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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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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 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 the climatic conditions where dependence on vertebrate dispersers is less common compared to 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*

Introduction

Unpredictable reproduction in trees (“masting”) could be an evolved response to thwart seed consumers^(1,2,3), but then there is a conundrum: the volatility that limits seed predators could be just as deleterious to mutualist pollen and seed dispersers^(4,2,5,6), while also concentrating competition within offspring^(7,8). For natural enemies and mutualists alike, masting effects depend on three elements (fig. 1), i) year-to-year *volatility*, or the time-dependent magnitude of variation, ii) *quasi-periodicity*, the lag between high seed-production years, and iii) *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^(10,11,12), but they operate together: the costs and benefits of masting depend on the interactions between them and the foraging ranges of consumers and dispersers^(13,9). Meta-analyses provide important insights at the aggregate population or species scale⁽¹⁴⁾ but miss the volatility within and synchronicity between trees^(15,16,17). 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 of 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 inter-annual variation in one host tree by accessing others^(13,9) (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^(4,2,22); 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^(24,25,26) or not⁽²⁷⁾. The mast interval could be prolonged where large crops deplete reserves that require years to replenish^(28,29,21,30) 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 (e.g. Kelly et al⁽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 from 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^(35,36,37,38,39) 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^(42,38,41,40), but our analysis evaluates variation globally, spanning seasonal and a-seasonal 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 an spring-time temperature anomaly of 1°C is not comparable between highly seasonal taiga and a-seasonal 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 analyzed together, in part, because a joint analysis requires substantial data 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^(15,43,9,17,44). Understanding spatial scales⁽⁴⁵⁾, allocation tradeoffs^(46,47), responses to climate^(48,42,49,39,50), and effects on consumers^(51,9) and dispersers^(4,2) 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, synchronous variability. All three elements vary between species and regions. The commonly used coefficient of variation (CV) omits time and frequency, one 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 (e.g., [fig. 1c](#)) (Supplementary information). Estimating periodicity requires a definition for what constitutes a mast year^(30,52,53,54), which is challenging because there is no identifiable threshold (e.g., [fig. 1c](#)) despite detectable indicators on trees (e.g., 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, *P. monticola* ([fig. 1a](#)) and *A. grandis* ([fig. 1b](#)) share biennial variation but differ in the secondary concentration of variance at 3 to 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 eco-region 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 evaluate 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^(4,2,9) ([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^(29,23) ([fig. 2a](#)). We further hypothesized that warm climates favor low volatility and high synchronicity^(2,14,40), while dry climates (high moisture deficit) favor high volatility and synchronicity^(45,41) ([fig. 2a](#)). To test those hypotheses, we begin by extracting the three components of masting ([fig. 1](#)) from inter-annual 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 low 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), due to the fact that 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 mutualist, because 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, especially strong for volatility and periodicity and less so for synchronicity (fig. 6). Volatility is 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), fig. S2). This negative relationship between volatility and period holds within phylogenetic groups, where there are more negative than positive correlations between volatility and period (fig. S2). High volatility aligns

with short periods in most temperate groups (in *Abies*, *Quercus*, *Fagus*, residual Fagaceae, Pinaceae, and Magnoliaceae), some tropical species (in Meliaceae, Melastomataceae), and some with mixed tropical/temperate affinities (residual Sapindaceae). Correlations in other large temperate groups (in *Pinus*, *Acer*, Cupressaceae, Betulaceae, and Oleaceae), as well as in mixed tropical/temperate groups (in Annonaceae, Araliaceae, Moraceae, Symplocaceae, 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 (fig. S3). Volatile species have low synchronicity in many families of mixed temperate/tropical affinity (blue in fig. S3). High volatility combines with high synchronicity in the temperate genera *Fagus* and *Abies*, but only weakly in *Quercus* (brown in fig. S3). 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^(4,2,14). These selective forces are further complicated by the fact that at least some animal dispersers are also seed predators (e.g., 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^(4,2,23,6,62).

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 (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 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). 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^(15,16,17). 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^(67,22).

The finding that volatile species tend to have short periods (fig. 6), including within multiple phylogenetic groups (fig. S2), 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 (i.e., genetic differences among populations⁽⁶⁸⁾) and gene \times environment interactions that affect seed enemies and dispersers^(69,5) 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 have to consider that previous studies include few species^(24,25,26). 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 \times seed size)⁽⁵⁸⁾; they also are 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 from Schopmeyer et al⁽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 *Quercus alba* than *Q. falcata*. In general, we find that red oaks (*Q. falcata*, *Q. rubra*, *Q. velutina*, *Q. coccinea*) have longer periods than white oaks (*Q. alba*, *Q. montana*, *Q. pubescens*, *Q. robur*, *Q. stellata*, *Q. serrata*), Cerris oaks (*Q. cerris*, *Q. ilex*, *Q. suber*) and *Fagus* (fig. 6b), perhaps related to the two-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 (Fig. S1). 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^(71,72,73). Despite the fact that it is not uncommon for a given tree species to have multiple pollinators and seed dispersers⁽⁷⁴⁾, the diet breadth of seed consumers (e.g., 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 the 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 allows 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 Clark et al. ⁽⁹⁾, with only key elements that relate to mast syndromes summarized here. Model fitting includes approximately 12 million tree-years from 898 species (fig. S1). MASTIF model is open-access with 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 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 the uncertainty in fraction of the crop that is observed,

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

where $q_{ijr,t}$ is an estimate of the fraction of the crop observed, and $(a_{ijr,t}, b_{ijr,t})$ are parameters selected have mean fraction $q_{ijr,t}$ (i.e., 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,

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

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 $i = 1, \dots, n_j$ 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 ⁽⁷⁵⁾.

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 (i.e., mature) for trees that have 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 subsequently $[\rho_{ijr,t} = 1|\rho_{ij,t+1} = 0] = 0$. 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 eq. (3) are the currently imputed values in Gibbs sampling.

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

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

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 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 ^(76,77). Predictors in the design vector $\mathbf{x}_{ijr,t}$ include known climate and habitat variables combined with variable selection by 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

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

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-year of observations (139,785 trees and 2,841,238 tree-years from 468 species). Detailed data distribution can be found in the supplementary csv file. We set T to be half of the threshold, i.e, $T = 5$ yr. Likewise, *periodicity* emphasizes variance at low frequency,

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

with variance

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

The span of variance captures the quasi-periodic nature of masting, being broad where period is unpredictable (fig. 1d). 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 multi-year 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:

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

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

where ISP is individual standardized productivity^(58,63). It is defined as seeds per tree times mass per seed and 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 of 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 that 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, i.e., the product of fecundities for each pair of trees k .

Analyses at ecoregion-species level

We evaluated variations in the $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$ jointly at ecoregion-species level ($n = 583$) through 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 csv file). The remaining (85%) species that are 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. But 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⁽⁷⁸⁾.

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⁽⁷⁹⁾. We used the continuous character mapping method from the R package *phytools*⁽⁸⁰⁾ to visualize the phylogenetic coherence in volatility, periodicity, and synchronicity.

To account for phylogeny in the joint model of three masting syndromes, we depart 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^(81,82) 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 modeling 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 (e.g., Fig. S3). Relationships between masting syndromes within each phylogenetic group were evaluated using Pearson's correlation coefficient.

Joint modeling 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 (gm per seed). Traits information are obtained from collections in our labs and supplemented with the TRY database⁽⁸³⁾. Genus-

or family-level means were used where seed size and foliar nutrients were missing at the species level. Similarly, genus- or family- modes were used for dispersal and pollination syndromes. Foliar N:P were 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 include soil fertility (Cation Exchange Capacity, CEC), mean annual temperature, and accumulated annual moisture deficit (differences between potential evapotranspiration and precipitation) averaged at ecoregion-species level. We used generalized joint attribute modeling (GJAM)⁽⁷⁷⁾ to allow for the dependence between mast components and the fact that masting components are non-negative (they are non-Gaussian),

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

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⁽⁷⁷⁾.

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

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 are obtained at <https://soilgrids.org/>. Climate data are extracted from Terraclimate at <http://www.climatologylab.org/> and CHELSA at <https://chelsa-climate.org/>.

Code availability

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

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Author contributions statement

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.A, D.A, Y.B, M.B, T.B, R.B, T.C, M.C, R.C, S.C, J.J.C, C.C, J.C, F.C, B.C, A.C, A.J.D, N.D, S.D, M.D, L.D, J.E, T.J.F, W.F, J.F.F, C.A.G, G.S.G, G.G, C.H.G, A.G, Q.G, A.H, A.H, Q.H, J.H, K.H, I.I, J.F.J, V.J, T.K, J.M.K, G.K, H.K, J.G.L, J.M.L, F.L, T.L, J.L, J.A.L, D.M, A.M, E.J.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, L.P, T.P, J.P, M.D.R, C.D.R, K.C.R, F.R, P.S, J.D.S, C.L.S, B.S, S.S, M.S, M.S, M.A.S, N.L.S, J.N.S, S.S, J.J.S, M.S, 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 statement

The authors declare no competing interests.

Figure caption

Fig. 1: Illustration of three masting components for *Pinus monticola* and *Abies grandis* from the central Cascades, U.S.A. Crop counts for these species (a, b) vary between individual trees, and they drift over time. The frequency of counts (c) in both species 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 and their standard deviations 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).

Fig. 2: Hypothesized effects (a) and summary of results (b) of mutualists (green), resources (blue), and climate (red) on the three masting components. Arrows with + and – represent positive and negative effects, respectively. We expect 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.

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 (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 animal seed dispersal (AD) and pollination (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. 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 Deviance Information Criterion (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.

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).

Fig. 5: Volatility, dispersal mode, climate anomalies, and foliar N:P. Each point locates species volatility (variability between years on log scales) with its coefficients to climatic anomalies in moisture deficit (panel a and c) and temperature (panel b and d). Coefficients were obtained from the fitted model (see methods). Overall sensitivity with no grouping by dispersal/pollination syndromes is shown as absolute values in the above panel (a, b); and with their signs in the below panel (c, 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 and b). Loess regressions on parameter estimates (dots), weighted by the standard errors of the estimate (error bars), summarize trends with their confidence intervals (the colored shades) in absolute sensitivity (a, b) and for the three dispersal groups (c, d).

