S.C. contributed data and revised the paper.

Competing interests

The authors declare no competing interests.

Additional information

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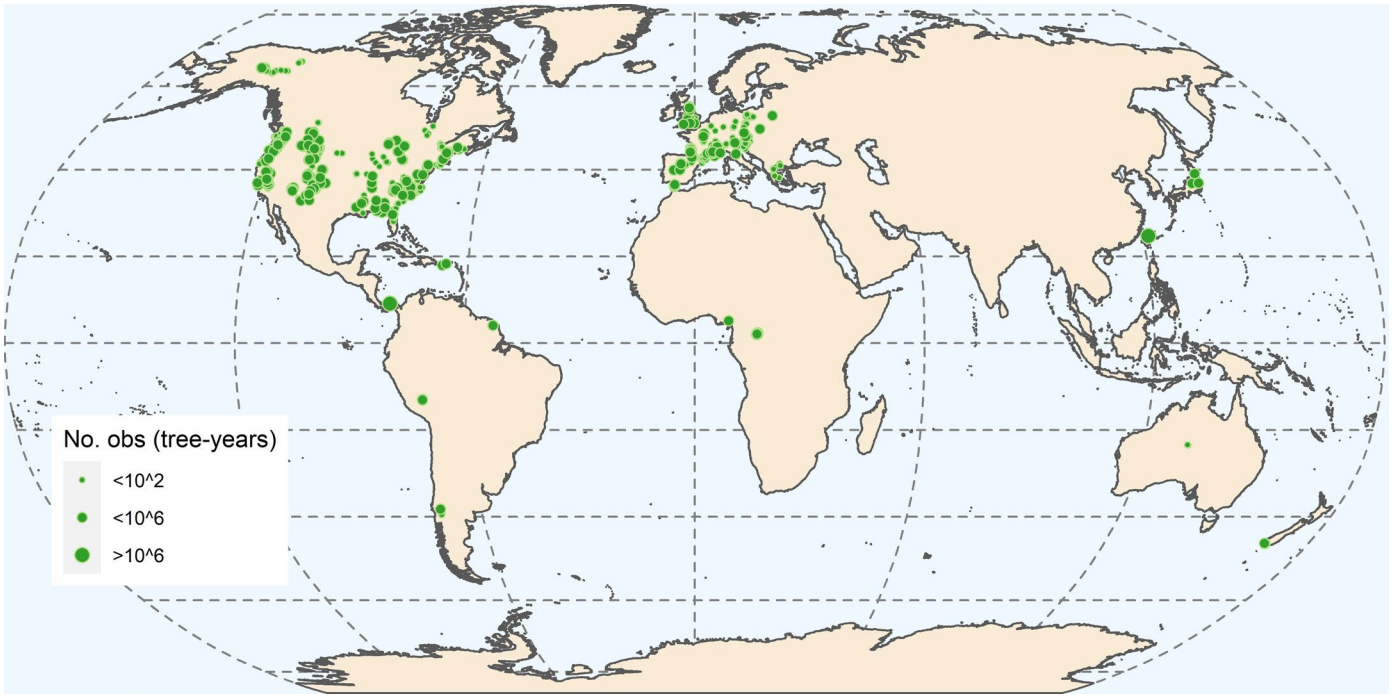

Extended Data Fig. 1 | MASTIF sites. The summary of MASTIF sites with symbol size proportional to observations. Detailed data distribution is in the supplementary csv file.

