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Nutrient scarcity as a selective pressure for mast seeding

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Introductory paragraph

Mast seeding is one of the most intriguing reproductive traits in nature. Despite its potential drawbacks in terms of fitness, the widespread existence of this phenomenon suggests that it should have evolutionary advantages under certain circumstances. Using a global dataset of seed production time series for 219 plant species from all the continents, we tested whether masting behaviour appears predominantly in species with low foliar N and P concentrations, when controlling for local climate and productivity. Here we show that masting intensity is higher in species with low foliar N and P concentrations and especially imbalanced N:P ratios, and that the evolutionary history of masting behaviour has been linked to that of nutrient economy. Our results support the hypothesis that masting is stronger in species growing under limiting conditions and suggest that this reproductive behaviour might have evolved as an adaptation to nutrient limitations and imbalances.

Main text

Mast seeding, often called *masting*, has long intrigued biologists as one of the most bizarre reproductive behaviours found in nature^{1,2}. This behaviour consists of the synchronous production of highly variable seed crops over time³. Masting has often been considered an evolutionary paradox because organisms that skip reproductive attempts should have lower fitness than those that reproduce at every opportunity⁴. Nonetheless, the fact that this reproductive behaviour is found in different lineages suggests that masting behaviour should be beneficial, at least under certain scenarios⁵.

The most widely accepted hypotheses explaining the selective advantages of masting are all related to *economies of scale*^{6,7}. Briefly, these hypotheses state that, in terms of fitness, it is more efficient for plants to produce large number of seeds every few to several years than producing a constant amount every year. This general mechanism includes the *predator satiation* hypothesis^{2,8–10}, where predators are starved during

years of null or low reproduction and satiated during high reproduction *mast* years, leaving large numbers of seeds intact. Another example is the *pollination efficiency* hypothesis^{6,11,12}, stating that, particularly for wind-pollinated plants, saturating the atmosphere with pollen in a given year is more efficient than producing regular amounts of pollen each year in order to ensure pollination. Given that masting is present in only a modest percentage of plant species¹³, such economies of scale are apparently advantageous only under certain circumstances. What those circumstances are remains, so far, under debate.

The environmental stress hypothesis¹⁴ suggests that masting behaviour should be stronger under unfavourable growing conditions or limitation of resources, conditions under which *economies of scale* should be more beneficial^{3,12,15}. This is because plants growing in unfavourable environments presumably experience more difficulties in acquiring the required resources to reproduce, as suggested by the *resource accumulation* hypothesis^{16,17}. According to this hypothesis, plants growing under favourable conditions will be able to accumulate the required amount of resources every year and, therefore, present a regular pattern in seed production, without exhibiting any underlying negative temporal autocorrelation that could indicate resource depletion after reproduction¹⁶. The opposite is true for plants growing in unfavourable conditions, which will exhibit high interannual variability and negative temporal autocorrelation in seed production due to potential resource depletion after seeding. However, there is no current empirical evidence suggesting that species with higher interannual variability in fruit production are more likely to exhibit negative temporal autocorrelation than species that produce seeds more regularly⁵. On the other hand, weather variability has been found to be a key factor driving interannual variability in fruit production in many plant species^{12,18–21}. Temporal patterns in weather events (i.e., temporal variability and autocorrelation) could, therefore, potentially shape the temporal patterns of fruit production²².

Foliar nutrient concentrations play a key role in plant ecophysiology and ecosystem functioning: photosynthetic rates are linked to foliar nitrogen (N) and phosphorus (P) concentrations^{23–25}. Together with carbon, they are the basis of ecological stoichiometry^{26,27} and are fundamental parts of the *elementome* or the *biogeochemical niche*²⁸, useful for inferring ecological traits from the elemental composition of organisms²⁹. Carbon (C), and especially N and P have been suggested to be potential resources determining seed production and masting behaviour^{15,30–32} because seeds and fruits are enriched with N and P compared to vegetative tissues³³. Low foliar concentrations of N and P would imply lower photosynthetic rates²³ that would in turn result in reduced accumulation of C, in addition to low accumulation of N and P. Thus, based on the *resource budget* model, plant species with low foliar N and P concentrations would be expected to exhibit stronger masting behaviour in terms of variability and negative temporal autocorrelation.

Both foliar N and P have been reported to be positively correlated with investment in plant reproduction^{34–36}. Additionally, the interaction between foliar N and P, (i.e., the N:P ratio) has been suggested to be an important indicator of plant nutritional status, to promote vegetative productivity^{37–40} and to relate to reproductive effort³⁶ and ecological strategies²⁸. The lower N:P ratio of seeds compared to vegetative tissues suggest that nutrient imbalances may constrain reproduction more than growth³⁸. Previous studies have reported that plants and shoots producing flowers often exhibit lower N:P values than those that do not^{38,41}, highlighting the role of nutrient imbalances in plant reproduction. However, no study has yet been focused on the evolutionary linkage between plant reproduction and foliar nutrient stoichiometry over a large set of species.

Here we hypothesize that mast seeding behaviour evolved predominantly in plant species with low foliar N and P concentrations and high N:P ratios. To test this hypothesis, we first explored the relationship between temporal variability and autocorrelation in reproductive effort using a global dataset of 219 plant species from

all the continents to see if higher variability in seed production is related to higher potential resource depletion (negative temporal autocorrelation)⁵. We then fitted phylogenetic linear models to test whether masting intensity, here defined as the combination of temporal variability and autocorrelation using the consecutive disparity (D) index^{42,43}, was related to foliar N, P and N:P ratio, while controlling for the evolutionary history of the species and other potentially influencing factors such as local climate and productivity of the regions where species were sampled. Finally, we tested the model of evolution of masting behaviour by means of ancestral character reconstructions and explored whether it has evolved in concert with foliar N and P economies.

Results

Redefining masting intensity: temporal variability, potential resource depletion and their evolutionary relationships

Our results indicated that temporal variability (here calculated as the proportional variability index⁴⁴ PV, see **Methods**) in seed production is evolutionary conserved (**Figure S1a**), showing a strong phylogenetic signal⁴⁵. In contrast, lag-1 temporal autocorrelation (AR1, indicating potential resource depletion when it takes negative values) is not phylogenetically conserved. Additionally, temporal variability and autocorrelation are not evolutionary correlated. Hence, species exhibiting higher temporal variability do not necessarily exhibit any particular pattern of temporal autocorrelation (**Figure S1b**). Masting intensity, defined as D in this study (see **Methods**), accounted for both features of masting behaviour (**Figure 1**), temporal variability and potential resource depletion (negative AR1 coefficients), hence defining masting behaviour more broadly than the coefficient of variation (CV) alone, as it is typically assessed⁴². Masting intensity was also preserved phylogenetically (**Figure 1**). Our results suggest that most species exhibit low or intermediate masting intensity, while only a few exhibit strong masting behaviour (see histogram in **Figure 1a**).