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 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.

References

- [1] D. H. Janzen, “Seed predation by animals,” *Annual Review of Ecology and Systematics*, vol. 2, no. 1, pp. 465–492, 1971.
- [2] D. Kelly and V. L. Sork, “Mast seeding in perennial plants: Why, how, where?,” *Annual Review of Ecology and Systematics*, vol. 33, no. 1, pp. 427–447, 2002.
- [3] P. A. Jansen, F. Bongers, and L. Hemerik, “Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent,” *Ecological Monographs*, vol. 74, no. 4, pp. 569–589, 2004.
- [4] C. M. Herrera, P. Jordano, J. Guitian, and A. Traveset, “Annual variability in seed production by woody plants and the masting concept: Reassessment of principles and relationship to pollination and seed dispersal,” *American Naturalist*, vol. 152, no. 4, pp. 576–594, 1998.
- [5] A. M. Siepielski and C. W. Benkman, “Conflicting selection from an antagonist and a mutualist enhances phenotypic variation in a plant,” *Evolution*, vol. 64, no. 4, pp. 1120–1128, 2010.
- [6] Y. Y. Wang, J. Zhang, J. M. LaMontagne, F. Lin, B. H. Li, J. Ye, Z. Q. Yuan, X. G. Wang, and Z. Q. Hao, “Variation and synchrony of tree species mast seeding in an old-growth temperate forest,” *Journal of Vegetation Science*, vol. 28, no. 2, pp. 413–423, 2017.
- [7] L. Huang, C. Jin, L. Zhou, K. Song, S. Qian, D. Lin, L. Zhao, B. Chen, E. Yan, R. Michalet, and Y. Yang, “Benefit versus cost trade-offs of masting across seed-to-seedling transition for a dominant subtropical forest species,” *Journal of Ecology*, vol. 109, no. 8, pp. 3087–3098, 2021.
- [8] B. Seget, M. Bogdziewicz, J. Holeksa, M. Ledwon, F. Milne-Rostkowska, L. Piechnik, A. Rzepczak, and M. Zywiec, “Costs and benefits of masting: economies of scale are not reduced by negative density-dependence in seedling survival in sorbus aucuparia,” *New Phytologist*, vol. 233, no. 4, pp. 1931–1938, 2022.
- [9] J. S. Clark, C. Nunez, and B. Tomasek, “Foodwebs based on unreliable foundations: spatiotemporal masting merged with consumer movement, storage, and diet,” *Ecological Monographs*, vol. 89, no. 4, p. e01381, 2019.
- [10] D. Janzen, “Herbivores and the number of tree species in tropical forests,” *The American Naturalist*, vol. 104, no. 940, pp. 501–528, 1970.
- [11] E. D. Clotfelter, A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and E. D. Ketterson, “Acorn mast drives long-term dynamics of rodent and songbird populations,” *Oecologia*, vol. 154, no. 3, pp. 493–503, 2007.
- [12] W. Chen, J. Zhong, W. P. Carson, Z. Tang, Z. Xie, S. Sun, and Y. Zhou, “Proximity to roads disrupts rodents’ contributions to seed dispersal services and subsequent recruitment dynamics,” *Journal of Ecology*, vol. 107, no. 6, pp. 2623–2634, 2019.
- [13] L. M. Curran and M. Leighton, “Vertebrate responses to spatiotemporal variation in seed production of mast-fruited dipterocarpaceae,” *Ecological Monographs*, vol. 70, no. 1, pp. 101–128, 2000.

- [14] I. S. Pearse, J. M. LaMontagne, M. Lordon, A. L. Hipp, and W. D. Koenig, “Biogeography and phylogeny of masting: do global patterns fit functional hypotheses?,” *New Phytologist*, vol. 227, no. 5, pp. 1557–1567, 2020.
- [15] C. H. Greenberg, “Individual variation in acorn production by five species of southern appalachian oaks,” *Forest Ecology and Management*, vol. 132, no. 2, pp. 199–210, 2000.
- [16] J. S. Clark, S. LaDeau, and I. Ibanez, “Fecundity of trees and the colonization-competition hypothesis,” *Ecological Monographs*, vol. 74, no. 3, pp. 415–442, 2004.
- [17] X. Chen, D. G. Brockway, and Q. Guo, “Characterizing the dynamics of cone production for longleaf pine forests in the southeastern united states,” *Forest Ecology and Management*, vol. 429, pp. 1–6, 2018.
- [18] Z. Pucek, W. Jedrzejewski, B. Jedrzejewska, and M. Pucek, “Rodent population-dynamics in a primeval deciduous forest (bialowieza-national-park) in relation to weather, seed crop, and predation,” *Acta Theriologica*, vol. 38, no. 2, pp. 199–232, 1993.
- [19] M. Bogdziewicz, R. Zwolak, and E. E. Crone, “How do vertebrates respond to mast seeding?,” *Oikos*, vol. 125, no. 3, pp. 300–307, 2016.
- [20] K. M. Christensen and T. G. Whitham, “Impact of insect herbivores on competition between birds and mammals for pinyon pine seeds,” *Ecology*, vol. 74, no. 8, pp. 2270–2278, 1993.
- [21] E. E. Crone and J. M. Rapp, “Resource depletion, pollen coupling, and the ecology of mast seeding,” *Year in Ecology and Conservation Biology*, vol. 1322, pp. 21–34, 2014.
- [22] M. A. Steele and X. Yi, “Squirrel-seed interactions: The evolutionary strategies and impact of squirrels as both seed predators and seed dispersers,” *Frontiers in Ecology and Evolution*, vol. 8, no. 259, 2020.
- [23] I. S. Pearse, W. D. Koenig, and D. Kelly, “Mechanisms of mast seeding: resources, weather, cues, and selection,” *New Phytologist*, vol. 212, no. 3, pp. 546–562, 2016.
- [24] D. H. Janzen, “Tropical blackwater rivers, animals, and mast fruiting by the dipterocarpaceae,” *Biotropica*, pp. 69–103, 1974.
- [25] S. J. Smaill, P. W. Clinton, R. B. Allen, and M. R. Davis, “Climate cues and resources interact to determine seed production by a masting species,” *Journal of Ecology*, vol. 99, no. 3, pp. 870–877, 2011.
- [26] A. J. Tanentzap, W. G. Lee, and D. A. Coomes, “Soil nutrient supply modulates temperature-induction cues in mast-seeding grasses,” *Ecology*, vol. 93, no. 3, pp. 462–469, 2012.
- [27] M. Fernández-Martínez, I. Pearse, J. Sardans, F. Sayol, W. D. Koenig, J. M. LaMontagne, M. Bogdziewicz, A. Collalti, A. Hacket-Pain, G. Vacchiano, J. M. Espelta, J. Peñuelas, and I. A. Janssens, “Nutrient scarcity as a selective pressure for mast seeding,” *Nature Plants*, vol. 5, no. 12, pp. 1222–1228, 2019.
- [28] R. C. Rosecrance, S. A. Weinbaum, and P. H. Brown, “Alternate bearing affects nitrogen, phosphorus, potassium and starch storage pools in mature pistachio trees,” *Annals of Botany*, vol. 82, no. 4, pp. 463–470, 1998.
- [29] A. Sala, K. Hopping, E. J. B. McIntire, S. Delzon, and E. E. Crone, “Masting in whitebark pine (*pinus albicaulis*) depletes stored nutrients,” *New Phytologist*, vol. 196, no. 1, pp. 189–199, 2012.
- [30] V. L. Sork, “Evolutionary ecology of mast-seeding in temperate and tropical oaks (*quercus* spp.),” *Vegetatio*, vol. 107, no. 1, pp. 133–147, 1993.
- [31] A. Sharma, D. C. Weindorf, D. D. Wang, and S. Chakraborty, “Characterizing soils via portable x-ray fluorescence spectrometer: 4. cation exchange capacity (cec),” *Geoderma*, vol. 239, pp. 130–134, 2015.
- [32] P. Hazelton and B. Murphy, *Interpreting soil test results: What do all the numbers mean?* CSIRO publishing, 2016.