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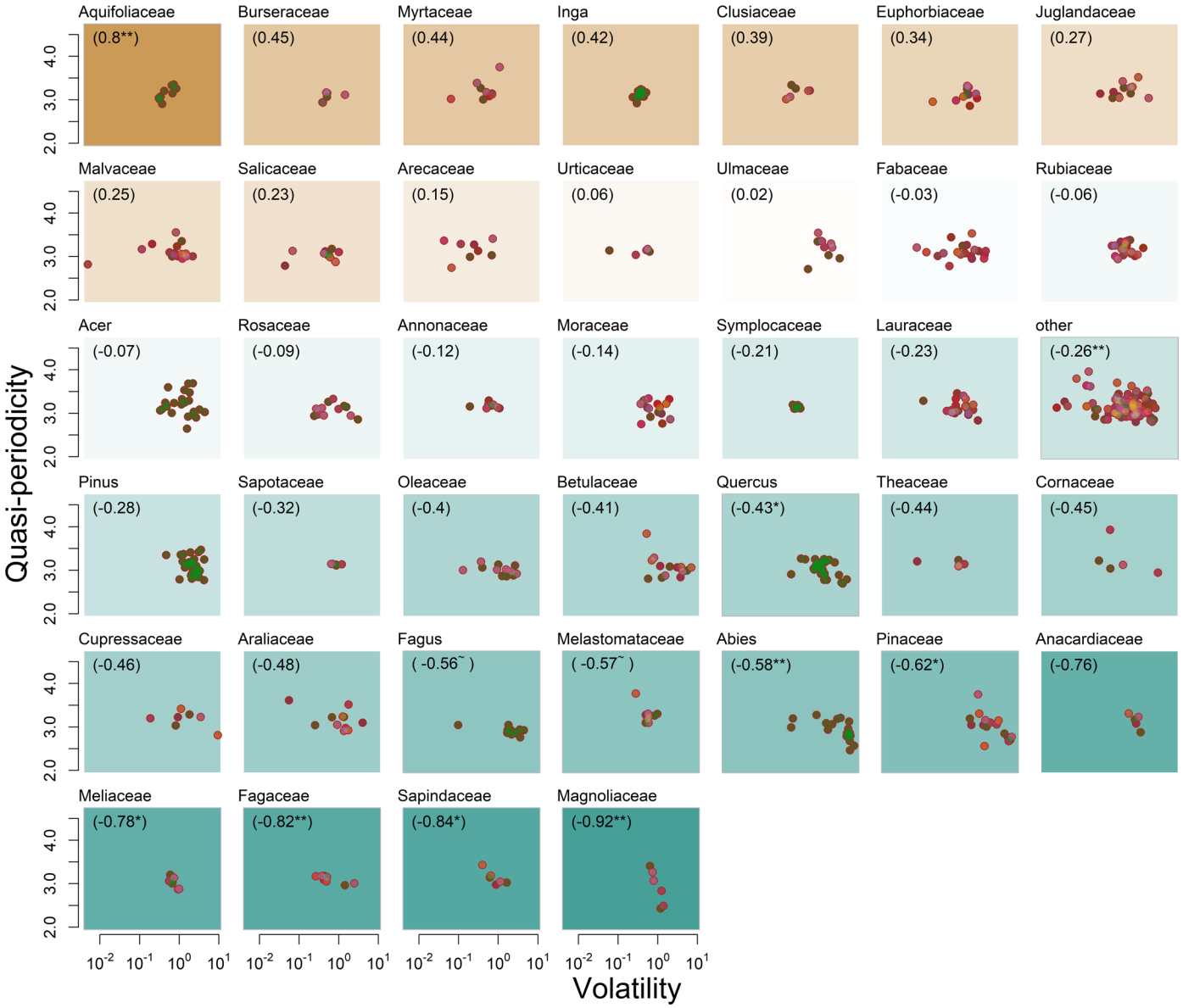

Extended Data Fig. 2 | Correlations between volatility and quasi-periodicity. Correlations between volatility and quasi-periodicity at ecoregion/species level within phylogenetic groups (see methods). Top-left labels include Pearson's correlation coefficients (two-sided test), including those that are significant (-, *, **, and ***) indicate 0.1, 0.05, 0.01, and 0.001 significant level, respectively. Shading represents positive (brown) and negative (teal) correlations. Colors of the points indicate different genera within each phylogenetic group. Across all ecoregion/species level observations, volatility is negatively correlated with quasi-periodicity (-0.28, 95% CI = (-0.36,-0.21)).