Phylogenetic models indicated a statistically significant negative interaction between foliar N and P explaining variability in masting intensity across species (**Table 1, Figure 2**). Model results indicated that when foliar P is low, increasing foliar N increases masting intensity as N:P increases. The inverse situation (high masting intensity at very low N:P ratios) is also possible according to model results, despite being a less likely scenario (we only had 19 species with $N:P < 8$ in our dataset). The highest masting intensity was found in species with high N:P while the lowest was found in species with high foliar N and P concentrations. Species with low foliar N and P concentrations showed intermediate values of masting intensity. Temporal variability of the local climate or productivity of the region from where species were sampled did not explain variation in masting intensity. Mean annual precipitation, however, was positively related to masting intensity (**Table 1**). Temporal variability in seed production was negatively related to mean annual temperature and positively related to temporal variability of annual precipitation. Additionally, species with higher foliar P exhibited lower temporal variability. When assessing temporal variability using the CV, we found that species from regions with higher temporal variability in productivity also presented higher CV of seed production ($\beta=0.22 \pm 0.08$, $P=0.004$, $\lambda=0.58$). Potential resource depletion was more likely to occur in species living in climates exhibiting negative temporal autocorrelation in annual precipitation (**Table 1**). Interestingly, the model also showed a positive interaction between foliar N and P, indicating that potential resource depletion after seeding was more likely to occur in species with low foliar N and P.

Our analyses also revealed the evolutionary processes linking masting behaviour and foliar nutrient concentrations (**Table S1**). We found that adaptive processes - Ornstein-Uhlenbeck (OU) models based on ancestral character reconstructions (**Figure S2**) - are the models that better explain current patterns in masting intensity, linked to foliar nutrient concentrations. Adaptive OU models explaining evolutionary history of masting

intensity with N, P and N×P (a measure of total N and P foliar concentration) assumed that species evolved toward different optimum values depending on whether they present high or low masting intensity (masting and non-masting species) (OUM model). However, a single optimum for all species was equally likely for foliar N, P and N×P (less than 2 units of AICc between models were found, OU1, see **Methods**). Nonetheless, given that OUM models with different optimum values performed equally well for foliar N, P and N×P (**Table S1**), OUM models are used to illustrate our results. The model that best fitted the data for foliar N:P was an adaptive OU model with different optimum and phenotypic variation for high and low masting intensity species (OUMV model).

Results from OU models indicated that masting species had, on average, $9.5 \pm 0.4\%$ and $18.3 \pm 0.5\%$ lower foliar N and P concentrations, respectively, than non-masting species (**Figure 3, Table S2**). Foliar N:P ratio was $11.4 \pm 0.2\%$ (mean \pm standard error of the mean) higher in masting species, while N×P, combined availability of N and P, was $28.7 \pm 1.0\%$ lower than in non-masting species. These results were consistent when using five different thresholds of masting intensity (see **Methods**) to classify species as masting or non-masting species (**Table S2**). Like masting intensity, both foliar N and P concentrations were preserved throughout the phylogeny (**Figure S3**).

Discussion

The role of foliar nutrients in seed production

Our results suggest that masting intensity co-evolved with species-specific optimal foliar N and P concentrations and that species with lower N and especially lower P, and therefore high N:P, exhibit higher masting intensity (**Figure 3**). Hence, our analyses supported our initial hypothesis stating that masting behaviour evolved predominantly in plant species with low foliar N and P concentrations and high N:P ratios. This observed evolutionary pattern may have originated because of different underlying

mechanisms driven by environmental and physiological constraints. One potential mechanism explaining these findings could be the physiological role of foliar N and P concentrations in plants. Foliar N is well known for being the primary limiting nutrient for reproduction^{34,35} and vegetative growth^{46,47}. Elevated foliar P concentrations, and low N:P ratios, have been shown to allow larger seed crops in multiple species^{15,36,41,48}, coinciding with fast growing species according to the *growth rate* hypothesis²⁶. P is also essential to maintain water-use efficiency and growth, particularly during drought conditions⁴⁹. Both nutrients are essential elements of ribosomes and, therefore, play a major role in organismal metabolism⁵⁰. The production of seeds, which are structures enriched with N and P³³, may potentially benefit from high concentrations of nutrients even more than vegetative tissues.

Low foliar N and P concentrations and high N:P imbalance are often indicative of unfavourable environments for plant growth^{15,51,52}, such as infertile soils. These poor growing conditions are often related to dry or cold climates where decomposition of organic matter is constrained, rates of nutrient mineralisation and weathering are low^{49,53}, or disturbances (e.g., wildfires) are frequent⁵⁴. However, differences in foliar N and P concentrations may not always reflect differences in nutrient availability across species, as coexisting species may have different elemental compositions (the *biogeochemical niche* hypothesis²⁸). Nonetheless, plants with high foliar N and P concentrations must either be growing in environments without nutrient limitations or have developed mechanisms that allow them to sustain high foliar nutrient concentrations even if they are growing under unfavourable conditions. In any case, these higher concentrations of nutrients should confer a competitive advantage in terms of C acquisition, because higher N and P concentrations are, on average, linked to higher photosynthetic rates²³.

Evolutionary history of masting intensity and foliar nutrients

Being capable to invest more in reproduction does not explain masting behaviour by itself, because equal average seed crops over time could lead to different reproductive behaviours¹⁵. The necessary link between the ecological stoichiometry and masting theoretical backgrounds lies in the *resource accumulation* hypothesis^{16,17}. Plant species with lower or imbalanced availability of N and P may present more difficulties in acquiring the necessary amount of C, N and P to successfully produce seeds regularly, thereby mechanistically producing a reproductive behaviour aligned with high masting intensity: high interannual variability and negative temporal autocorrelation (i.e., potential resource depletion). The combination of low and imbalanced nutrient availability, causing high variability in seed production and potential resource depletion after crops, and environmental variability that synchronises the reproduction of individuals through weather cues^{7,19} would finally shape the reproductive behaviour of masting species. In fact, our results also revealed that mean annual precipitation, and its temporal variability and autocorrelation, are related to the reproductive behaviour of plant species (**Table 1**). These results indicate that even nutrient-rich species can present masting behaviour if they grow under climates with highly fluctuating weather conditions. Therefore, we suggest that the interaction between weather conditions and the availability of nutrients, both conditioning photosynthetic rates, are the triggering factor of the common nonlinear (often exponential-like) response²² between seed production and weather variability in masting species^{8,18,21}.

As a result of the environmental and physiological constraints, species may have been selected to exhibit distinctive reproductive behaviours in order to increase their fitness. Nutrient-rich species may not have developed a resource-conservative masting-like reproduction strategy because of their capacity to produce abundant seeds with regularity, avoiding losing reproduction attempts. Instead, because the investment in reproduction in terms of C and nutrients should be proportionally more expensive for nutrient-poor or nutrient-imbalanced species, the pressure to exhibit more cost-efficient

reproduction may have selected such species to produce fewer but larger reproductive events in order to take advantage of one or more *economies of scale*^{6,7,11}. As a side effect of these massive reproductive events, negative temporal autocorrelation would also have appeared in masting species because of potential resource depletion (**Figure S1**). Hence, these particular traits would have been preserved throughout evolutionary history (**Figure 1**) because foliar functional traits and masting intensity have co-evolved (**Figure 3, Table S2**). Nonetheless, our results do not discard other potential selective pressures that may have triggered the evolution of masting behaviour. Some species may have been selected to mast to improve their pollination efficiency⁵⁵, to escape seed predation from voracious predators^{8,9} or because of interspecific competition in different ways (e.g., seedling establishment). Also, a selective pressure towards reproducing more constantly could happen in animal-pollinated species, where a more constant production of flowers would favour populations of pollinators and, hence, pollination. Further research on reproductive behaviour of early plants, such as bryophytes, and taxa from different realms using concepts from the masting literature may facilitate better understanding of the evolution of different reproductive behaviours in nature.