- [33] J. J. Elser, K. Acharya, M. Kyle, J. Cotner, W. Makino, T. Markow, T. Watts, S. Hobbie, W. Fagan, J. Schade, J. Hood, and R. W. Sterner, “Growth rate–stoichiometry couplings in diverse biota,” *Ecology Letters*, vol. 6, no. 10, pp. 936–943, 2003.
- [34] D. Kelly, A. Geldenhuys, A. James, E. Penelope Holland, M. J. Plank, R. E. Brockie, P. E. Cowan, G. A. Harper, W. G. Lee, M. J. Maitland, A. F. Mark, J. A. Mills, P. R. Wilson, and A. E. Byrom, “Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change,” *Ecology Letters*, vol. 16, no. 1, pp. 90–98, 2013.
- [35] E. M. Schaubert, D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie, “Masting by eighteen new zealand plant species: The role of temperature as a synchronizing cue,” *Ecology*, vol. 83, no. 5, pp. 1214–1225, 2002.
- [36] J. M. Espelta, P. Cortés, R. Molowny-Horas, B. Sánchez-Humanes, and J. Retana, “Masting mediated by summer drought reduces acorn predation in mediterranean oak forests,” *Ecology*, vol. 89, no. 3, pp. 805–817, 2008.
- [37] I. M. Pérez-Ramos, J. M. Ourcival, J. M. Limousin, and S. Rambal, “Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment,” *Ecology*, vol. 91, no. 10, pp. 3057–3068, 2010.
- [38] W. D. Koenig, J. M. H. Knops, W. J. Carmen, and I. S. Pearse, “What drives masting? the phenological synchrony hypothesis,” *Ecology*, vol. 96, no. 1, pp. 184–192, 2015.
- [39] A. P. Wion, P. J. Weisberg, I. S. Pearse, and M. D. Redmond, “Aridity drives spatiotemporal patterns of masting across the latitudinal range of a dryland conifer,” *Ecography*, vol. 43, no. 4, pp. 569–580, 2020.
- [40] J. M. LaMontagne, I. S. Pearse, D. F. Greene, and W. D. Koenig, “Mast seeding patterns are asynchronous at a continental scale,” *Nature Plants*, vol. 6, no. 5, pp. 460–465, 2020.
- [41] G. Vacchiano, A. Hacket-Pain, M. Turco, R. Motta, J. Maringer, M. Conedera, I. Drobyshev, and D. Ascoli, “Spatial patterns and broad-scale weather cues of beech mast seeding in europe,” *New Phytologist*, vol. 215, no. 2, pp. 595–608, 2017.
- [42] J. S. Clark, D. M. Bell, M. C. Kwit, and K. Zhu, “Competition-interaction landscapes for the joint response of forests to climate change,” *Glob Chang Biol*, vol. 20, no. 6, pp. 1979–91, 2014.
- [43] J. M. Lamontagne and S. Boutin, “Local-scale synchrony and variability in mast seed production patterns of picea glauca,” *Journal of Ecology*, vol. 95, no. 5, pp. 991–1000, 2007.
- [44] J. N. Straub, A. G. Leach, R. M. Kaminski, A. W. Ezell, and T. D. Leininger, “Red oak acorn yields in green-tree reservoirs and non-impounded forests in mississippi,” *Wildlife Society Bulletin*, vol. 43, no. 3, pp. 491–499, 2019.
- [45] D. Ascoli, G. Vacchiano, M. Turco, M. Conedera, I. Drobyshev, J. Maringer, R. Motta, and A. Hacket-Pain, “Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction,” *Nature Communications*, vol. 8, 2017.
- [46] A. J. Hacket-Pain, A. D. Friend, J. G. Lageard, and P. A. Thomas, “The influence of masting phenomenon on growth–climate relationships in trees: explaining the influence of previous summers’ climate on ring width,” *Tree Physiology*, vol. 35, no. 3, pp. 319–330, 2015.
- [47] A. B. Berdanier and J. S. Clark, “Divergent reproductive allocation trade-offs with canopy exposure across tree species in temperate forests,” *Ecosphere*, vol. 7, no. 6, pp. e01313–n/a, 2016.
- [48] M. D. Redmond, F. Forcella, and N. N. Barger, “Declines in pinyon pine cone production associated with regional warming,” *Ecosphere*, vol. 3, no. 12, p. art120, 2012.
- [49] A. V. Whipple, N. S. Cobb, C. A. Gehring, S. Mopper, L. Flores-Rentería, and T. G. Whitham, “Long-term studies reveal differential responses to climate change for trees under soil- or herbivore-related stress,” *Frontiers in Plant Science*, vol. 10, no. 132, 2019.

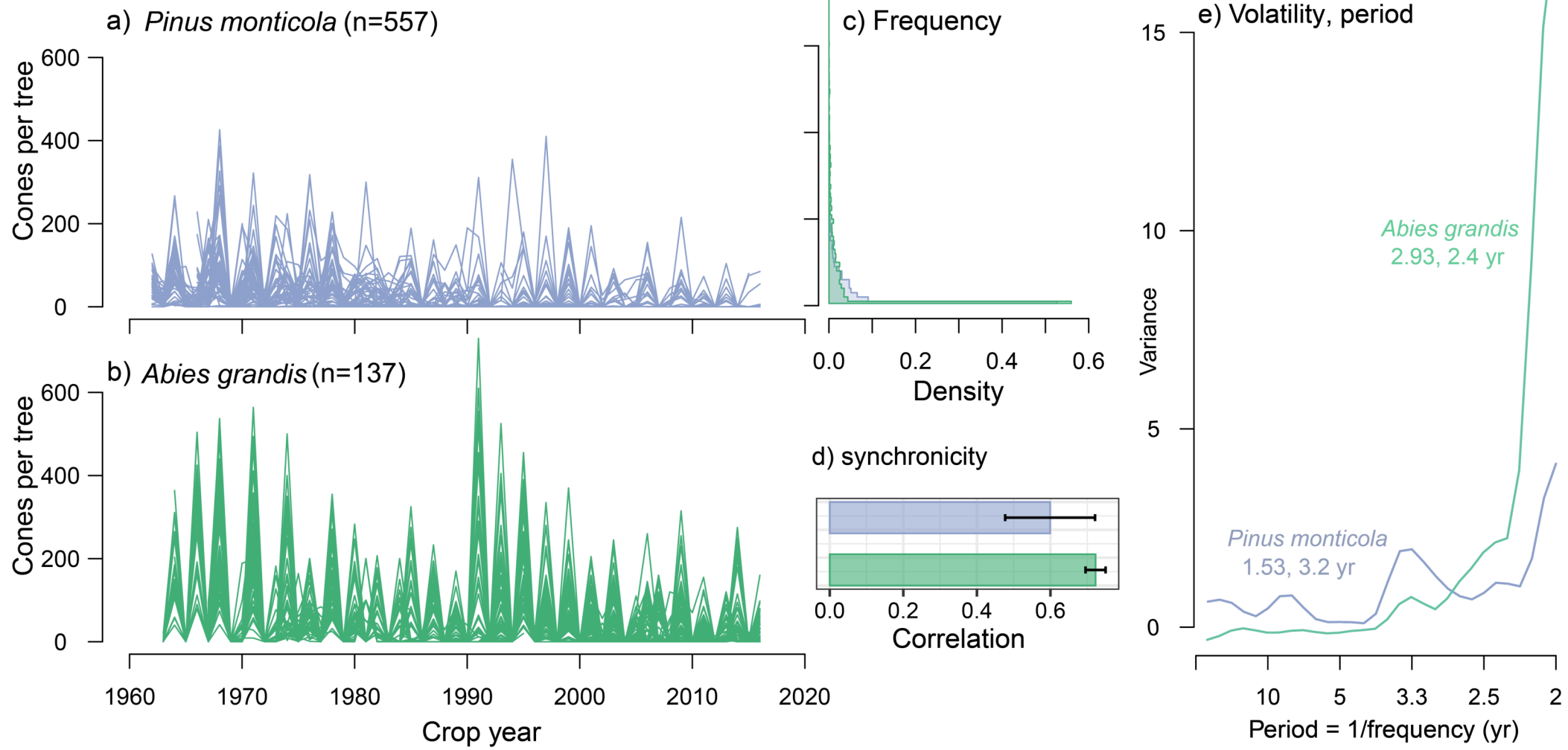
- [50] M. Bogdziewicz, D. Kelly, P. A. Thomas, J. G. A. Lageard, and A. Hacket-Pain, “Climate warming disrupts mast seeding and its fitness benefits in european beech,” *Nature Plants*, vol. 6, no. 2, pp. 88–94, 2020.
- [51] J. M. Espelta, R. Bonal, and B. Sanchez-Humanes, “Pre-dispersal acorn predation in mixed oak forests: interspecific differences are driven by the interplay among seed phenology, seed size and predator size,” *Journal of Ecology*, vol. 97, no. 6, pp. 1416–1423, 2009.
- [52] A. Yamauchi, “Theory of mast reproduction in plants: Storage-size dependent strategy,” *Evolution*, vol. 50, no. 5, pp. 1795–1807, 1996.
- [53] W. D. Koenig and J. M. H. Knops, “The mystery of masting in trees: Some trees reproduce synchronously over large areas, with widespread ecological effects, but how and why?,” *American Scientist*, vol. 93, no. 4, pp. 340–347, 2005.
- [54] J. M. LaMontagne and S. Boutin, “Quantitative methods for defining mast-seeding years across species and studies,” *Journal of Vegetation Science*, vol. 20, no. 4, pp. 745–753, 2009.
- [55] J. S. Clark, “Individuals and the variation needed for high species diversity in forest trees,” *Science*, vol. 327, no. 5969, pp. 1129–1132, 2010.
- [56] M. Shibata, T. Masaki, T. Yagihashi, T. Shimada, and T. Saitoh, “Decadal changes in masting behaviour of oak trees with rising temperature,” *Journal of Ecology*, vol. 108, no. 3, pp. 1088–1100, 2020.
- [57] J. S. Clark, R. Andrus, M. Aubry-Kientz, Y. Bergeron, M. Bogdziewicz, D. C. Bragg, D. Brockway, N. L. Cleavitt, S. Cohen, B. Courbaud, R. Daley, A. J. Das, M. Dietze, T. J. Fahey, I. Fer, J. F. Franklin, C. A. Gehring, G. S. Gilbert, C. H. Greenberg, Q. Guo, J. HilleRisLambers, I. Ibanez, J. Johnstone, C. L. Kilner, J. Knops, W. D. Koenig, G. Kunstler, J. M. LaMontagne, K. L. Legg, J. Luongo, J. A. Lutz, D. Macias, E. J. B. McIntire, Y. Messaoud, C. M. Moore, E. Moran, J. A. Myers, O. B. Myers, C. Nunez, R. Parmenter, S. Pearse, S. Pearson, R. Poulton-Kamakura, E. Ready, M. D. Redmond, C. D. Reid, K. C. Rodman, C. L. Scher, W. H. Schlesinger, A. M. Schwantes, E. Shanahan, S. Sharma, M. A. Steele, N. L. Stephenson, S. Sutton, J. J. Swenson, M. Swift, T. T. Veblen, A. V. Whipple, T. G. Whitham, A. P. Wion, K. Zhu, and R. Zlotin, “Continent-wide tree fecundity driven by indirect climate effects,” *Nature Communications*, vol. 12, no. 1, p. 1242, 2021.
- [58] T. Qiu, R. Andrus, M.-C. Aravena, D. Ascoli, Y. Bergeron, R. Berretti, D. Berveiller, M. Bogdziewicz, T. Boivin, R. Bonal, D. C. Bragg, T. Caignard, R. Calama, J. J. Camarero, C.-H. Chang-Yang, N. L. Cleavitt, B. Courbaud, F. Courbet, T. Curt, A. J. Das, E. Daskalakou, H. Davi, N. Delpierre, S. Delzon, M. Dietze, S. D. Calderon, L. Dormont, J. Espelta, T. J. Fahey, W. Farfan-Rios, C. A. Gehring, G. S. Gilbert, G. Gratzer, C. H. Greenberg, Q. Guo, A. Hacket-Pain, A. Hampe, Q. Han, J. Hille Ris Lambers, K. Hoshizaki, I. Ibanez, J. F. Johnstone, V. Journé, D. Kabeya, C. L. Kilner, T. Kitzberger, J. M. H. Knops, R. K. Kobe, G. Kunstler, J. G. A. Lageard, J. M. LaMontagne, M. Ledwon, F. Lefevre, T. Leininger, J.-M. Limousin, J. A. Lutz, D. Macias, E. J. B. McIntire, C. M. Moore, E. Moran, R. Motta, J. A. Myers, T. A. Nagel, K. Noguchi, J.-M. Ourcival, R. Parmenter, I. S. Pearse, I. M. Perez-Ramos, L. Piechnik, J. Poulsen, R. Poulton-Kamakura, M. D. Redmond, C. D. Reid, K. C. Rodman, F. Rodriguez-Sanchez, J. D. Sanguinetti, C. L. Scher, W. H. Schlesinger, H. Schmidt Van Marle, B. Seget, S. Sharma, M. Silman, M. A. Steele, N. L. Stephenson, J. N. Straub, I. F. Sun, S. Sutton, J. J. Swenson, M. Swift, P. A. Thomas, M. Uriarte, G. Vacchiano, T. T. Veblen, A. V. Whipple, T. G. Whitham, A. P. Wion, B. Wright, S. J. Wright, K. Zhu, J. K. Zimmerman, *et al.*, “Limits to reproduction and seed size-number trade-offs that shape forest dominance and future recovery,” *Nature Communications*, vol. 13, no. 1, p. 2381, 2022.
- [59] S. B. Vander Wall, “How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 365, no. 1542, pp. 989–997, 2010.
- [60] R. Zwolak, M. Bogdziewicz, A. Wrobel, and E. E. Crone, “Advantages of masting in european beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis,” *Oecologia*, vol. 180, no. 3, pp. 749–758, 2016.

- [61] C. Larue, E. Austruy, G. Basset, and R. J. Petit, “Revisiting pollination mode in chestnut (*castanea* spp.): an integrated approach,” *Botany Letters*, vol. 168, no. 3, pp. 348–372, 2021.
- [62] G. Garcia, B. Re, C. Orians, and E. Crone, “By wind or wing: pollination syndromes and alternate bearing in horticultural systems,” *Philosophical Transactions of the Royal Society B*, vol. 376, no. 1839, p. 20200371, 2021.
- [63] V. Journe, R. Andrus, M.-C. Aravena, D. Ascoli, R. Berretti, D. Berveiller, M. Bogdziewicz, T. Boivin, R. Bonal, T. Caignard, R. Calama, J. J. Camarero, C.-H. Chang-Yang, B. Courbaud, F. Courbet, T. Curt, A. J. Das, E. Daskalidou, H. Davi, N. Delpierre, S. Delzon, M. Dietze, S. Donoso Calderon, L. Dormont, J. Maria Espelta, T. J. Fahey, W. Farfan-Rios, C. A. Gehring, G. S. Gilbert, G. Gratzner, C. H. Greenberg, Q. Guo, A. Hacket-Pain, A. Hampe, Q. Han, J. H. R. Lambers, K. Hoshizaki, I. Ibanez, J. F. Johnstone, D. Kabeya, R. Kays, T. Kitzberger, J. M. H. Knops, R. K. Kobe, G. Kunstler, J. G. A. Lageard, J. M. LaMontagne, T. Leininger, J.-M. Limousin, J. A. Lutz, D. Macias, E. J. B. McIntire, C. M. Moore, E. Moran, R. Motta, J. A. Myers, T. A. Nagel, K. Noguchi, J.-M. Ourcival, R. Parmenter, I. S. Pearse, I. M. Perez-Ramos, L. Piechnik, J. Poulsen, R. Poulton-Kamakura, T. Qiu, M. D. Redmond, C. D. Reid, K. C. Rodman, F. Rodriguez-Sanchez, J. D. Sanguinetti, C. L. Scher, H. S. V. Marle, B. Seget, S. Sharma, M. Silman, M. A. Steele, N. L. Stephenson, J. N. Straub, J. J. Swenson, M. Swift, P. A. Thomas, M. Uriarte, G. Vacchiano, T. T. Veblen, A. V. Whipple, T. G. Whitham, B. Wright, S. J. Wright, K. Zhu, J. K. Zimmerman, R. Zlotin, M. Zywiec, and J. S. Clark, “Globally, tree fecundity exceeds productivity gradients,” *Ecology Letters*, vol. n/a, no. n/a, 2022.
- [64] C. C. Smith, J. L. Hamrick, and C. L. Kramer, “The advantage of mast years for wind pollination,” *The American Naturalist*, vol. 136, no. 2, pp. 154–166, 1990.
- [65] C. K. Augspurger, “Reproductive synchrony of a tropical shrub: Experimental studies on effects of pollinators and seed predators in *hybanthus prunifolius* (violaceae),” *Ecology*, vol. 62, no. 3, pp. 775–788, 1981.
- [66] E. E. Crone, “Responses of social and solitary bees to pulsed floral resources,” *The American Naturalist*, vol. 182, no. 4, pp. 465–473, 2013.
- [67] W. D. Koenig, D. Kelly, V. L. Sork, R. P. Duncan, J. S. Elkinton, M. S. Peltonen, and R. D. Westfall, “Dissecting components of population-level variation in seed production and the evolution of masting behavior,” *Oikos*, vol. 102, no. 3, pp. 581–591, 2003.
- [68] A. Satake and D. Kelly, “Studying the genetic basis of masting,” *Philosophical Transactions of the Royal Society B*, vol. 376, no. 1839, p. 20210116, 2021.
- [69] R. C. Mueller, B. D. Wade, C. A. Gehring, and T. G. Whitham, “Chronic herbivory negatively impacts cone and seed production, seed quality and seedling growth of susceptible pinyon pines,” *Oecologia*, vol. 143, no. 4, pp. 558–565, 2005.
- [70] C. S. Schopmeyer *et al.*, “Seeds of woody plants in the united states.,” *Seeds of woody plants in the United States.*, no. 450, 1974.
- [71] M. J. Crawley and C. R. Long, “Alternate bearing, predator satiation and seedling recruitment in *quercus robur* l.,” *Journal of Ecology*, vol. 83, no. 4, pp. 683–696, 1995.
- [72] R. H. Manson, R. S. Ostfeld, and C. D. Canham, “The effects of tree seed and seedling density on predation rates by rodents in old fields,” *Écoscience*, vol. 5, no. 2, pp. 183–190, 1998.
- [73] R. Zwolak, P. Celebias, and M. Bogdziewicz, “Global patterns in the predator satiation effect of masting: A meta-analysis,” *Proceedings of the National Academy of Sciences*, vol. 119, no. 11, p. e2105655119, 2022.
- [74] J. Bascompte, “Mutualistic networks,” *Frontiers in Ecology and the Environment*, vol. 7, no. 8, pp. 429–436, 2009.
- [75] J. S. Clark, M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers, “Seed dispersal near and far: Patterns across temperate and tropical forests,” *Ecology*, vol. 80, no. 5, pp. 1475–1494, 1999.

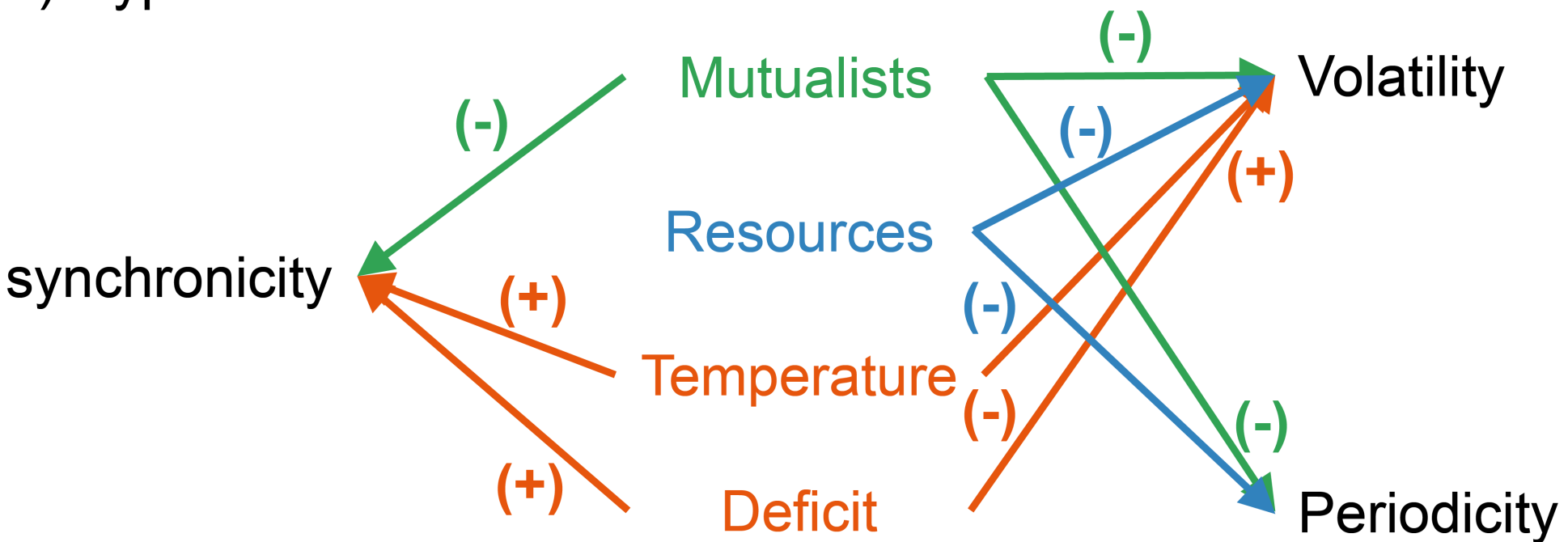
- [76] J. Tobin, “Estimation of relationships for limited dependent variables,” *Econometrica*, vol. 26, no. 1, pp. 24–36, 1958.
- [77] J. S. Clark, D. Nemergut, B. Seyednasrollah, P. J. Turner, and S. Zhang, “Generalized joint attribute modeling for biodiversity analysis: median-zero, multivariate, multifarious data,” *Ecological Monographs*, vol. 87, no. 1, pp. 34–56, 2017.
- [78] D. M. Olson, E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. Powell, E. C. Underwood, J. A. D’amico, I. Itoua, H. E. Strand, J. C. Morrison, *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*, vol. 51, no. 11, pp. 933–938, 2001.
- [79] A. E. Zanne, D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J. McGlinn, B. C. O’Meara, A. T. Moles, P. B. Reich, D. L. Royer, D. E. Soltis, P. F. Stevens, M. Westoby, I. J. Wright, L. Aarssen, R. I. Bertin, A. Calaminus, R. Govaerts, F. Hemmings, M. R. Leishman, J. Oleksyn, P. S. Soltis, N. G. Swenson, L. Warman, and J. M. Beaulieu, “Three keys to the radiation of angiosperms into freezing environments,” *Nature*, vol. 506, no. 7486, pp. 89–92, 2014.
- [80] L. J. Revell, “phytools: an r package for phylogenetic comparative biology (and other things),” *Methods in Ecology and Evolution*, vol. 3, no. 2, pp. 217–223, 2012.
- [81] R. Freckleton, P. P. Harvey, H. and M. Pagel, “Phylogenetic analysis and comparative data: A test and review of evidence,” *The American Naturalist*, vol. 160, no. 6, pp. 712–726, 2002.
- [82] J. D. Hadfield and S. Nakagawa, “General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters,” *Journal of Evolutionary Biology*, vol. 23, no. 3, pp. 494–508, 2010.
- [83] J. Kattge, G. Boenisch, S. Diaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D. A. Werner, T. Aakala, M. Abedi, A. T. R. Acosta, G. C. Adamidis, K. Adamson, M. Aiba, C. H. Albert, J. M. Alcantara, C. C. Alcazar, I. Aleixo, H. Ali, B. Amiaud, C. Ammer, M. M. Amoroso, M. Anand, C. Anderson, N. Anten, J. Antos, D. M. G. Apgaua, T.-L. Ashman, D. H. Asmara, G. P. Asner, M. Aspinwall, O. Atkin, I. Aubin, L. Baastrop-Spohr, K. Bahalkeh, M. Bahn, T. Baker, W. J. Baker, J. P. Bakker, D. Baldocchi, J. Baltzer, A. Banerjee, A. Baranger, J. Barlow, D. R. Barneche, Z. Baruch, D. Bastianelli, J. Battles, W. Bauerle, M. Bauters, E. Bazzato, M. Beckmann, H. Beeckman, C. Beierkuhnlein, R. Bekker, G. Belfry, M. Belluau, M. Beloiu, R. Benavides, L. Benomar, M. L. Berdugo-Lattke, E. Berenguer, R. Bergamin, J. Bergmann, M. B. Carlucci, L. Berner, M. Bernhardt-Roemermann, C. Bigler, A. D. Bjorkman, C. Blackman, C. Blanco, B. Blonder, D. Blumenthal, K. T. Bocanegra-Gonzalez, P. Boeckx, S. Bohlman, K. Boehning-Gaese, L. Boisvert-Marsh, W. Bond, B. Bond-Lamberty, A. Boom, C. C. F. Boonman, K. Bordin, E. H. Boughton, V. Boukili, D. M. J. S. Bowman, S. Bravo, M. R. Brendel, M. R. Broadley, K. A. Brown, H. Bruelheide, F. Brunnich, H. H. Bruun, D. Bruy, S. W. Buchanan, S. F. Bucher, N. Buchmann, R. Buitenwerf, D. E. Bunker, J. Buerger, S. Burrascano, D. F. R. P. Burslem, B. J. Butterfield, C. Byun, M. Marques, M. C. Scalon, M. Caccianiga, M. Cadotte, M. Cailleret, J. Camac, J. Julio Camarero, C. Company, G. Campetella, J. A. Campos, L. Cano-Arboleda, R. Canullo, M. Carbognani, F. Carvalho, F. Casanoves, B. Castagneyrol, J. A. Catford, J. Cavender-Bares, B. E. L. Cerabolini, M. Cervellini, E. Chacon-Madrigo, K. Chapin, F. S. Chapin, S. Chelli, S.-C. Chen, A. Chen, P. Cherubini, F. Chianucci, B. Choat, K.-S. Chung, M. Chytry, D. Ciccarelli, L. Coll, C. G. Collins, L. Conti, D. Coomes, J. H. C. Cornelissen, W. K. Cornwell, P. Corona, M. Coyea, J. Craine, D. Craven, J. P. G. M. Croomsigt, A. Cseceserits, K. Cufar, M. Cuntz, A. C. da Silva, K. M. Dahlin, M. Dainese, I. Dalke, M. Dalle Fratte, A. T. Dang-Le, J. Danihelka, M. Dannoura, S. Dawson, A. J. de Beer, A. De Frutos, J. R. De Long, B. Dechant, S. Delagrange, N. Delpierre, G. Derroire, A. S. Dias, M. H. Diaz-Toribio, P. G. Dimitrakopoulos, M. Dobrowolski, D. Doktor, P. Drevojan, N. Dong, J. Dransfield, S. Dressler, L. Duarte, E. Ducouret, S. Dullinger, W. Durka, P. Duursma, O. Dymova, A. E-Vojtko, R. L. Eckstein, H. Ejtehadi, J. Elser, T. Emilio, K. Engemann, M. B. Erfanian, A. Erfmeier, A. Esquivel-Muelbert, G. Esser, M. Estiarte, T. F. Domingues, W. F. Fagan, J. Fagundes, D. S. Falster, Y. Fan, J. Fang, E. Farris, F. Fazlioglu, Y. Feng, F. Fernandez-Mendez, C. Ferrara, J. Ferreira, A. Fidelis, B. Finegan, J. Firn, T. J. Flowers, D. F. B. Flynn, V. Fontana, E. Forey, C. Forgiarini, L. Francois, M. Frangipani, D. Frank, C. Frenette-Dussault, G. T. Freschet, E. L. Fry, N. M. Fyllas, G. G. Mazzochini, S. Gachet, R. Gallagher, G. Ganade, F. Ganga, P. Garcia-Palacios,

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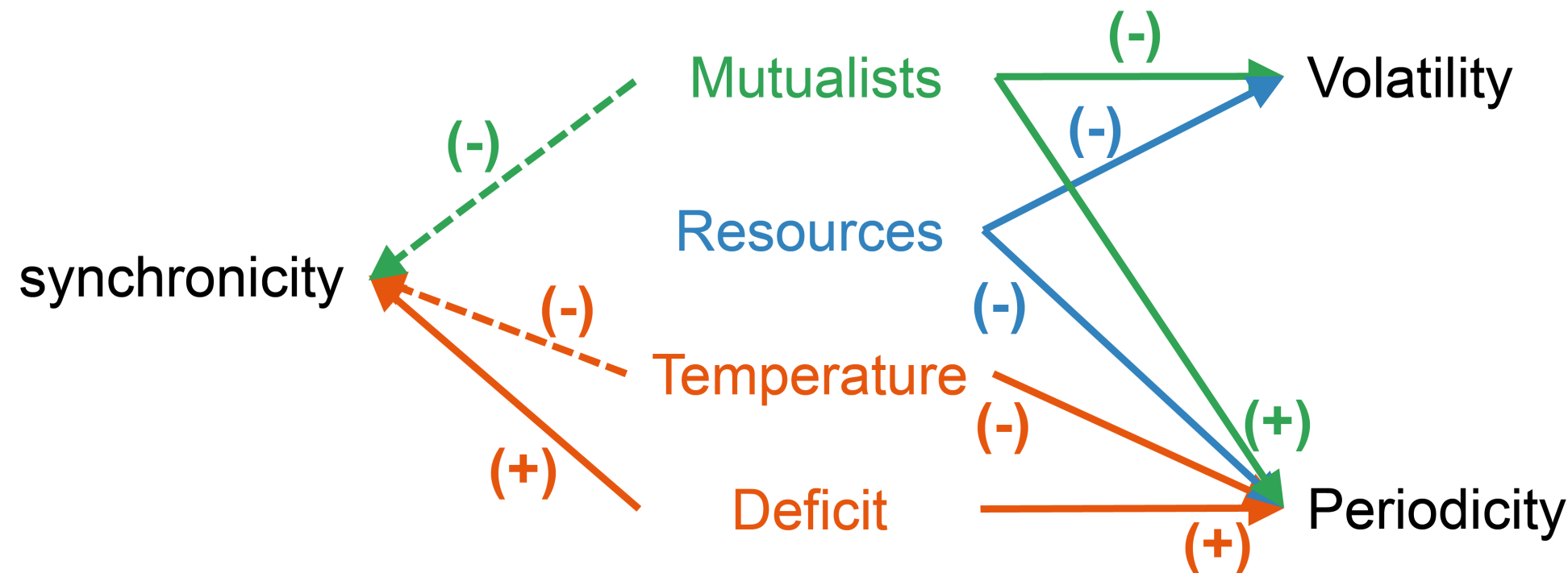
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 870 Bi, G. Zotz, C. Wirth, and N. Network, “Try plant trait database – enhanced coverage and open
 871 access,” *Global Change Biology*, vol. 26, no. 1, pp. 119–188, 2020.