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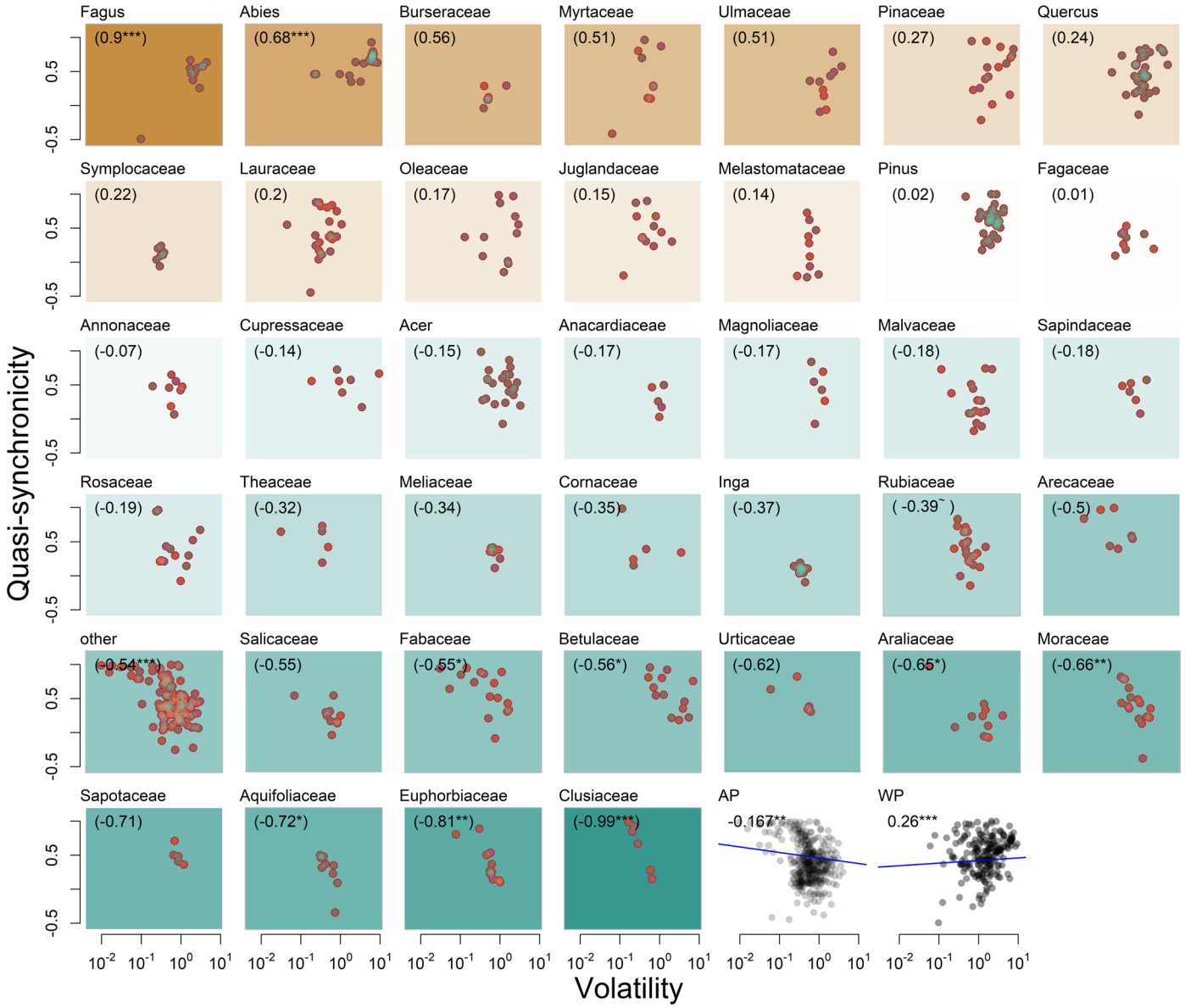

Extended Data Fig. 3 | Correlations between volatility and synchronicity. Correlations between volatility and synchronicity at the ecoregion-species level within phylogenetic groups (see Methods). Symbology follows the extended data fig. 2. Volatility is negatively associated with synchronicity for animal pollinated (AP) species (-0.17, 95% CI = (-0.06,-0.26)) while positively associated with synchronicity for wind pollinated (WP) species (0.26, 95% CI = (0.13,0.39)). Blue lines in AP and WP panels indicate linear regression.

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection.
Data analysis	R statistical software (v 4.0.2) was used in this work. All analyses used published R packages, with details stated in the section Methods. The packages include phytools v0.7-70, gjam v2.5.1, mastif v1.0.1

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Seed production data are available at the Duke Data Repository (https://doi.org/10.7924/r4348ph5t). Species traits are downloaded from TRY Plant Trait database at https://www.try-db.org/TryWeb/Home.php. Cation exchange capacity data are obtained at https://soilgrids.org/. Climate data are extracted from Terraclimate at http://www.climatologylab.org/ and CHELSA at https://chelsa-climate.org/.

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Population characteristics	Not applicable
Recruitment	Not applicable
Ethics oversight	Not applicable

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We quantified three masting syndromes, including volatility, periodicity, and synchronicity, for 583 species-ecoregions from 2,841,238 mature tree-years that has at least 10 years of data. The synthesis covers all vegetated continents across the globe. We used two data types including crop counts and seed traps.
Research sample	Each sample is a tree-year observation, i.e., an individual tree at a given year.
Sampling strategy	This study use all data from crop counts and seed traps. The methods that accounts for dependences between the two data types are detailed in the paper with citation Clark et al., 2019 (Ecological Monographs).
Data collection	Seed traps were used to capture seeds falling from trees. Seed trap data were collected by emptying the traps multiple times each year. Crop counts were collected with binoculars. All authors collected data.
Timing and spatial scale	Observations ranged from year 1960 to the present and were collected in North America, South and Central America, Africa, Europe, Asia, and Oceania. Seed trap were emptied multiple times every year. Crop counts were collected annually when trees were fruiting.
Data exclusions	No data were excluded in this study.
Reproducibility	No experiments were performed in this study. Previous published data and existing R packages from CRAN were used in this study. Results can be reproduced following the method section.
Randomization	Randomization is not applicable because no experiments were performed in this study
Blinding	Blinding is not applicable because no experiments were performed in this study

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Temperature and moisture deficit conditions are detailed in the paper with citation Qiu et al., 2022 (nature communications)
Location	Plot coordinates are detailed in the paper with citation Qiu et al., 2022 (nature communications)
Access & import/export	Individual authors that contribute data determined the access to the plot
Disturbance	No disturbance was caused by the study

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☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging