

Mutualist dispersers and the global distribution of masting: mediation by climate and fertility

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Abstract

The benefits of masting (volatile, quasi-synchronous seed production at lagged intervals) include satiation of seed predators, but these benefits come with the 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 the 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 12.1 million tree-years worldwide, we quantified three components of masting that have not previously been analyzed together: 1) volatility (frequency-weighted year-to-year variation); 2) periodicity (lag between high-seed years); and 3) synchronicity (tree-to-tree correlation). Results show that mast avoidance (low volatility, low synchronicity) by species dependent on mutualist dispersers explains more variation than any other effect. Nutrient-demanding species, species that are most common on nutrient-rich and warm/wet sites have low volatility and short periods. The prevalence of masting in cold/dry sites coincides with climates 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, fertility, and nutrient demands.

Keywords: *masting, periodicity, pollination, synchronicity, seed production, seed dispersal, traits, volatility*

1 Introduction

2 Unpredictable reproduction in trees (“masting”) could be an evolved response to thwart seed consumers
3 (Janzen, 1971; Kelly and Sork, 2002; Jansen et al., 2004), but then there is a conundrum: the volatility
4 that limits seed predators could be just as deleterious to mutualist pollen and seed dispersers (Herrera
5 et al., 1998; Kelly and Sork, 2002; Wang et al., 2017), while also concentrating competition within off-
6 spring (Huang et al., 2021; Seget et al., 2022). For natural enemies and mutualists alike, masting effects
7 depend on three elements (fig. 1), i) year-to-year *volatility*, or the time-dependent magnitude of varia-
8 tion, ii) *quasi-periodicity*, the lag between high seed-production years, and iii) *quasi-synchronicity*, the
9 tendency for individuals to produce large seed crops in the same years (Clark et al., 2019). Explanations
10 for forest diversity invoke combinations of these three elements (Janzen, 1970; Clotfelter et al., 2007;
11 Chen et al., 2019), but they operate together: the costs and benefits of masting depend on the interac-
12 tions between them and the foraging ranges of consumers and dispersers (Curran and Leighton, 2000;
13 Clark et al., 2019). Meta-analyses provide important insights at the aggregate population or species
14 scale (Pearse et al. (2020)) but miss the volatility within and synchronicity between trees (Greenberg,
15 2000; Clark et al., 2004; Chen et al., 2018). Efforts to generalize species- and site-specific results confront
16 a diversity of methods, measurements, and scales used in each study. In this paper we integrate raw
17 data at the individual tree-scale from all vegetated continents to allow formal inference on the joint
18 distribution of masting components. We show that variation of masting components across the diversity
19 of tree species depends on how seeds and pollen are dispersed, indicating that mutualists may be just as
20 important as consumers for the evolution of masting. Results show mediation of these effects by climate,
21 soil fertility, and nutrient demand.

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

32 The adaptive foundation for masting may involve escape from natural enemies that are satiated by
33 large, quasi-synchronized crops and limited by intervening lean years (Pucek et al., 1993; Bogdziewicz
34 et al., 2016), but this same variation can likewise negatively impact mutualists (fig. 2a). Scatter-hoarding
35 birds and rodents can be both seed predators and mutualists, consuming the entire seed crop in some
36 years, while also aiding reproduction through seed burial (Christensen and Whitham, 1993). Predator
37 satiation is most likely with high reproductive volatility, long periods between high-yield years, and
38 synchronicity between trees; this synchronicity reduces a consumer’s capacity to simply average over
39 inter-annual variation in one host tree by accessing others (Curran and Leighton, 2000; Clark et al.,
40 2019) (fig. 2a). For example, erratic seed production by individual trees (volatile and quasi-periodic)
41 may not deter natural enemies if high-production years are asynchronous between trees (Clark et al.,
42 2019). Any negative effects of quasi-periodic variation on a tree’s consumers would be amplified by
43 high year-to-year variation, especially when concentrated at long lags (Kelly and Sork, 2002; Crone and
44 Rapp, 2014), again, defined here as *volatility*. Weighing against the benefits of unreliable fruiting for its
45 deleterious effects on enemies are the negative effects on mutualist dispersers (Herrera et al., 1998; Kelly
46 and Sork, 2002; Steele and Yi, 2020); the predator satiation hypothesis might not benefit species that
47 are reliant on specialized pollinators and seed dispersers.

48 While volatility amplifies the effects of periodicity and synchronicity on enemies and benefactors
49 alike, this same volatility could be mediated by resource availability and climate (Crone and Rapp, 2014;
50 Pearse et al., 2016) (fig. 2). Limited resources might promote reproductive variation in trees (Janzen,
51 1974; Smaill et al., 2011; Tanentzap et al., 2012) or not (Fernández-Martínez et al., 2019). The mast
52 interval could be prolonged where large crops deplete reserves that require years to replenish (Rosecrance
53 et al., 1998; Sala et al., 2012; Crone and Rapp, 2014; Sork, 1993) or not (Pearse et al., 2020; Fernández-
54 Martínez et al., 2019). In this global analysis, we use cation exchange capacity (CEC), a widely used
55 index of soil fertility (Sharma et al., 2015; Hazelton and Murphy, 2016), and foliar nitrogen (N) and
56 phosphorous (P) concentrations (Fernández-Martínez et al., 2019) to quantify the association between
57 masting and resource supply (CEC) and resource demand: nutrient demanding species tend to have high

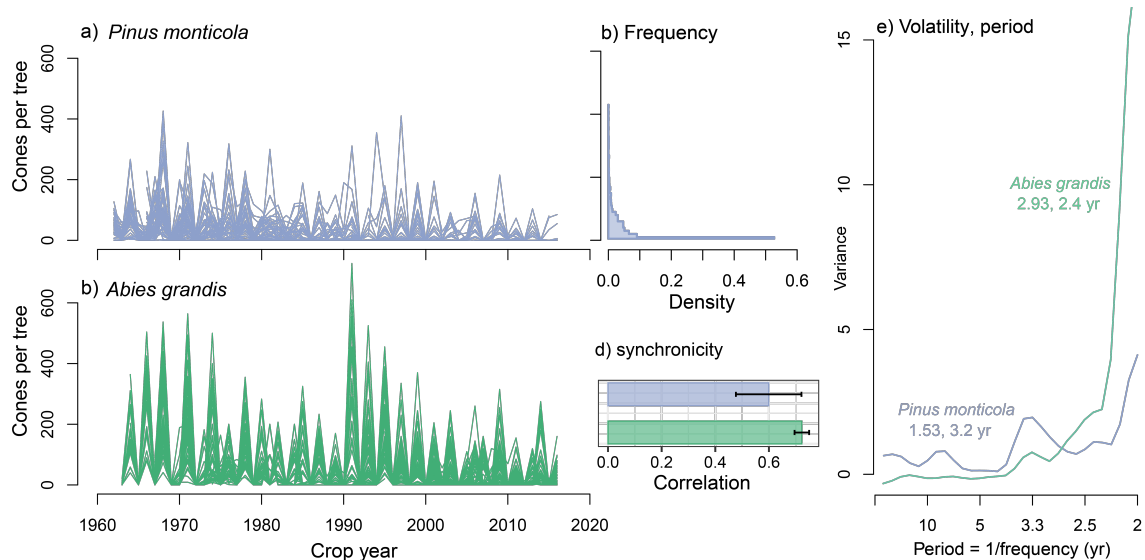


Fig. 1: *Pinus monticola* and *Abies grandis* from the central Cascades. Crop counts for these species (a, b) vary between individual trees, and they drift over time. The frequency of *P. monticola* counts (c) shows that zeros dominate, and there is no threshold that could be used to define masting events. *A. grandis* shows higher synchronicity between individuals (mean pairwise correlations between trees are shown in d) and higher volatility, especially concentrated at the 2-yr period (e). *P. monticola* also shows variance concentrated at 2-yr, with a secondary peak at 3.4 yr. The (volatility, period) for this example are shown beneath species names in (e) (Methods).

58 foliar N and P (Elser et al., 2003).

59 In addition to site differences in resources and climate norms, weather anomalies might contribute
60 to large seed crops (e.g. Kelly et al. (2013)), especially for species with limited dependence on stored
61 reserves (Janzen, 1971; Pearse et al., 2016). An *anomaly* is defined here as the difference between a
62 climate variable in a given year from the average of that variable for that site (the site *norm*). At least
63 for a few species at one or a few sites, warm and wet years may be associated with low seed production
64 (Schauber et al., 2002; Espelta et al., 2008; Pérez-Ramos et al., 2010; Koenig et al., 2015; Wion et al.,
65 2020) and increased reproductive synchronicity (LaMontagne et al., 2020; Vacchiano et al., 2017) (fig. 2a).

66 Because the distribution of species across environments is uneven, species differences cannot be fully
67 assessed from observational data, which dominate the masting literature. For example, climate anomalies
68 in specific seasons are clearly important for many temperate species (Clark et al., 2014; Koenig et al.,
69 2015; Vacchiano et al., 2017; LaMontagne et al., 2020), but our analysis evaluates variation globally,
70 spanning seasonal and a-seasonal environments. The effect of a climate anomaly such as temperature
71 or moisture must depend on the climate norm at each site, including seasonality. For example, the
72 estimated effect of an spring-time temperature anomaly of 1°C is not comparable between highly seasonal
73 taiga and a-seasonal wet tropics, where the notion of spring is not relevant. Including an interaction
74 between anomalies and norms in data models cannot clarify their respective contributions, because species
75 are not observed across the same combinations of norms and anomalies in the data. For this reason,
76 environmental anomalies are limited here to annual variation in temperature and moisture deficit, and
77 comparisons between species in fig. 2a include the caveat that we are not observing all of them in all of
78 the same settings.

79 The three components of masting have not been analyzed together, in part, because a joint analysis re-
80 quires substantial data at the individual (tree-year) scale. Unless individuals are perfectly synchronized,
81 periodicity at the population scale underestimates periodicity at the individual scale; in fact, asyn-
82 chronicity can entirely mask periodic reproduction where observed with population-scale data. Studies
83 that examine both individual and population variation show that fecundity is typically quasi-synchronous
84 at best (Greenberg, 2000; Lamontagne and Boutin, 2007; Clark et al., 2019; Chen et al., 2018; Straub
85 et al., 2019). Understanding spatial scales (Ascoli et al., 2017), allocation tradeoffs (Hackett-Pain et al.,
86 2015; Berdanier and Clark, 2016), responses to climate (Redmond et al., 2012; Clark et al., 2014; Whipple
87 et al., 2019; Wion et al., 2020; Bogdziewicz et al., 2020), and effects on consumers (Espelta et al., 2009;
88 Clark et al., 2019) and dispersers (Herrera et al., 1998; Kelly and Sork, 2002) all require joint analysis
89 of reproductive variance within and between individuals.

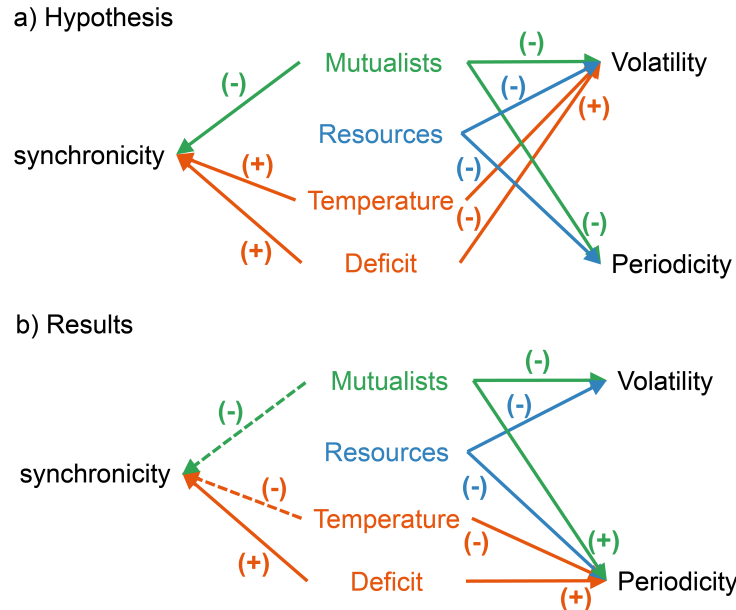


Fig. 2: a) Hypothesized effects of mutualists (green), resources (blue), and climate (red) on the three masting components. Arrows with + and - represent positive and negative effects, respectively. Tree species with low volatility, short periodicity, and low synchronicity benefit most from their mutualist pollinators and dispersers. Resources reduce volatility and periodicity. High temperature decreases volatility while promoting synchronicity. Dry sites have higher volatility and synchronicity than wet sites. b) Summary of results from the joint model in fig. 3. Dashed lines indicate that 90% credible intervals contain zero.

90 Synthesis is challenged not just by the incompatible reference used in literature studies (Supplement),
 91 but also by a need for measures of volatile, periodic, synchronous variability. All three elements vary
 92 between species and regions. The commonly used coefficient of variation (CV) omits time and frequency,
 93 one of the defining features of masting, and applications of CV to log values cannot properly incorporate
 94 zeros. This is important, because zero is the most frequent observation in many data sets (e.g., fig. 1c)
 95 (Supplement). Estimating periodicity requires a definition for what constitutes a mast year (Sork, 1993;
 96 Yamauchi, 1996; Koenig and Knops, 2005; LaMontagne and Boutin, 2009), which is challenging because
 97 there is no identifiable threshold (e.g., fig. 1c). The interval between mast years that would come from
 98 imposing an artificial threshold can range widely, in part due to variation within and between trees
 99 (Clark, 2010; Shibata et al., 2020). Using methods developed in this study, *P. monticola* (fig. 1a) and
 100 *A. grandis* (fig. 1b) share biennial variation but differ in the secondary concentration of variance at 3
 101 to 4 yr in *P. monticola*. The period-weighted variance spectrum (to emphasize low-frequency) gives
 102 estimates of 2.4 and 3.2 yr in *P. monticola* and *A. grandis*, respectively (fig. 1e). Not only are both
 103 species strongly biennial, they are also quasi-synchronous, with mean pairwise individual correlations
 104 being especially high for *A. grandis* (0.72 ± 0.12 compared with 0.60 ± 0.27 in *P. monticola*) (fig. 1d).
 105 Quasi-synchronicity between trees within a species can extend over regions (LaMontagne et al., 2020;
 106 Vacchiano et al., 2017; Ascoli et al., 2017), but it is not global. In our case, regional variation is defined
 107 at the eco-region scale, and synchronicity is evaluated at the 1-km scale (Methods).

108 Our approach that leads to the summaries in fig. 1 takes the perspective of each tree as a time series,
 109 with dependence between individuals, using a state-space representation for maturation and fecundity
 110 status (Clark et al., 2004, 2014). A model that allows for dependent observations is especially important
 111 for masting, where synchronicity means that a single individual may offer almost the same information as
 112 an entire population. In our approach, dependent observations are taken up by the correlation structure
 113 contained in the posterior distribution of latent states, one for each tree-year. The approach can allow for
 114 either year effects or autoregressive [AR(p) with lag p] terms as alternative ways to incorporate variation
 115 over time. Zeros are accommodated by a hidden Markov process for maturation status and allowance for
 116 failed crops with censoring (see Methods). Year effects that are random by ecoregion have the advantage
 117 that they do not assume a fixed AR structure over time (Clark et al., 2019).

118 In three steps, we evaluate masting across species with contrasting reliance on mutualist dispersers at
 119 the global scale, and how the relationship between masting and mutualists varies with resources, climate,
 120 and phylogeny. We hypothesized that mutualist pollinators and dispersers select for low volatility, short

121 periods, and low synchronicity (Herrera et al., 1998; Kelly and Sork, 2002; Clark et al., 2019) (fig. 2a). We
 122 expected that nutrient-demanding species and species that commonly occur on fertile sites tend toward
 123 low volatility, rapid replenishment times following large crops and, thus, short periods (Sala et al., 2012;
 124 Pearse et al., 2016) (fig. 2a). We further hypothesized that warm climates favor low volatility and high
 125 synchronicity (Kelly and Sork, 2002; Pearse et al., 2020; LaMontagne et al., 2020), while dry climates
 126 (high moisture deficit) favor high volatility and synchronicity (Ascoli et al., 2017; Vacchiano et al., 2017)
 127 (fig. 2a). To test those hypotheses, we begin by extracting the three components of masting (fig. 1)
 128 from inter-annual and inter-tree variation (Clark et al., 2019) using methods that derive from signal-
 129 processing for the time-series aspect of data and tree-to-tree correlation. Second, individual time series
 130 were aggregated by ecoregion-species, weighted by fecundity to emphasize large producers (Clark et al.,
 131 2021; Qiu et al., 2021) (Methods). Finally, we evaluated the effects of pollen and seed dispersal modes,
 132 resources, and climate on the joint response of masting components, both including and controlling for
 133 phylogeny.

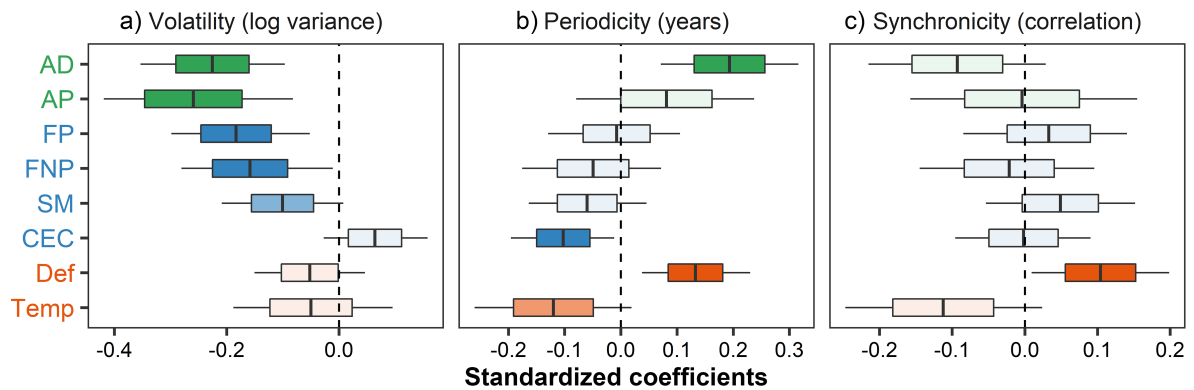


Fig. 3: **Variables that contribute to the joint response of masting components** including volatility (a), periodicity (b), and synchronicity (c) at ecoregion-species scales. Predictors include vertebrate dispersers (animal seed dispersal (AD), animal pollination (AP)), resources (soil cation exchange capacity (CEC), foliar P (FP), and foliar N:P ratio (FNP)), seed mass (SM), and climate (mean annual temperature (Temp), accumulated moisture deficit (Def)). Dispersal and pollination syndromes are included as two-level factors, so the negative coefficients for animal seed dispersal (AD) and pollination (AP) have as mirror images the (positive) effects of wind dispersal and pollination (not shown). 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. Colors 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 hypotheses.

134 Results

135 Across all species in the study, dependence on mutualist dispersers is linked to low masting volatility
 136 (fig. 3a). Volatility for species that depend on animals for seed and/or pollen dispersal is substantially
 137 lower than that for wind-pollinated flowers and wind-dispersed seeds. The link between volatility and
 138 dispersal syndrome is mediated by resources and climate (fig. 3a). In addition to wind dispersal (the
 139 positive mirror images of negative AD and AP in fig. 3a), high volatility is associated with low nutrient
 140 demand (low foliar P and N:P) and with fertile soils (cation exchange capacity, CEC in fig. 3a). Of
 141 course, there is within-species variation in response to fertility (Qiu et al., 2022), which is distinct from
 142 the mean CEC on which species are located, as used in this study. There is a weak tendency for low
 143 volatility in cold, moist climates (credible intervals include zero for Temp and Def in fig. 3a). High
 144 volatility is further associated with small seeds ($SM < 0$).

145 The volatility relationships are not isolated from the two other components of masting. High peri-
 146 odicity values in fig. 3b mean that there are long periods between high-yield years. High synchronicity
 147 values in fig. 3c mean that individuals produce large crops in the same years, and vice versa. Because
 148 period and synchronicity are important only for trees with non-negligible seed production, both are
 149 weighted here by individual fecundity (see Methods). In the case of synchronicity, the distribution of
 150 pairwise correlations for trees of the same species within 1 km of one another (see Methods) has the

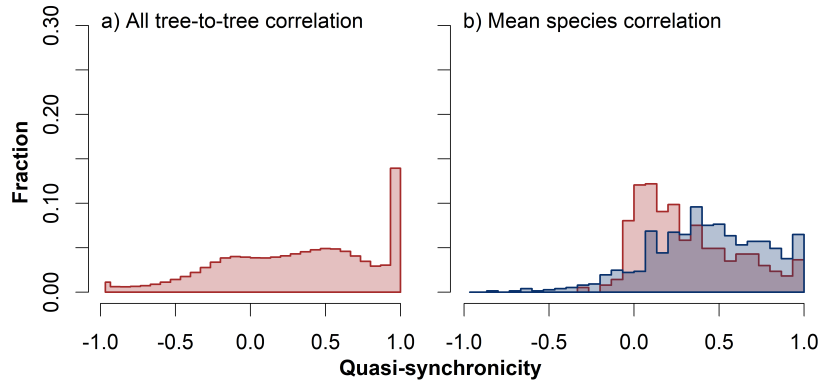


Fig. 4: **Quasi-synchronicity at individual and species level** a) Correlations between every pair of trees of the same species within 1 km show a mode near one, but a broad range. b) Species average correlations are concentrated near zero (red), but fecundity-weighted correlations are substantially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

151 mode near +1, but is broadly distributed over negative and positive values (fig. 4a). When aggregated
 152 to the species level (averaged over pairwise correlations for the species), the distribution shifts to pre-
 153 dominantly positive values (fig. 4b, red). When weighted by fecundity, these averages increase further
 154 (fig. 4b, blue), due to the fact that large producers have the highest levels of synchronicity.

155 The long periods associated with animal seed dispersal (fig. 3b) may not have meaningful effects on
 156 consumers or mutualist, because these species are weakly synchronized (fig. 3c). For consumers that
 157 can move between host trees, weak synchronicity means that there will be individuals producing seed
 158 in many years. Short periods are associated with warm, wet, infertile sites (negative Temp and CEC,
 159 positive Def in fig. 3b). The quasi-synchronicity that is strongest for wind dispersal is amplified in cold,
 160 dry climates (negative AD and Temp, positive Def in fig. 3c).

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

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

184 Taken over all ecoregion-species combinations, volatile seed production is most common for species
 185 with short periods between productive years (correlation = -0.28, 95% CI = (-0.36,-0.21), fig. S1). This
 186 negative relationship between volatility and period holds within phylogenetic groups, where there are
 187 more negative than positive correlations between volatility and period (fig. S1). High volatility aligns
 188 with short periods in most temperate groups (in *Abies*, *Quercus*, *Fagus*, residual Fagaceae, Pinaceae,
 189 and Magnoliaceae), some tropical species (in Meliaceae, Melastomataceae), and some with mixed tropi-
 190 cal/temperate affinities (residual Sapindaceae). Correlations in other large temperate groups (in *Pinus*,

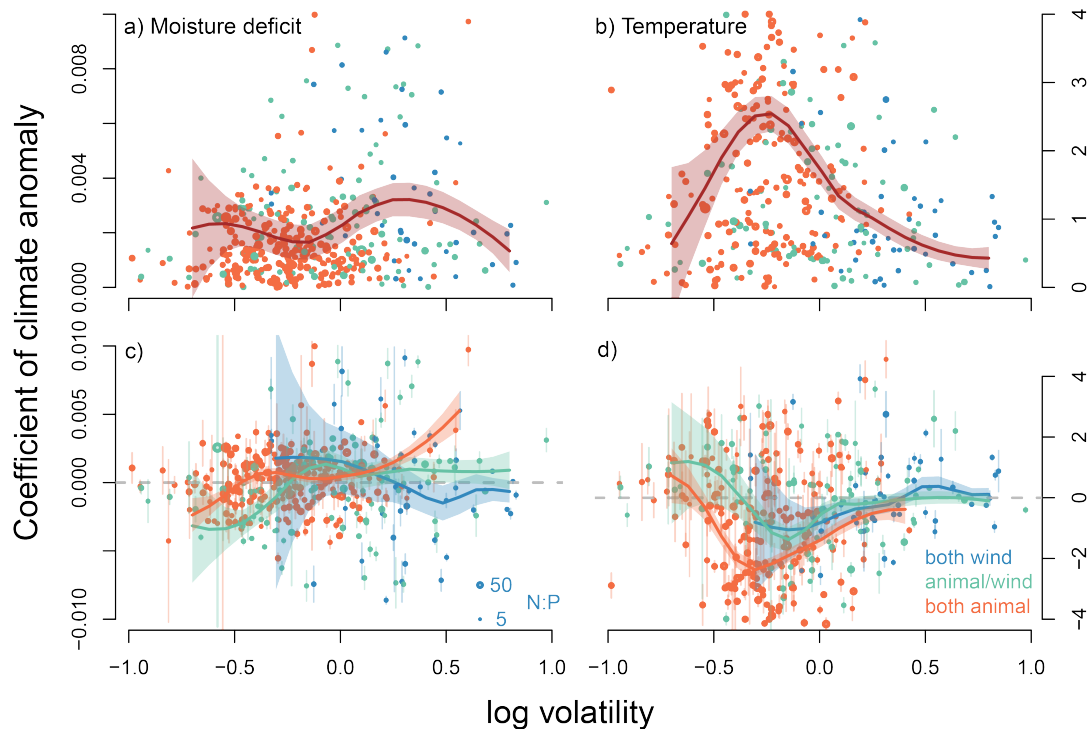


Fig. 5: **Volatility, dispersal mode, climate anomalies, and foliar N:P.** Each point locates species volatility (variability between years) with its response to climatic anomalies in moisture deficit of the previous and current year (panel a and c) and temperature of the previous year (panel b and d). Overall sensitivity is shown as absolute values above (a, b); and with their signs below (c, d). 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 and b). Loess weighted regressions on parameter estimates (dots), weighted by parameter variance (error bars are standard errors of the estimates), summarize trends in absolute sensitivity (a, b) and the three dispersal groups (c, d).

191 *Acer*, Cupressaceae, Betulaceae, and Oleaceae), as well as in mixed tropical/temperate groups (in An-
 192 nonaceae, Araliaceae, Moraceae, Symplocaceae, Lauraceae), are negative but not significantly less than
 193 zero. Conversely, positive relationships are dominated by one mostly temperate group (Aquifoliaceae),
 194 others being non-significant, but predominantly tropical.

195 Across species, the relationship between volatility and synchronicity is weak (correlation = -0.039,
 196 95% CI = (-0.12, 0.043)), but strong correlations emerge within many phylogenetic groups (fig. S2).
 197 Volatile species have low synchronicity in many families of mixed temperate/tropical affinity (blue in
 198 fig. S2). High volatility combines with high synchronicity in the temperate genera *Fagus* and *Abies*, but
 199 only weakly in *Quercus* (brown in fig. S2). For the majority of species groups, high synchronicity is
 200 associated with low volatility.

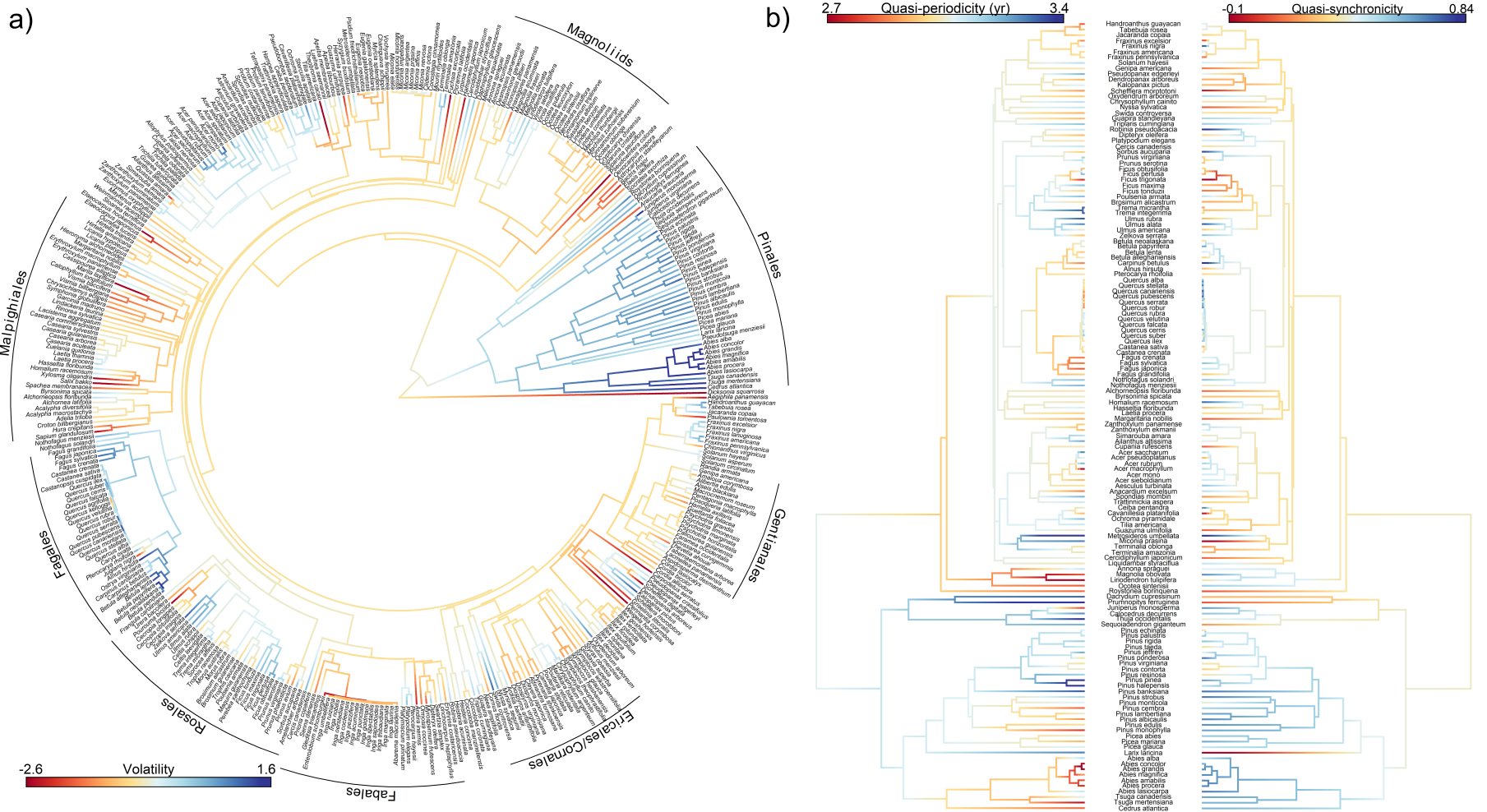


Fig. 6: (a) Volatility (on log scale) has a phylogeny component (*Pagel's* $\lambda = 0.83$, $p < 10^{-9}$, $n = 394$). (b) Quasi-periodicity (left) exhibits a weaker phylogenetic coherence compared to volatility (*Pagel's* $\lambda = 0.52$, $p = 0.0023$, $n = 142$). Quasi-synchronicity (right) shows 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 level of 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 (Herrera et al., 1998; Kelly and Sork, 2002; Pearse et al., 2020). These selective forces are further complicated by the fact that at least some animal dispersers are also seed predators. While animal-dispersed species are overall less volatile, there are notable exceptions. For example, the volatile Fagaceae (fig. 6a) have primarily wind-dispersed pollen, but depend on scatterhoarding seed dispersers–mutualists that suffer in low-yield years and disperse and satiate in high-yield years (Vander Wall, 2010; Zwolak et al., 2016). Perhaps as an exception that supports the rule, within Fagaceae the lowest volatility is estimated for *Castanea* with primarily insect-dispersed pollen (Larue et al., 2021). The strong connection between mast volatility and wind dispersal (fig. 3a) supports the hypothesis that animal pollination may suffer from volatile masting (Herrera et al., 1998; Kelly and Sork, 2002; Pearse et al., 2016; Wang et al., 2017; Garcia et al., 2021).

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. 1b). 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 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, where reproductive output is two orders of magnitude lower than in the wet tropics (Journe et al., 2022), 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 (Ascoli et al., 2017). Even the increased volatility with soil fertility fits this negative relationship between fecundity and volatility: mean fecundity declines with foliar P (Qiu et al., 2022) as volatility increases (foliar nutrients and soil CEC in fig. 3a). Despite the limitations of comparing environmental responses across species that differ in their distribution of exposures to environment, results are not consistent with the expectation that volatility at the species level is driven in a specific direction by climate anomalies (Kelly et al., 2013).

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 (Smith et al., 1990). Synchronized flowering may increase pollinator visitation rates (Augsburger, 1981; Crone, 2013); 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). The association of wind pollination with high volatility but not with long periods agrees with the largely untested notion that pollination efficiency benefits when flowering effort varies and it is quasi-synchronous, but without added benefit of long intervals between mast years (Janzen, 1971).

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 (Greenberg, 2000; Clark et al., 2004; Chen et al., 2018). Low and even negative correlations characterize populations on the 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 have to 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 (Fig. S2) suggests the potential for region/species-scale adaptation in response to variable predation pressure (Koenig et al., 2003; Steele and Yi, 2020).

The finding that volatile species tend to have short periods (fig. 6), including within multiple phylogenetic groups (fig. S1), 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

258 does not preclude a need for extended replenishment following high-yields *within individuals* in ways that
259 differ between species. Although less studied, it is also important to understand how local adaptation
260 (i.e., genetic differences among populations (Satake and Kelly, 2021)) and gene \times environment interac-
261 tions that affect seed enemies and dispersers (e.g., Mueller et al. (2005)) may contribute to the evolution
262 of volatility, periodicity and synchronicity.

263 If consistently high nutrient concentrations obviate the need for prolonged nutrient recovery, then we
264 expect the observed negative association between foliar nutrients and volatility (fig. 3a). By allowing for
265 the effects of both foliar nutrient concentrations and site fertility, our results diverge from previous studies
266 suggesting low volatility on fertile sites. However, comparisons have to consider that previous studies
267 include few species (Janzen, 1974; Smaill et al., 2011; Tanentzap et al., 2012). The effects of nutrient
268 demand versus supply can be confounded by the fact that nutrient-demanding species are most abundant
269 on fertile sites. By including differences in foliar nutrients as a species-level trait with the CEC where
270 trees occur, this global analysis finds that low volatility is associated with nutrient-demanding species,
271 not low-fertility sites. The association of high volatility and short periods with nutrient-rich habitats
272 (CEC in fig. 3) could result from accelerated nutrient replenishment on fertile soils. However, as noted
273 above, volatile species are not those with short periods in general. Not only do nutrient-demanding
274 species (as reflected in foliar nutrient content) produce less seed (Qiu et al., 2022); they also are less
275 volatile (fig. 3a). Limited effects of resources on synchronicity can be related to the weak effects of soil
276 CEC on seed production (Qiu et al., 2022) and intense competition on nutrient-rich sites (Clark et al.,
277 2014).