Methods

Datasets

Masting database

Data on interannual reproductive effort (seed or fruit production) were compiled from Web of Science searches, scanning the literature cited of published papers to look for more records of reproductive effort, contacting managers of wildlife surveys, forestry districts, and regional seed surveys, and soliciting datasets in the Ecolog listserv (<https://listserv.umd.edu/archives/ecolog-l.html>). See Pearse et al.¹⁴ for more information on data collection methods and characteristics of the dataset.

We only included records when: i) data were available for more than four consecutive years per species at a given site (with clear geographical coordinates), ii) records could be clearly assigned to plants of a particular species, iii) records were not measured in such an indirect way their accuracy could be jeopardised (e.g., anticipated correlations with gamete abundance), iv) data represented seed or fruit production, or inflorescence set only for those cases where inflorescences are strongly linked to seed or fruit production, and v) records from iteroparous perennial plants whose seed set could not be explained by changes in population size. We did not include records of pollen production nor from records from agricultural settings.

Overall, the reproductive effort dataset contained 1084 records of reproductive effort including 363 plant species (trees, shrubs, vines, grasses and herbs) from 205 studies, ranging from 1900 to 2014 and covering the six majorly vegetated continents (Africa (17), North America (466), Europe (280), Japan (68), New Zealand (67), Central America (118) and other regions (68)). On average, records were 11.9 years long, although 131 studies had more than 20 years of data¹⁴.

For each site and species, we calculated the proportional variability index in seed production (PV)⁴⁴ as a measure of temporal variability. The PV index overcomes several statistical and mathematical issues of the CV index⁴⁴. The PV index was calculated as:

$$PV = \frac{2 \sum z}{n(n-1)}$$

Where z is calculated as:

$$z = 1 - \frac{\min(z_i, z_j)}{\max(z_i, z_j)}$$

Where “ z ” represents the list of individual values (seed production per year) from which to calculate the pairwise comparisons and “ n ” indicates the number of values in a

variable. We also calculated the lag-1 temporal autocorrelation (AR1) as a measure of potential resource depletion using the *acf* function in R, and the consecutive disparity index (D)^{42,43} as a measure of masting intensity. We defined masting intensity as D because, like the PV index, this index also overcomes several statistical and mathematical limitations of the coefficient of variation (CV = standard deviation × mean⁻¹), including dependence on the mean, dependence on the length of the time series, and bias associated with non-Gaussian data commonly used to describe masting^{13,14}. More importantly, we used D because it combines two of the main features describing masting behaviour: temporal variability and lag-1 autocorrelation (AR1) in seed production⁴². D is defined as:

$$D = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1} + k}{p_i + k} \right|$$

Where p_i is the series value (seed production in our case) at time i , n is the series length and k is a constant (often one unit) to avoid numerical indetermination in time series with 0 values. D is high when temporal variability is high and lag-1 temporal autocorrelation is negative (i.e., strong masting behaviour, showing potential resource depletion after large seed crops^{20,31}). Conversely, D is low when temporal variability is low and temporal autocorrelation is close to zero or positive (i.e., describing a constant pattern of seed production and hence, no masting behaviour). Given that the CV is still the most widely used index to assess temporal variability in masting studies, we also calculated the CV of seed production per species and site to compare its results with those shown by the PV index. When multiple records from the same species were available, we calculated the average masting intensity (D), temporal variability (PV and CV) and the potential resource depletion coefficient (AR1) per species.

Climate, productivity and foliar nutrients

We extracted mean annual temperature (MAT, °C) and precipitation (MAP, mm yr⁻¹) and their seasonality (MAT_s [standard deviation of monthly values × 100] and MAP_s [CV]) for each location in our masting database from the WorldClim2 database⁵⁶. The climate database contains long-term means (1950-2000), calculated on a 30 arc-second grid. Data for variability and autocorrelation for temperature and precipitation was extracted from the CRU TS v3.25 dataset⁵⁷. To estimate site productivity we used a remotely-sensed gross primary production (GPP) database⁵⁸. For annual temperature and precipitation of the CRU TS and the GPP global databases we calculated D, PV and AR1 indices for each pixel. We then extracted climate (i.e., MAT_D, MAP_D, MAT_{PV}, MAP_{PV}, MAT_{AR1} and MAP_{AR1}) and productivity (i.e., GPP_D, GPP_{PV} and GPP_{AR1}) data for each site and species in our masting database and calculated the average per species. We used these variables in our statistical analyses to control for site-specific differences in temporal variability and autocorrelation patterns of climate and productivity.

Data for foliar concentration of N and P for the species in our database were gathered from the TRY trait database (<https://www.try-db.org/TryWeb/Home.php>)⁵⁹, the BIEN database (<http://bien.nceas.ucsb.edu/bien/>)⁶⁰, the ICP Forests database on foliar elemental concentration⁶¹ (www.icp-forests.net), and the Catalan Forest Inventory (<http://www.creaf.uab.cat/iefc/>). To estimate an average value per species, we first calculated the mean value per species and database. We then merged all databases and calculated the mean values per species. Species names in our database were checked and corrected using The Plant List database in the R package *Taxonstand*⁶². Phylogenetic analyses were performed using the plant phylogeny provided by Qian & Jin (2016). Out of the 363 species in the masting database, 219 species (~60%) names matched those in the phylogenetic tree, and therefore, only those were used for further analyses. Analyses using foliar N and P data were restricted to the 168 species (~46%) for which we could find data.

Data analyses

Evolutionary link between masting intensity, temporal variability and autocorrelation

To explore how well the phylogenetic ancestry can explain masting behaviour, we first estimated the phylogenetic signal (i.e. tendency for related species to resemble each other more than they resemble species drawn at random from the phylogenetic tree) of masting intensity (D) , PV and AR1 using the *phylosig* function in the R⁶⁴ package *phytools*⁶⁵. Phylogenetic signal was assessed by the lambda (λ) metric, which varies from 0 (where phylogenetic and trait similarity are totally independent) to 1 (where the traits are completely explained by shared ancestry). We then used continuous mapped phylogenetic trees (*contMap* function in R package *phytools*) to visualise their phylogenetic signal. Finally, we explored the evolutionary relationship between temporal variability, temporal autocorrelation and masting intensity using pairwise correlations correcting for the phylogeny. Relationships were shown using phylomorphospace plots⁶⁵, which depicts each species as a data point in a trait space, together with the phylogenetic relationship of each species-point.

Controls of masting intensity and its mode of evolution

We first tested whether masting intensity (D) was related to climate, productivity, foliar N and P concentrations and their interaction. To do so, we fitted phylogenetic linear models in which the response variable was masting intensity (D) and the predictors were foliar N and P concentrations and their interaction, MAT, MAP, MAT_s, MAP_s, MAT_D and MAP_D for climate and GPP and GPP_D for productivity. Phylogenetic models were fitted optimising lambda (i.e., the strength of phylogenetic signal) and using the *phylolm* function in the R *phylolm* package⁶⁶. The final model was achieved by removing the least significant terms from the full model, in a step-by-step process, until all variable estimates were significant. The same models were fitted for the PV and AR1, but changing the predictors from D to PV or AR1 respectively (e.g., MAT_{PV}

instead of MAT_D when predicting PV). Because the CV has been widely used to assess temporal variability, we also fitted a model using CV as the predictor variable to compare its results with those of the model using the PV index. Masting intensity and PV were transformed to natural logarithms to normalise model residuals. We used the package *visreg*⁶⁷ to visualise model results.

Evolution of masting intensity and foliar N and P and their interaction

To test the hypothesis that masting behaviour has evolved as an adaptation to nutrient imbalances and low foliar N and P concentrations, we performed three step analysis. First, we classified species as masting and non-masting. Second, we reconstructed the ancestral state between the two types of reproducing behaviour, and third, we fitted different evolutionary models to test whether foliar concentrations of N, P and N:P ratio and $N \times P$ (N times P, as a measure of the overall availability of nutrients) evolved under the reconstructed discrete selective regimes (masting or non-masting).

To define masting behaviour, and as a test for robustness of our results, we classified species as subsets that represent masting (high temporal variability and strong potential resource depletion) or non-masting (low temporal variability and no resource depletion) behaviours based on 5 different thresholds of masting intensity (D), selecting only the lower and upper bounds for the analyses and discarding the intermediate species. The selected percentile thresholds were: i) from 0% to 33% non-masting (N=38 species) and from 66% to 100% masting (N=58); ii) from 0% to 25% non-masting (N=32) and from 75% to 100% masting (N=43); iii) from 0% to 20% non-masting (N=27) and from 80% to 100% masting (N=34); iv) from 0% to 15% non-masting (N=22) and from 85% to 100% masting (N=26) and v) from 0% to 10% non-masting (N=16) and from 90% to 100% masting (N=17).

To reconstruct ancestral states of masting behaviour, for each of the five classifications we performed stochastic character mappings⁶⁸, which reconstructs the state of the

ancestors of a phylogeny based on the observed traits of the current species and the phylogenetic structure. Ancestral reconstructions were performed using the *make.simmap* function in the *phytools* R package⁶⁵, simulating 1000 stochastic ancestral reconstructions, specifying equal rates of transition amongst the character states and using the “*mcmc*” method.

Once we had the 1000 stochastic character mappings for each masting classification, we performed generalised Ornstein–Uhlenbeck Hansen models to test whether the inferred evolutionary trajectories in foliar concentrations of N, P, N:P and N×P (hereafter “continuous traits”) were associated with the two alternative masting behaviour strategies (hereafter “ancestral states”) and whether they followed an adaptive (Ornstein–Uhlenbeck: OU) or random (Brownian motion—BM) model of evolution^{69–71}. To do so, we used the OU function from *OUwie* R package⁷². We fitted five different models using the 1000 ancestral reconstructions mentioned above for each classification. The five different models represent different types of underlying evolutionary processes, being: i) single-state BM models (BM1), where evolutionary rates for the continuous traits are equal for all ancestral states, ii) BM models with different evolutionary rates for each ancestral state (BMS), iii) OU models with a single optimal value for the continuous traits for all ancestral states (OU1), iv) OU models with different optimal values but a single alpha (the strength of the pull towards the optimal values of the trait) and single theta (the rate of phenotypic variation around the optimal value) for each state (OUM), and v) OU models that assumed different optimal values with multiple rates of phenotypic evolution (theta) for each state (OUMV).

Models containing negative eigenvalues (non-sound models) were deleted when summarising our results²⁹. Different evolutionary models were compared using second-order Akaike information criterion (AICc) amongst all sound models. Those models with the lowest AICc were considered to be those that fitted the data best. For models assuming different optimal values of foliar N, P, N:P and N×P for masting and non-

421 masting species (i.e., OUM and OUMV models) we calculated the geometric mean of
422 the percentage differences of each model. Statistical differences in optimal values
423 estimated between subsets of masting and non-masting species by the OU models
424 with different state means (OUM and OUMV) were tested using paired *t*-tests. Given
425 that results pointed out to the same direction (see **Supplementary Information**) for all
426 masting intensity thresholds, we only show those from the intermediate (0% to 20% for
427 non-masting and 80% to 100% for masting). These analyses used the 168 species for
428 which we had data for masting intensity and foliar N and P concentrations. All statistical
429 analyses were performed with R statistical software version 3.5.1⁶⁴.

430 **Data availability**

431 The authors declare that the data supporting the findings of this study will be made
432 openly available upon acceptance at USGS ScienceBase. Any use of trade, firm, or
433 product names is for descriptive purposes only and does not imply endorsement by the
434 US Government.

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Author Contributions

M.F.-M., I.P., and I.A.J. conceived the paper. M.F.-M and F.S analyzed the data. M.F.-M., J.S., J.P., I.P., W.K., and J.M.L, provided data. All authors contributed substantially to the writing and discussion of the paper.