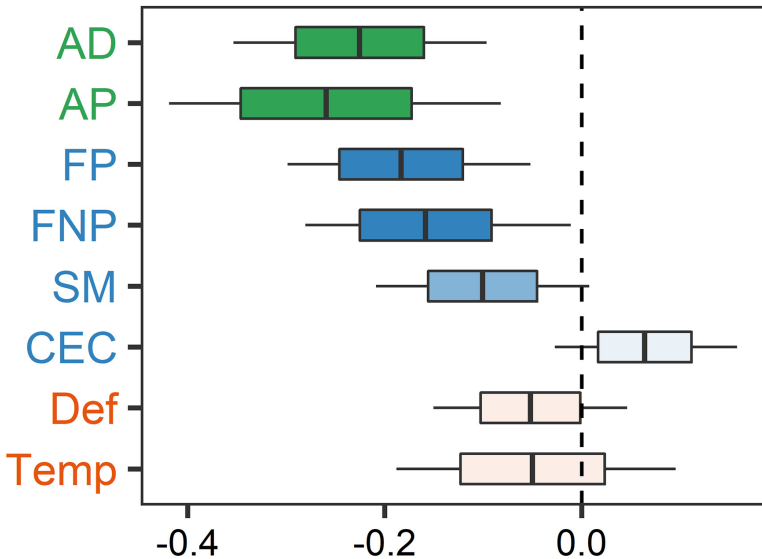
a) Hypotheses



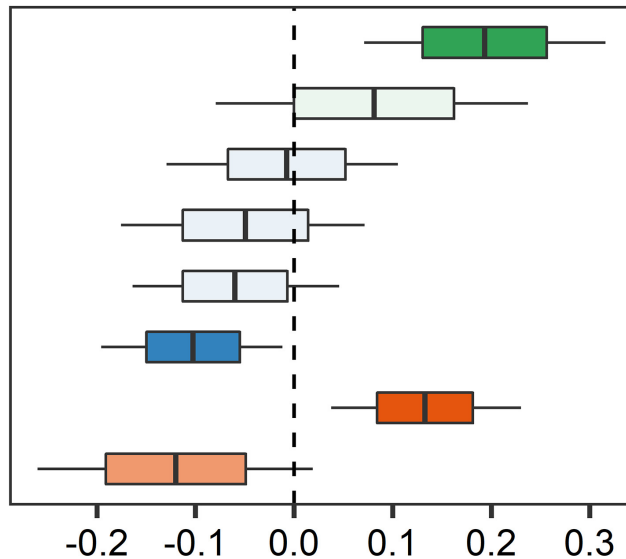
b) Results



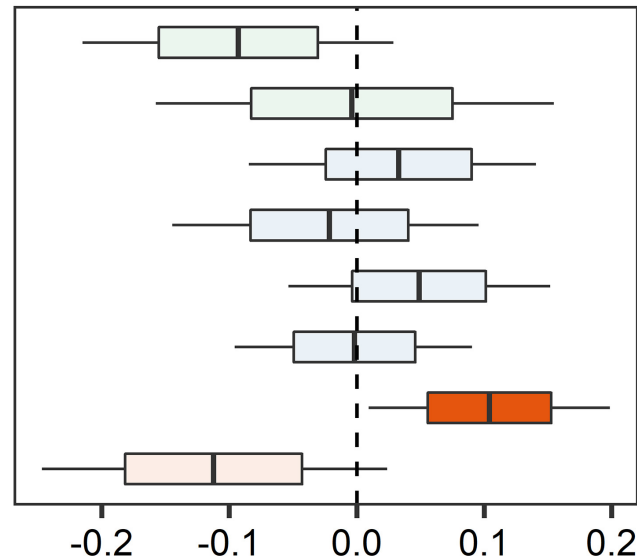
a) Volatility (log variance)

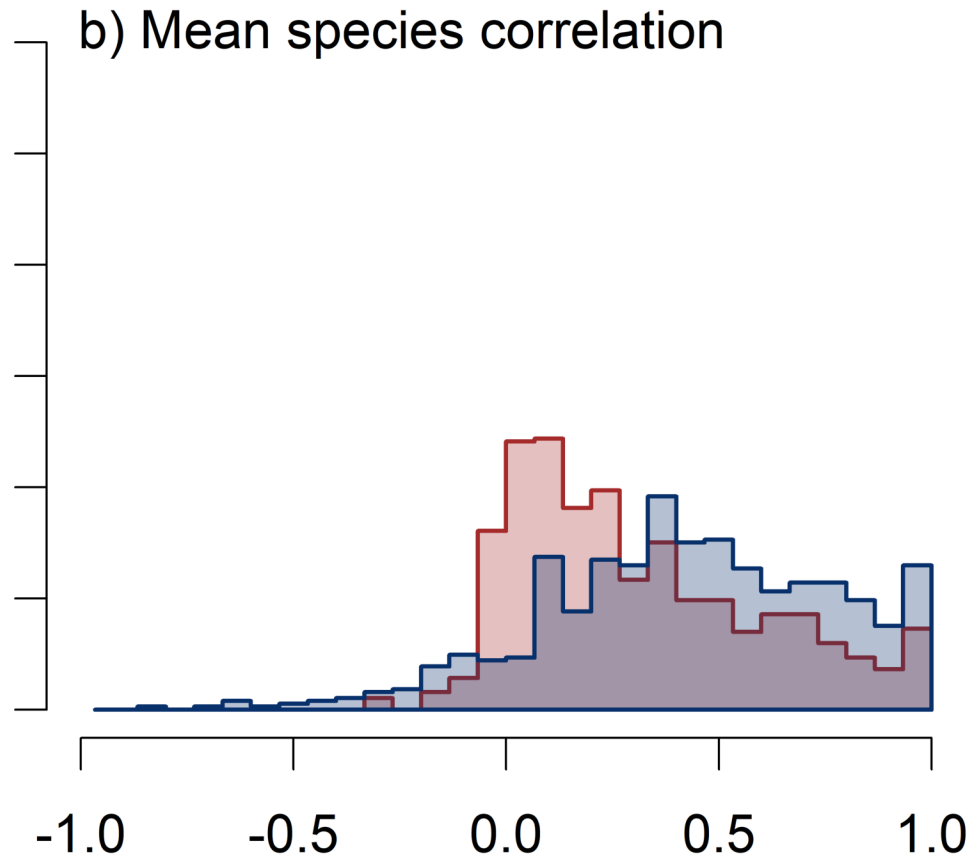
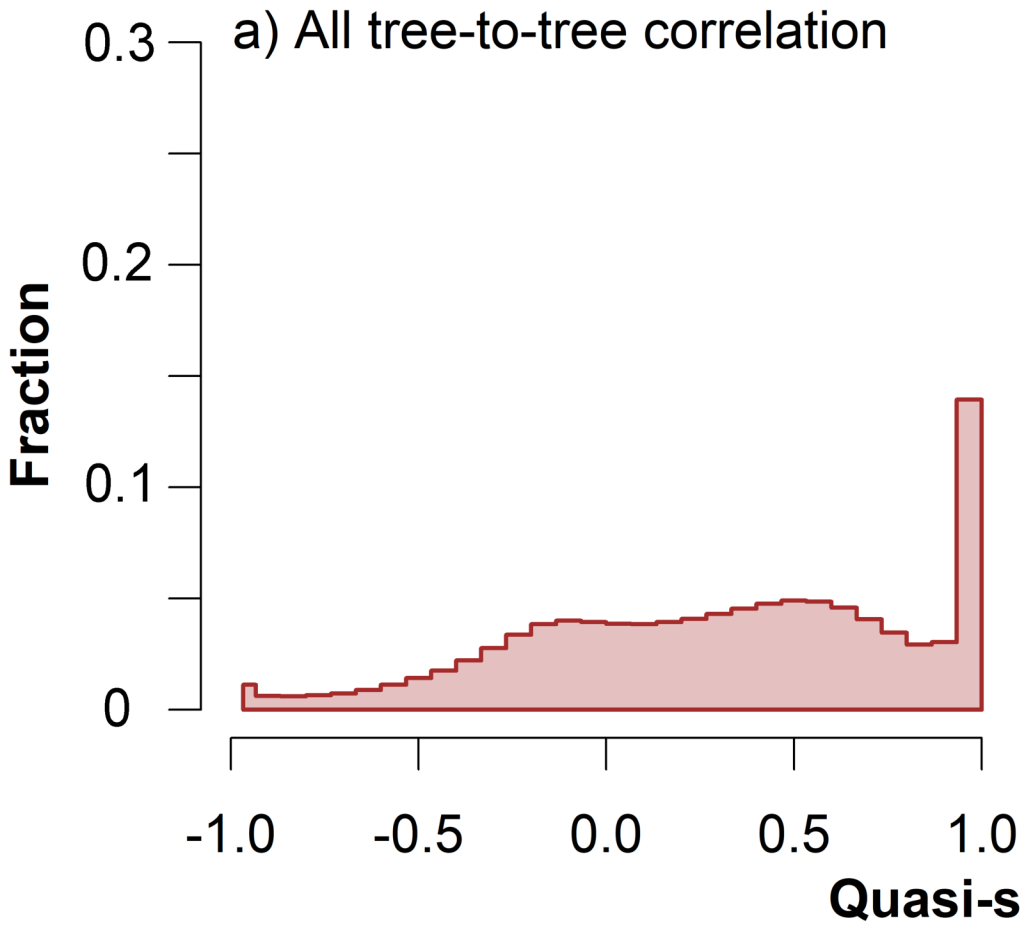