278 The expectation that large seeds might demand long recovery intervals was not supported by com-
279 parisons between species. Using data from Schopmeyer et al. (1974), Sork (1993) found a positive
280 relationship between acorn size and mast period for 18 temperate *Quercus* species. We find a negative
281 relationship at the global scale: species with large seeds are less volatile and have short periods in fig. 3a,
282 b. In the limited Schopmeyer et al. (1974) dataset, the negative correlation is driven by a longer interval
283 for *Quercus alba* than *Q. falcata*. In general, we find that red oaks (*Q. falcata*, *Q. rubra*, *Q. velutina*, *Q.*
284 *coccinea*) have longer periods than white oaks (*Q. alba*, *Q. montana*, *Q. pubescens*, *Q. robur*, *Q. stellata*,
285 *Q. serrata*), Cerris oaks (*Q. cerris*, *Q. ilex*, *Q. suber*) and *Fagus* (fig. 6b), perhaps related to the two-yr
286 development time for red oak seeds.

287 The negative association between masting intensity and fecundity suggests the view of masting as
288 desperation: an evolutionary option most common in species and settings where seed production is limited
289 primarily by climate and habitat and where animal dispersal is less common. There is no question that
290 predator satiation occurs, and seedling escape can result (Crawley and Long, 1995; Manson et al., 1998;
291 Zwolak et al., 2022). Still, at the global scale, species differences in masting depend on their reliance on
292 animal dispersers.

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

298 Methods

299 MASTIF summary

300 The MASTIF model allows us to jointly model individual trees, with their dependence on one another
301 and over time. This hierarchical, state-space model and the Gibbs sampling used for posterior simulation
302 are detailed in Clark et al. (2019), with only key elements that relate to mast syndromes summarized
303 here. Model fitting is open-access with R package MASTIF on CRAN.

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

311 The MASTIF model incorporates two data types including crop counts and seed traps. Crop counts
312 $c_{ijr,t}$ are conditionally beta-binomial, which allows for the uncertainty in fraction of the crop that is

313 observed,

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

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

317 Seed trap counts are conditionally Poisson,

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

318 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
 319 $S_j \times n_j$ kernel matrix that determines dispersal from each of $i = 1, \dots, n_j$ trees to S_j traps, depending
 320 tree-to-trap distances, and $\mathbf{f}_{jr,t}$ is the length- n_j vector of tree fecundities. The dispersal kernel follows
 321 Clark et al. (1999).

322 Fecundity is the product of latent states for maturation status and conditional fecundity, $f_{ijr,t} =$
 323 $\psi_{ij,t}\rho_{ijr,t}$ having the joint distribution $[\psi_{ijr,t}, \rho_{ijr,t}] = [\psi_{ijr,t}|\rho_{ijr,t}][\rho_{ijr,t}]$. (We use bracket notation $[x]$
 324 to indicate a distribution or density of x). Maturation is a one-way process, modelled as a probit hidden-
 325 Markov model. The maturation status $\rho_{ijr,t} \in \{0, 1\}$ is known to be 1 (i.e., mature) for trees that have
 326 been observed to produce seed in the past, i.e., $[\rho_{ijr,t} = 1|\rho_{ij,t-1} = 1] = 1$, and 0 if known to be immature
 327 subsequently $[\rho_{ijr,t} = 1|\rho_{ij,t+1} = 0] = 0$. For tree-years of unobserved maturation status, the probability
 328 of being mature in year t , given past and future status is the probit,

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

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

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

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

333 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
 334 year effect for ecoregion-species r , and σ^2 is the residual variance. The factors containing the indicator
 335 function specify that mature individuals have latent conditional fecundity sufficient to generate at least
 336 one seed. Importantly, the approach allows for observed zero fecundity for both seed traps and crop
 337 counts while latent fecundity remains finite. This approach follows the approach used in Tobit models
 338 for discrete zeros in otherwise continuous data (Tobin, 1958; Clark et al., 2017). Predictors in the design
 339 vector $\mathbf{x}_{ijr,t}$ include known climate and habitat variables combined with variable selection by DIC.

340 Masting syndromes

341 The analysis of masting components at individual level is based on the estimate of the fecundity, $f_{ijr,t}$,
 342 on the log (proportionate) scale. The mast syndrome consists of three elements $M = (M_v, M_p, M_c)$, the
 343 volatility M_v having units of variance in $\log f$, period M_p in years, and the dimensionless synchronicity
 344 M_c . The first two elements emerge from the spectral density $S_f(\omega)$, evaluated in the frequency ω domain.
 345 Technically, $S_f(\omega)$ is obtained by transforming the auto-covariance function $C(t)$ from the time domain
 346 to the frequency domain or, alternatively, by taking the Fourier transform of the autocorrelation function
 347 $C(t)/C(0)$. There is an associated spectral *variance*, obtained by integrating the spectral density over
 348 frequency

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

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

351 period-weighted spectral variance,

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

352 where T is the number of terms included in the summation. The subscripts of tree i , stand j , and
 353 ecoregion-species r are omitted to reduce clutter. Because short time series could be dominated by noise,
 354 we focused on trees that include at least 10 years of data (72,843 trees and 1,369,115 tree-years). We set
 355 T to the half of the threshold, i.e., $T = 5$ yr. Likewise, *periodicity* emphasizes variance at low frequency,

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

356 with variance

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

357 The span of variance captures the quasi-periodic nature of masting, being broad where period is unpre-
 358 dictable (fig. 1d). We obtained the spectral density $S_f(\omega_k)$ for each tree ($\log f_{ijr}$) using the R package
 359 `spectrum`. Volatility and periodicity complement currently-used metrics for masting. Volatility measures
 360 variance in the frequency domain, capturing the out-sized importance of variation at the multi-year scale,
 361 moving beyond lag-0 (CV) or lag-1 approaches. Periodicity side-steps the need to define a threshold
 362 productivity for mast years or the fact that a simple mean interval may not represent quasi-periodic
 363 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:

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

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

364 where ISP is individual standardized productivity (Qiu et al., 2022; Journe et al., 2022). It is defined as
 365 seeds per tree times mass per seed and divided by tree basal area and averaged across multiple years.