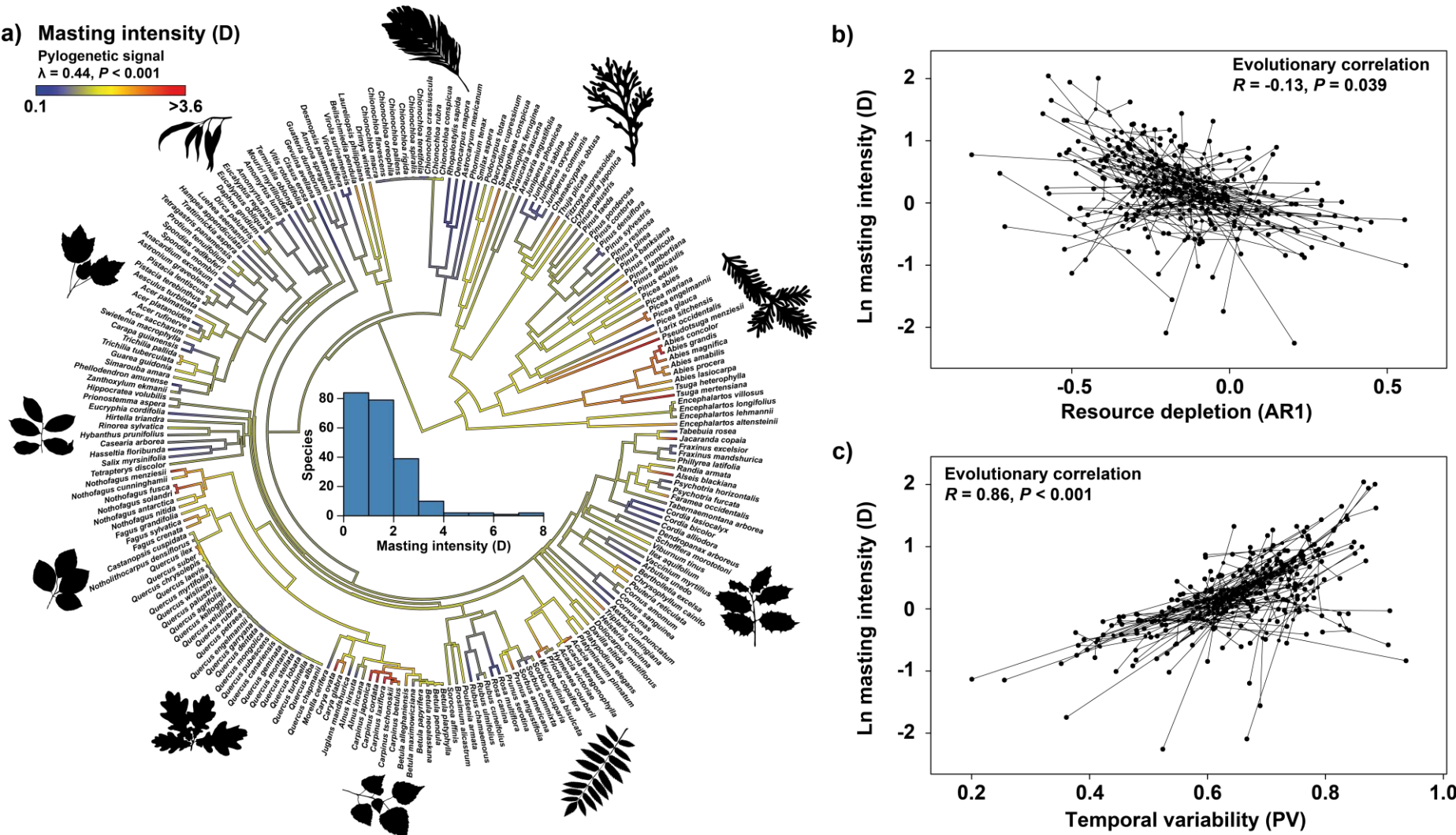
Figure captions

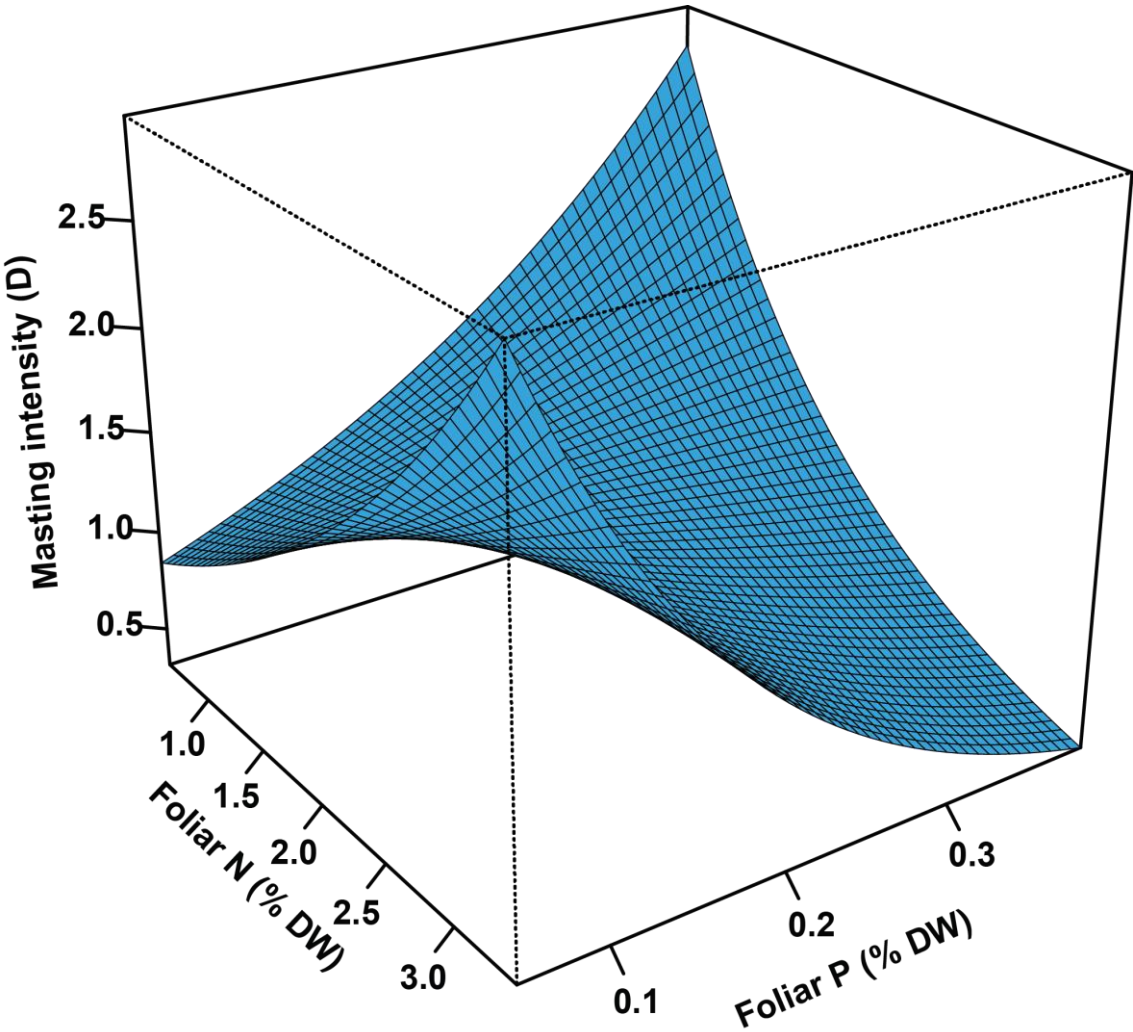
Figure 1: Masting behaviour intensity per species and its relationship with potential resource depletion (negative AR1) and temporal variability (PV) of reproductive effort. Panel (a) shows the reconstructed evolution of masting intensity based on the disparity (D) index (see **Methods**) and 219 species. The inset graph shows the distribution of values of masting intensity. Panels (b) and (c) are phylomorphospace plots showing the evolutionary correlation between masting intensity ($\ln(D)$, natural logarithm of disparity), potential resource depletion (AR1, negative values indicate potential resource depletion may happen) and temporal variability (PV). Plant silhouettes in panel (a) were drawn by FS and are available at PhyloPic (<http://phylopic.org>).

Figure 2: 3D graph showing the interaction between foliar N and P on masting intensity. Combined high foliar N and P concentrations decreased masting intensity, although the highest masting intensity was found in species with the highest N to P imbalances. Response surface of the negative interaction between N and P ($P = 0.007$) was estimated from a phylogenetic linear model (**Table 1**). See **Methods** for further information about the models.