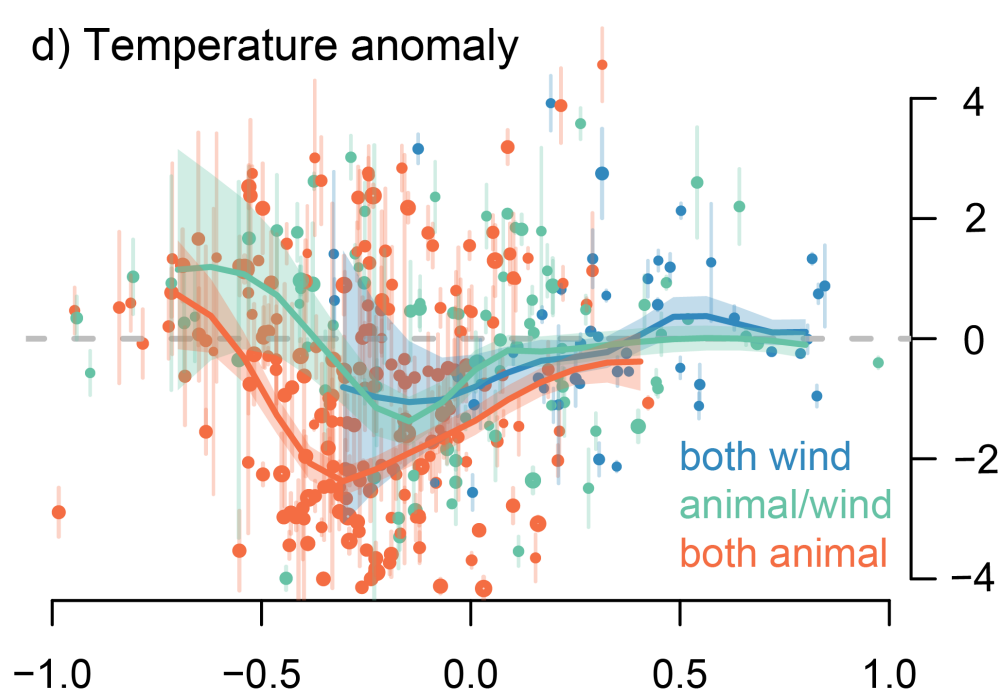
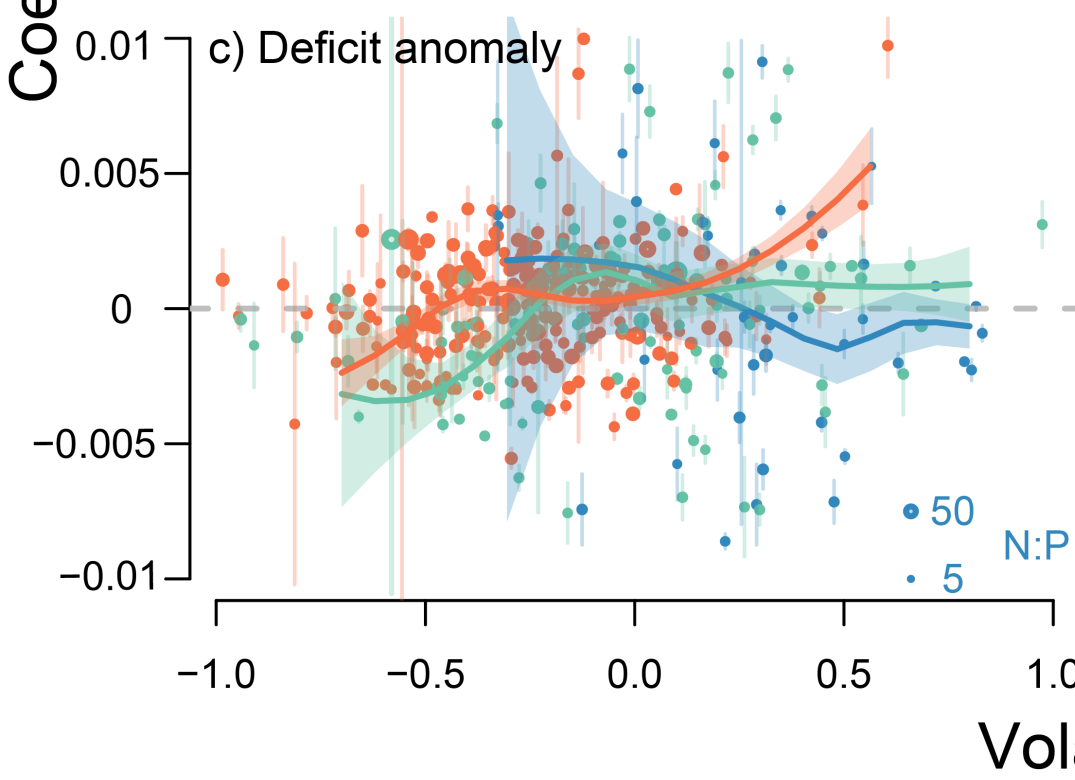
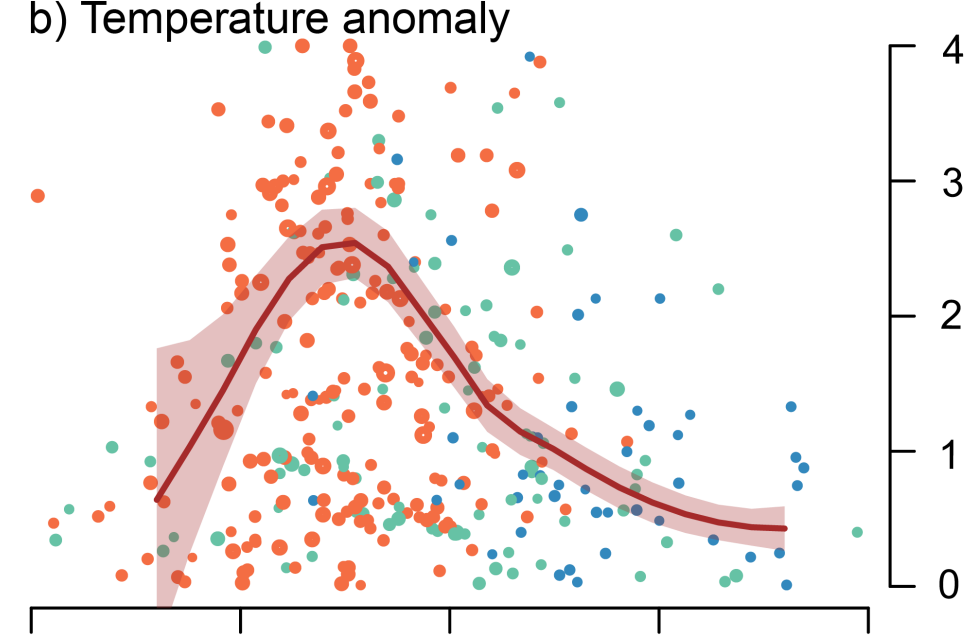
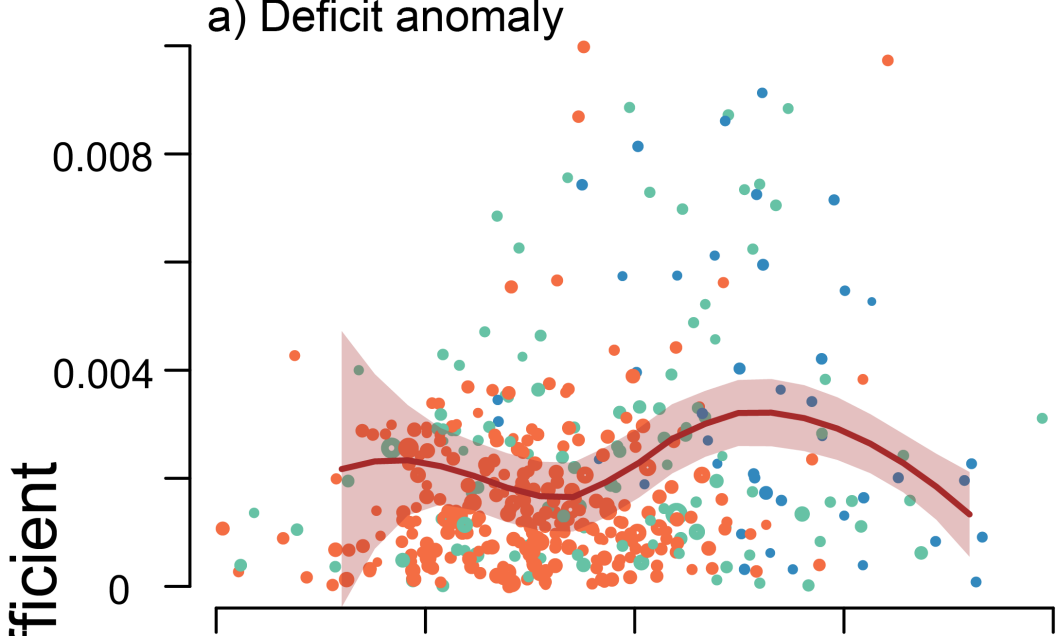
b) Periodicity (years)