366 We evaluated the weighted synchronicity at ecoregion-species level following a similar procedure as
 367 that of volatility and periodicity. Tree-to-tree correlation coefficients were calculated between all con-
 368 specific individuals within 1 km of one another. We included correlations $M_{c,k}$ over years for which both
 369 trees of a pair k that are estimated to be in the mature state. For the tree-to-tree correlations, both the
 370 correlation and the product of fecundities were calculated for each pair, the latter having large values
 371 for trees with high production. A weighted synchronicity over all trees of a species within 1 km was
 372 evaluated as

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

373 for all pairwise correlations $M_{c,kr}$ at ecoregion-species r , with weight C_k being the absolute value of the
 374 pairwise covariance, i.e., the product of fecundities for each pair of trees k .

375 Analyses at ecoregion-species level

376 We began by evaluating phylogenetic coherences in the masting syndromes. We then quantified the
 377 correlations among $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$ within each phylogenetic group. Finally, we evaluated
 378 variations in the M_r jointly at ecoregion-species level through incorporating phylogeny, species traits, soil,
 379 and climate covariates in a generalized joint attribute model (GJAM). Our analyses were implemented
 380 at ecoregion-species level because 15% of the species have within-species variations across ecoregions.
 381 The remaining (85%) species that are sampled at one ecoregion are primarily tropical species.

382 Phylogeny

383 We quantified the phylogenetic signal in volatility and quasi-periodicity using *Pagel's* λ . Species dif-
 384 ferences in masting syndromes were averaged across ecoregion-species combinations. Phylogeny was
 385 obtained for 375 species (84% of the total 447 species) from Zanne et al. (2014). We used the continuous
 386 character mapping method from the R package `phytools` (Revell, 2012) to visualize the phylogenetic
 387 coherence in volatility, periodicity, and synchronicity.

388 To account for phylogeny in the joint model of three masting syndromes, we depart from traditional
 389 assumptions concerning residual covariance, turning instead to direct inference on the effects of phy-
 390 logenetic groups. The aim to control for phylogenetic association in comparative studies (Freckleton
 391 et al., 2002; Hadfield and Nakagawa, 2010) suggests a capacity to take up variation that might be linked
 392 to relatedness in a general sense. Instead, current methods impose a highly specific assumption that
 393 residual variance between species traits results from a random walk that proceeds at a fixed rate across
 394 species pairs. However, natural selection would not operate in this way, not for a given species pair and
 395 certainly not across a large number of species. Residual variance constitutes all sources of variation that
 396 are not taken up by the mean structure of the model. Just as there could be massive phylogenetically
 397 constrained traits between specific species pairs that have diverged under differing intensities of selection,
 398 there could be minimally constrained pairs within the same comparative study where others are strong.
 399 The important modeling concern for valid inference on coefficients is a covariance matrix that can take up
 400 relationships that remain after accounting for the mean, regardless of their source, and without imposing
 401 specific assumptions about rates of divergence.

402 Our joint analyses of masting syndromes explored phylogenetic contributions with species groups
 403 treated as random effects and covariance that is unconstrained by assumptions on divergence rates.
 404 Rather than assume a fixed relationship between residual covariances, our approach provides a transpar-
 405 ent estimate for differences between species groups, allowing that they need not be anchored to pairwise
 406 divergence times. For genera having at least 10 species in the MASTIF data, species were grouped at
 407 the genus level. All remaining species in families having at least 5 species were grouped at the family
 408 level. Remaining species were aggregated into an 'other' group for purposes of model fitting, but they are
 409 displayed separately in the correlation plots (e.g., Fig. S2). Relationships between masting syndromes
 410 within each phylogenetic group were evaluated using Pearson's correlation coefficient.

411 Joint modeling of masting syndromes

412 To evaluate masting as a syndrome and the variables associated with it, we conducted joint analyses
 413 of mast attributes against predictors that include species traits, environment, and phylogeny. Species
 414 traits included dispersal mode (anemochory vs zoochory), pollination mode (animal vs wind pollinated
 415 syndromes), mean foliar N and P (percentage of dry mass), and seed size (gm per seed). Traits in-
 416 formation are obtained from collections in our labs and supplemented with the TRY database (Kattge
 417 et al., 2020). Environmental covariates include soil fertility (Cation Exchange Capacity, CEC), mean
 418 annual temperature, and total annual moisture deficit (differences between potential evapotranspiration
 419 and precipitation) averaged at ecoregion-species level. We used generalized joint attribute modeling
 420 (GJAM) (Clark et al., 2017) to allow for the dependence between mast components and the fact that
 421 mast components are non-negative (they are non-Gaussian),

$$422 \mathbf{w}_r \sim MVN(\mathbf{x}'_r \boldsymbol{\beta}, \Sigma) \times \prod_{l=1}^S I(w_{r,l} \leq 0)^{I(M_{r,l}=0)} I(w_{r,l} > 0)^{I(M_{r,l}=w_{r,l})} \quad (12)$$

422 where \mathbf{w}_r is the length- S vector holding the latent (and uncensored) mast response for ecoregion-species
 423 r and \mathbf{M}_r is the length- S observation vector ($S = 3$ for the three components). Covariates occupy the
 424 length- Q vector \mathbf{x}'_r , including species traits and environmental conditions. Responses to covariates are
 425 included in the $Q \times S$ matrix of coefficients $\boldsymbol{\beta}$. The latent variable has the mean vector $\mathbf{x}'_r \boldsymbol{\beta}$ and $S \times S$
 426 covariance matrix Σ . The product including indicator functions $I(\cdot)$ allows for negative values on the
 427 latent scale, essentially a multivariate Tobit (Clark et al., 2017).

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

434 Author contributions statement

435 J.S.C and T.Q. designed the study, performed analyses, and wrote the paper, J.S.C. compiled the
436 MASTIF data and wrote the MASTIF model and software, M.B, B.C., V.J, and G.K. co-wrote the
437 paper. All authors contributed data and revised the paper.

438 Competing interests statement

439 The authors declare no competing interests.

440 Data availability

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

446 Code availability

447 R statistical software v4.0.2 was used in this work. All analyses used published R packages, with details
448 stated in the section Methods. MASTIF includes code in R and C++, which is published on CRAN at
449 <https://cran.r-project.org/web/packages/mastif/index.html>.

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