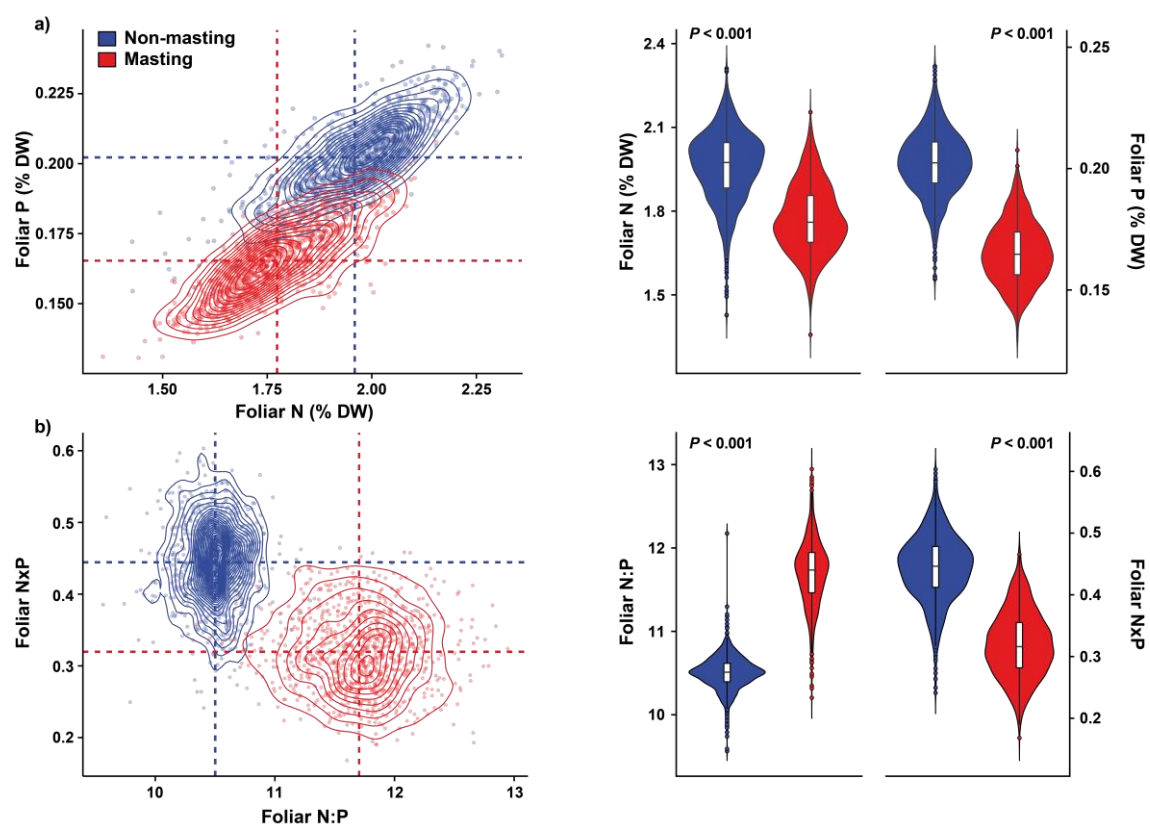
Figure 3: Different optimum values of foliar N and P for subsets of masting and non-masting species. Panel a shows model results for foliar N and P concentrations for a subset of species identified as masting (high masting intensity) and non-masting based on percentiles 20th and 80th of the D distribution (see **Methods**). Panel b shows model results for foliar N:P and N×P (overall nutrient availability) for masting and non-masting species. For panels a and b, 1000 and 927 stochastic character mapping simulations were respectively used (see **Table S2**). For foliar N:P results from OUMV models were used, while for N, P and N×P, OUM models were used (see **Table S1** and **Table S2**). See **Methods** for further information.

Table 1: Model summary of the phylogenetic linear models based on 168 species. Masting intensity was defined as the D index, PV indicates temporal variability and AR1 potential resource depletion coefficient (i.e., negative values indicate potential resource depletion). Beta (β) shows the standardised model coefficients, followed by the standard error of the mean (s.e.m), the *P*-value (*P*) and lambda (λ) indicating the phylogenetic signal in the models. See **Methods** for further information. **Acronyms:** mean annual precipitation (MAP), foliar nitrogen (N), foliar phosphorus (P), mean annual temperature (MAT), temporal autocorrelation at lag 1 (AR1).





670 **Figure 3**



671

672

	<i>β</i>	<i>s.e.m</i>	<i>P</i>	<i>λ</i>
<i>Masting intensity (D)</i>				
MAP	0.22	0.09	0.016	
N	0.04	0.10	0.708	
P	-0.04	0.10	0.674	
N×P	-0.19	0.07	0.007	0.47
<i>Temporal variability (PV)</i>				
MAP_{PV}	0.16	0.08	0.042	
MAT	-0.18	0.09	0.040	
P	-0.16	0.08	0.044	0.41
<i>Potential resource depletion (AR1)</i>				
MAP_{AR1}	0.27	0.08	0.001	
N	-0.09	0.10	0.001	
P	-0.05	0.10	0.008	
N×P	0.22	0.07	0.002	0.00

Supplementary Material

Figure S1: Evolutionary relationship between potential resource depletion coefficient (AR1) and temporal variability (PV) in seed production shown in a continuous trait phylogenetic reconstruction (a) and a phylomorphospace plot (b). Potential resource depletion and variability in seed production were not evolutionary correlated. Negative values of AR1 indicate that potential resource depletion may happen, see **Methods**. N=219 species.