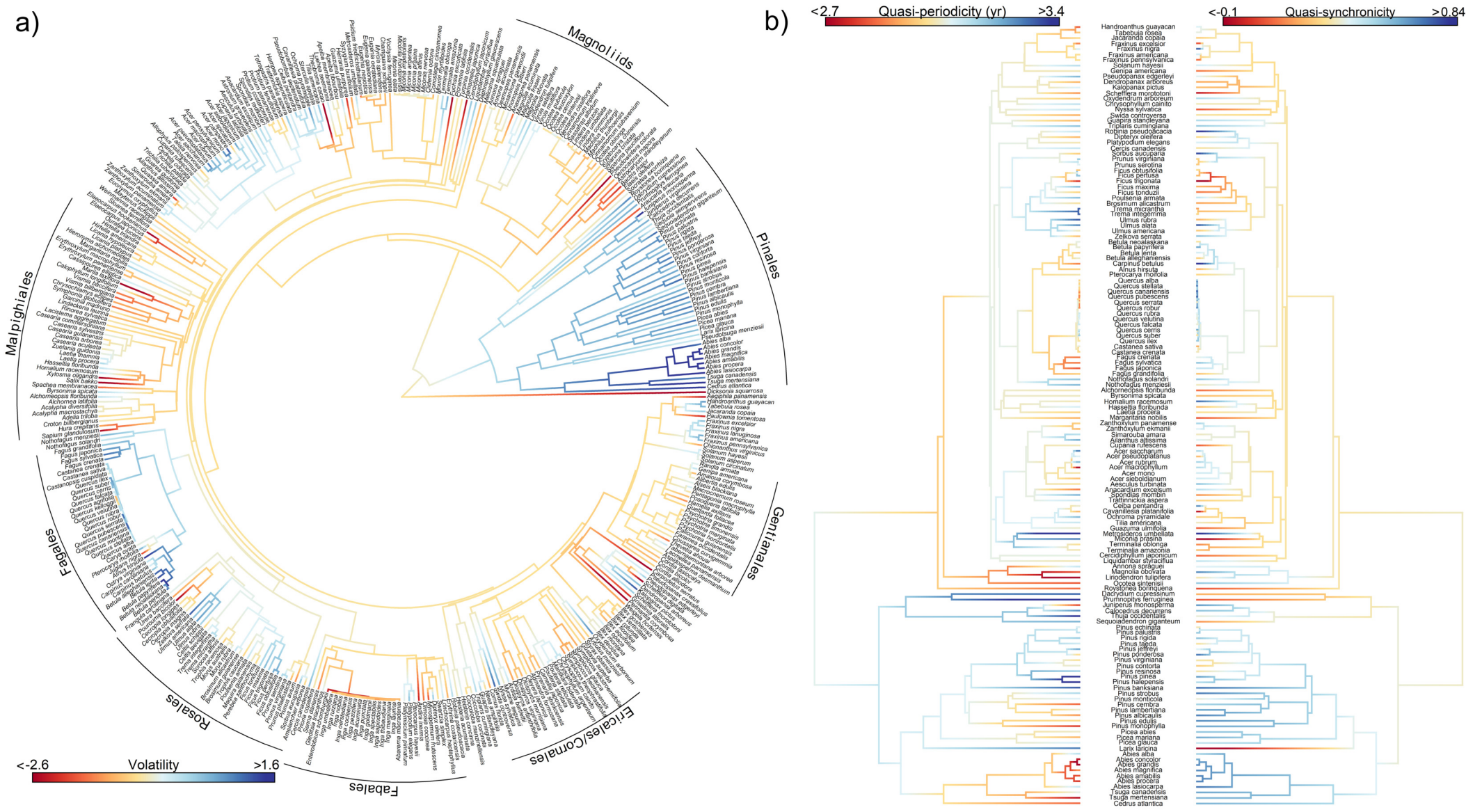


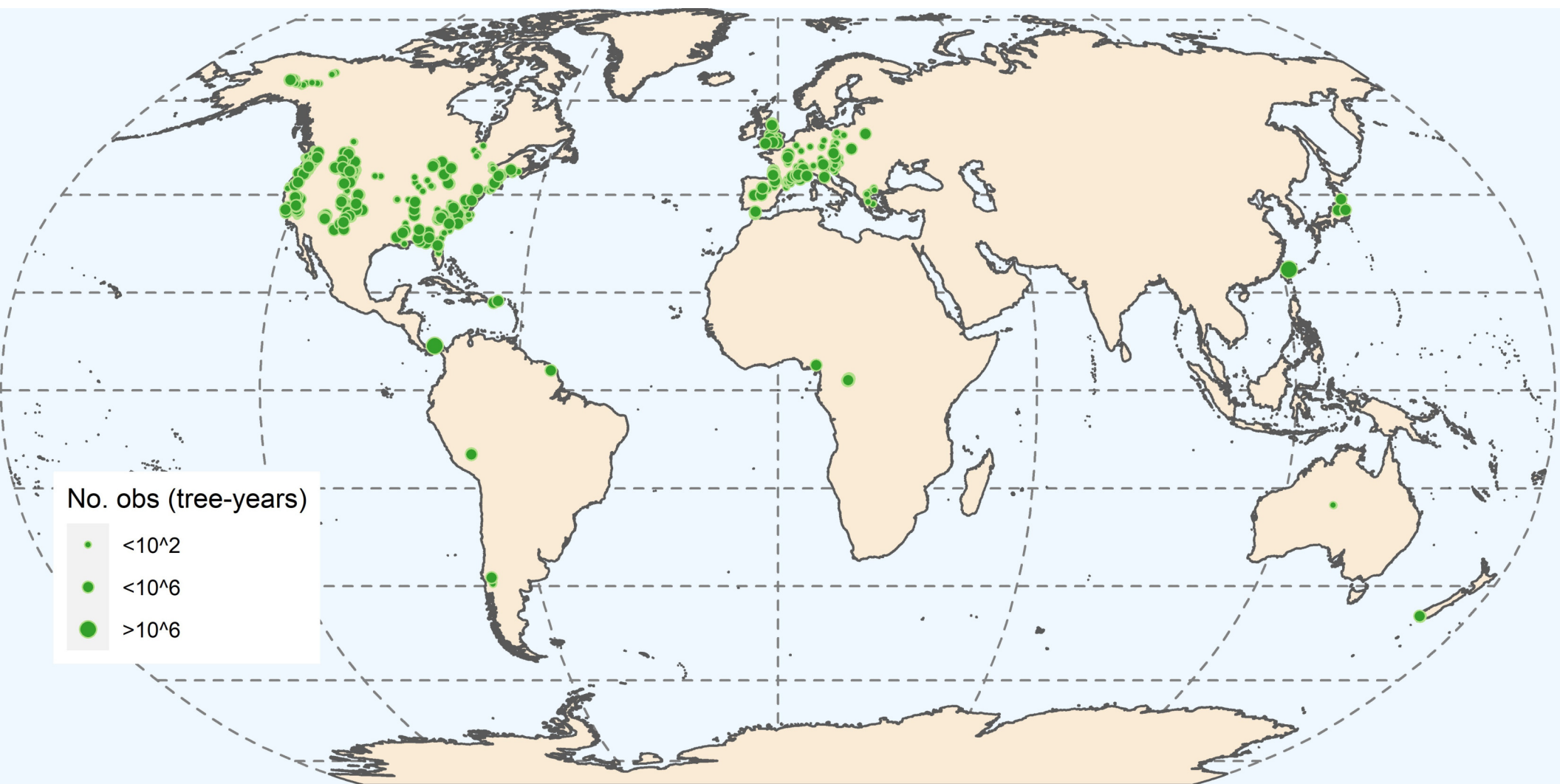
c) Synchronicity (correlation)

**Standardized coefficients**

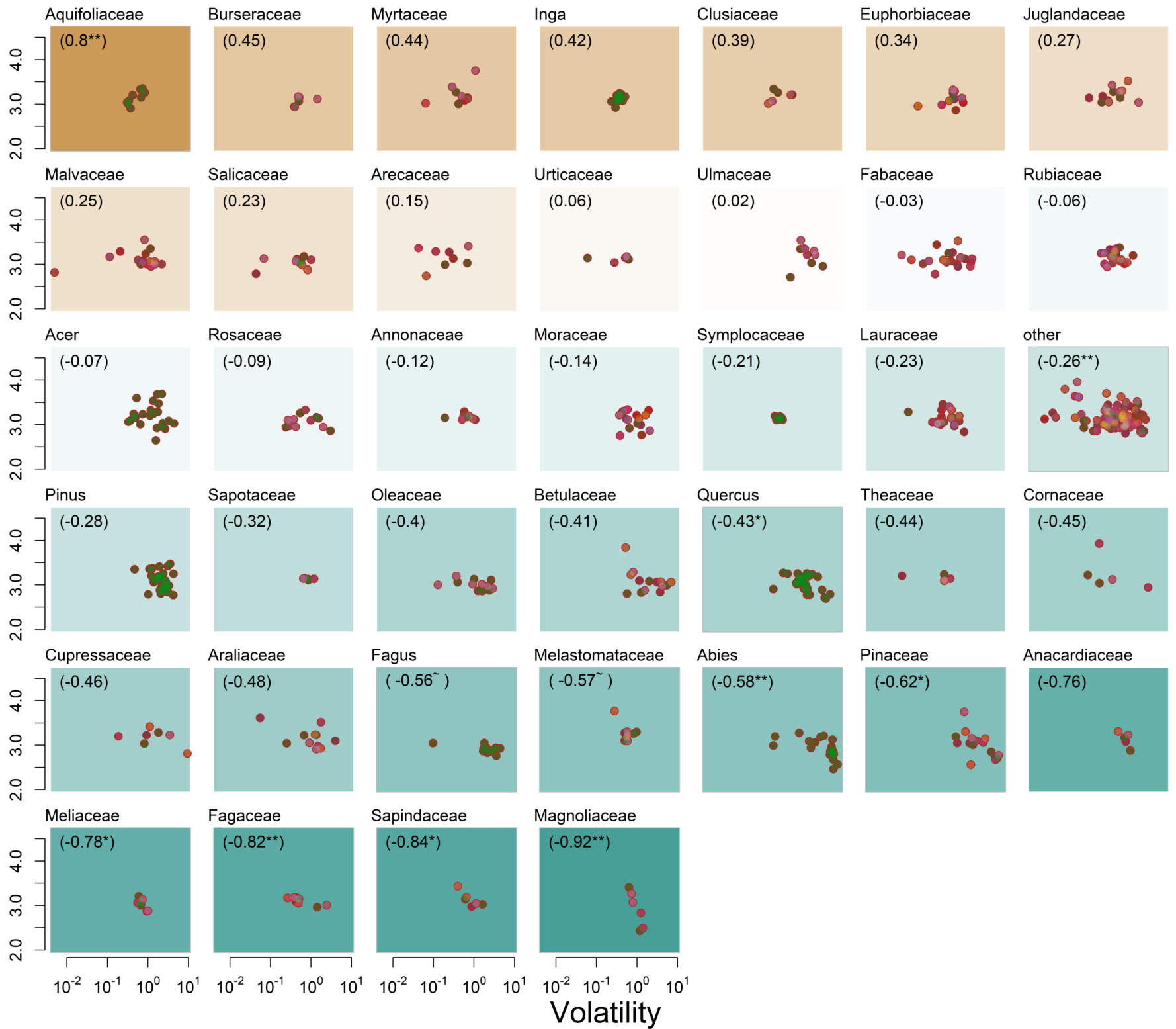








Quasi-periodicity



Quasi-synchronicity