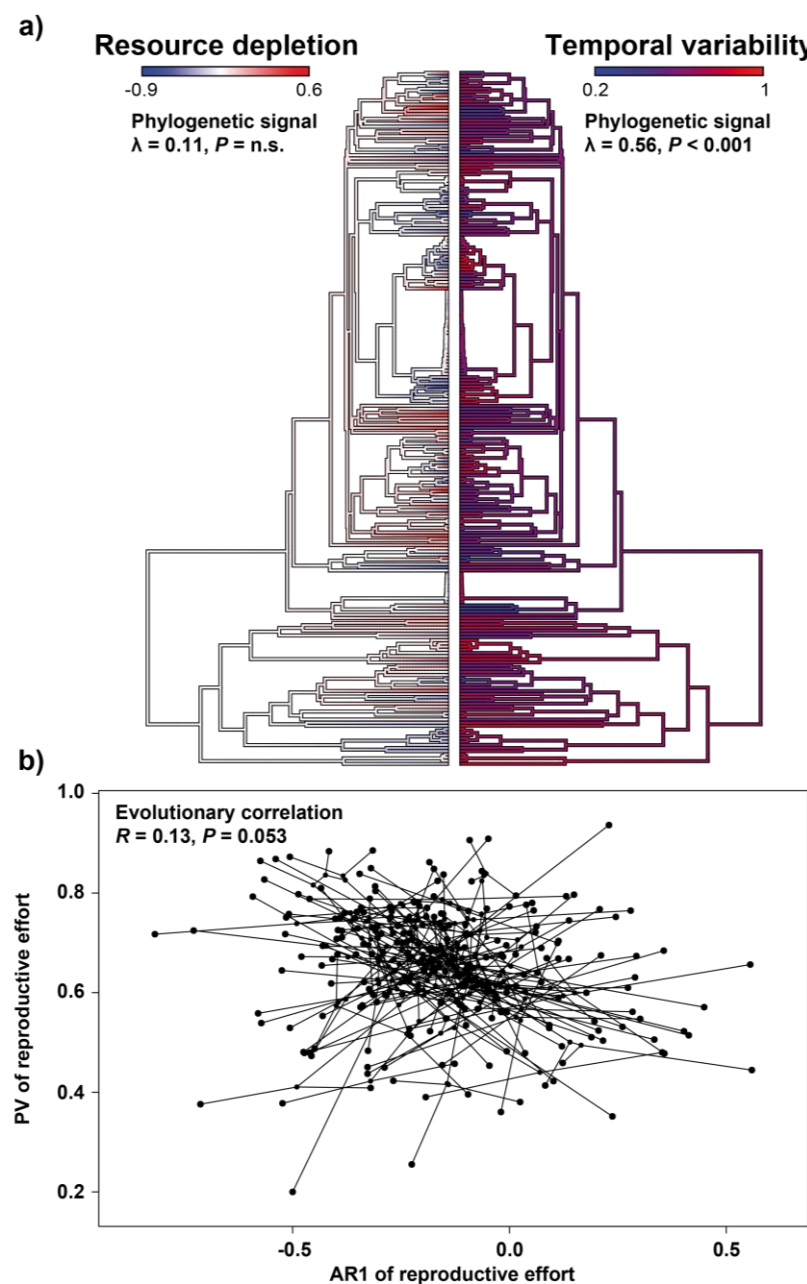


Figure S2: Phylogenetic tree including the subset of low (non-masting) and high masting intensity (masting) species used to perform the generalised Ornstein-Uhlenbeck model results presented in the main text (20th – 80th percentile thresholds for non-masting and masting species, **Figure 3**, **Table S1** and **S2**). The phylogenetic tree includes the estimated probability that ancestor nodes were masting or non-masting species (large circles) as pie charts. Small circles indicate the current category of the species. The ancestral character reconstruction was performed using 1000 stochastic character-mapped trees (see **Methods** for further information).

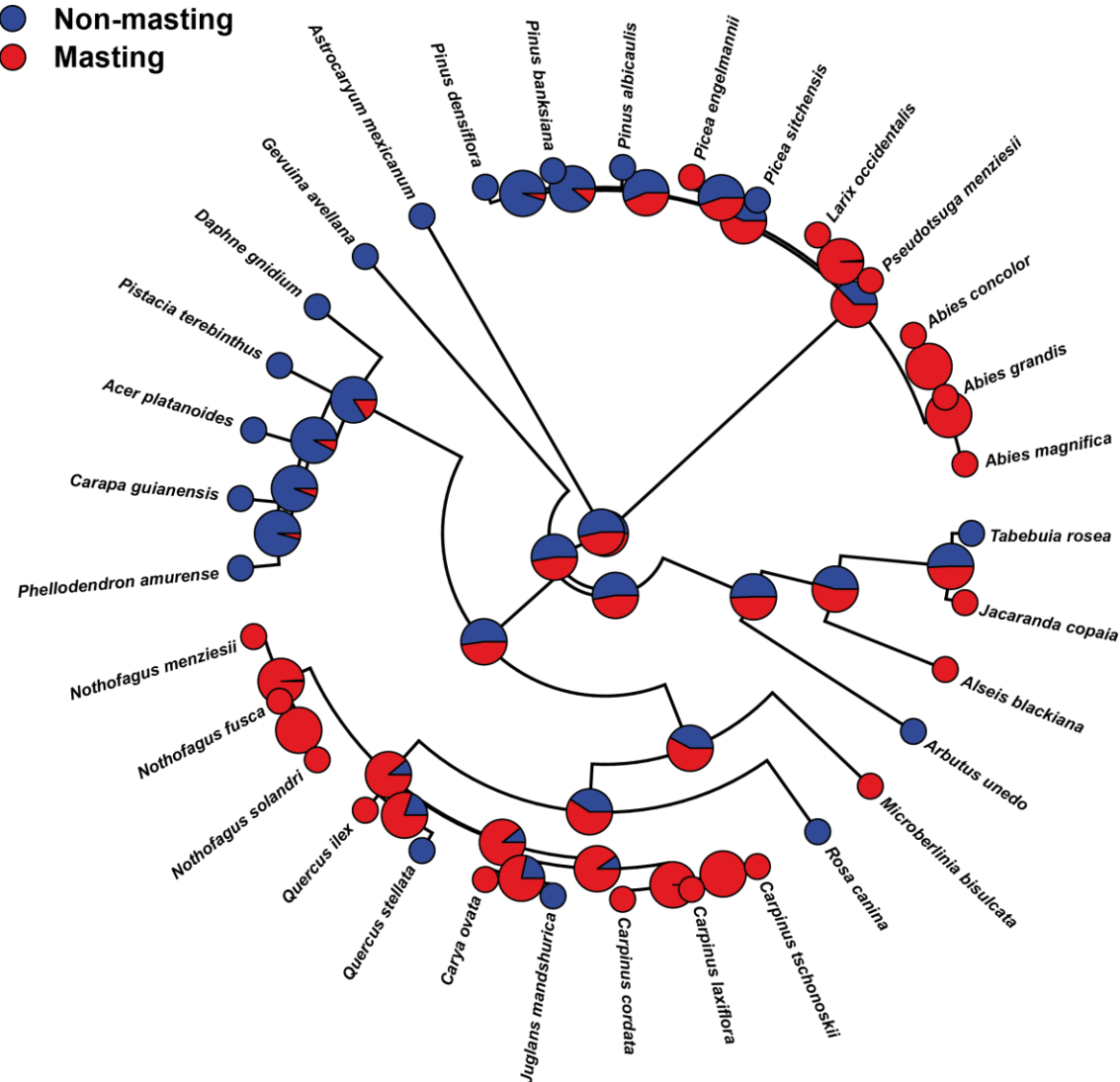


Figure S3: Evolutionary relationship between foliar N and P shown in a continuous trait phylogenetic reconstruction (a) and a phylomorphospace plot (b). Foliar N and P concentrations were evolutionary correlated. N=168 species.

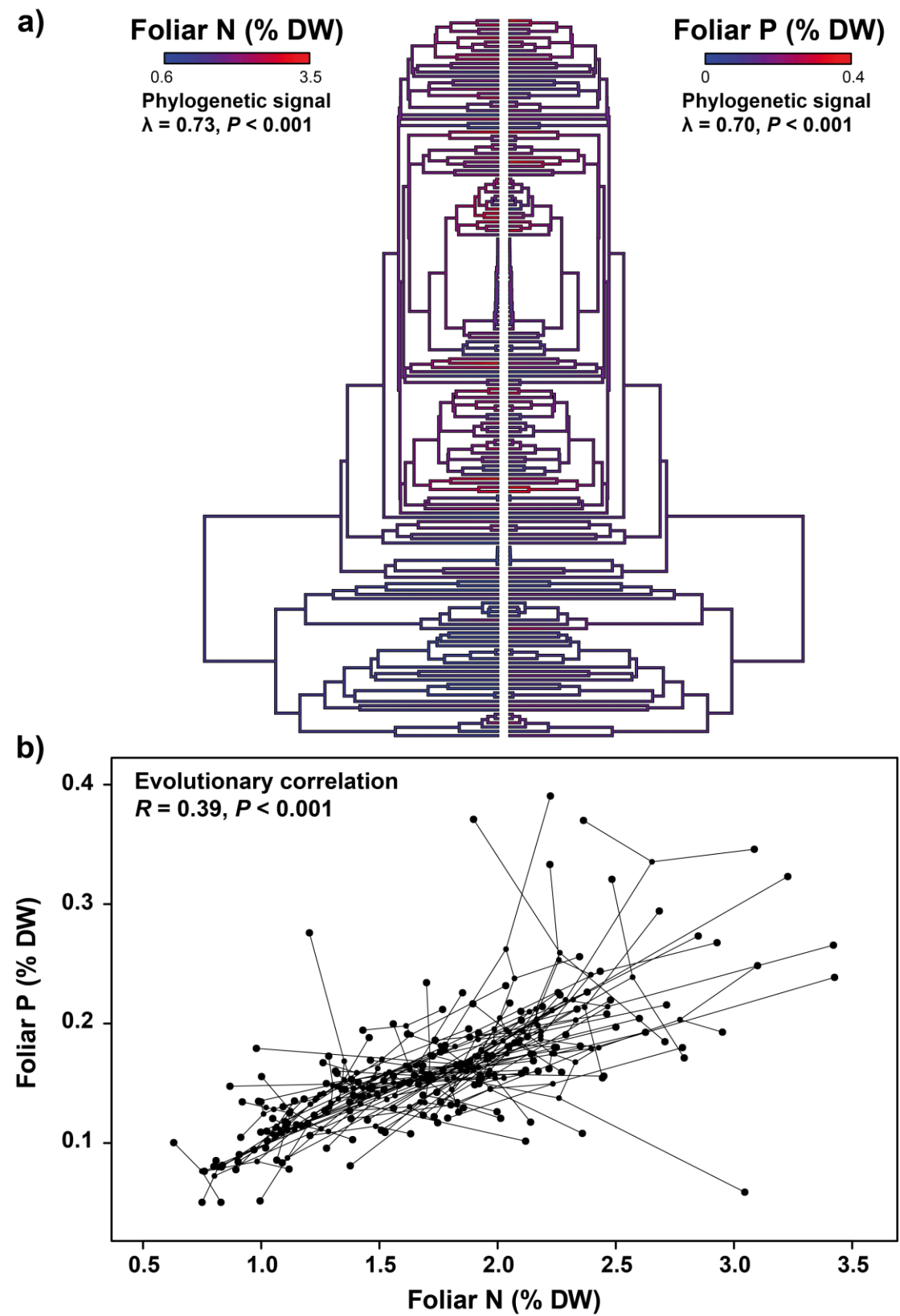


Table S1: Mean differences (ΔAICc , second-order Akaike information criterion) between each of the model's AICc and the model with the lowest AICc . Evolutionary models were Brownian motion (BM1, BMS) and generalised Ornstein-Uhlenbeck-based Hansen (OU1, OUM, OUMV), fitting "masting" and "non-masting" species-state and foliar nutrient concentrations (N: nitrogen, P: phosphorus, N:P: ratio N-to-P and, N×P: N times P (overall nutrient availability). Average AICc values were calculated using the subset of models in which none of them presented negative eigenvalues (sound models, column N). Non-masting and masting columns indicate the number of species used in each category depending on the percentile of masting intensity used to classify species as non-masting (i.e., higher than e.g., 33%) and masting (i.e., lower than e.g., 66%). Models with ΔAICc lower than 2 (indicating equal performance) were highlighted. See **Methods** for further information.

	BM1	BMS	OU1	OUM	OUMV	N	Non-masting	Masting
33 - 66%							38	58
N	36.36	30.79	0.00	1.35	3.19	1000		
P	42.52	46.34	0.51	1.39	0.00	1000		
N:P	123.81	98.59	18.25	20.23	0.00	903		
N×P	31.99	35.48	0.00	0.69	0.25	1000		
25 - 75%							32	43
N	35.51	26.82	0.00	1.11	2.43	1000		
P	33.48	36.88	0.00	0.77	1.04	1000		
N:P	112.98	85.34	21.92	23.69	0.00	906		
N×P	27.60	30.71	0.00	0.50	1.34	1000		
20 - 80%							27	34
N	29.05	17.30	0.00	1.11	1.28	1000		
P	29.46	32.96	0.00	0.54	1.35	1000		
N:P	97.95	72.61	19.86	21.29	0.00	927		
N×P	23.34	26.12	0.00	0.46	2.07	1000		
15 - 85%							22	26
N	25.21	18.42	0.00	0.68	2.34	1000		
P	23.22	27.27	1.08	0.27	0.00	998		
N:P	97.78	68.37	30.33	31.11	0.00	890		
N×P	15.37	18.94	0.25	0.00	0.96	1000		
10 - 90%							16	17
N	24.60	19.25	0.00	2.15	4.33	999		
P	14.88	17.99	0.00	1.78	3.96	999		
N:P	76.40	52.25	29.94	31.03	0.00	914		
N×P	11.35	13.51	0.00	1.89	4.31	1000		

709 **Table S2:** Estimated foliar nitrogen (N) and phosphorus (P) concentrations, N:P and N×P (overall nutrient availability) optimal values for
710 masting and non-masting species using OUMV and OUM models (see **Methods** for further information about the models), chosen based on the
711 lowest $\Delta AICc$ estimating different state means for masting and non-masting species (**Table S1**). Masting and non-masting species were
712 classified depending on the percentile of masting intensity (e.g., masting for higher than 66%, non-masting for lower than 33%, see subheaders
713 within the table). Columns 2.5%, 50 and 97.5% indicate, for masting and non-masting species, the percentiles of the optimal values based on
714 the sound models (without negative eigenvalues, N column) used. M>N% indicate the percentage of models in which masting species
715 presented average higher N, P, N:P or N×P optimal values than non-masting species. $\Delta M-N$, followed by s.e.m (standard error of the mean),
716 indicate the paired (across simulations) difference between optimal values in masting and non-masting species. P (t -test) shows the P -value of
717 the paired t -test testing for differences in the mean optimal values of masting and non-masting species. $\Delta M-N\%$, followed by s.e.m., indicates
718 the average percentual difference (geometric, paired differences) in mean optimal values between masting and non-masting species.

719

720 **Table S2:**

	Masting			Non-masting										
	2.5%	50%	97.5%	2.5%	50%	97.5%	M>N%	ΔM-N	s.e.m	P (t-test)	ΔM-N%	s.e.m	N	Model
33 - 66%														
N	1.59	1.78	1.92	1.70	1.92	2.13	20.5%	-0.15	0.01	<0.001	-7.6%	0.4%	1000	OUM
P	0.15	0.17	0.18	0.17	0.20	0.21	6.2%	-0.03	0.00	<0.001	-14.7%	0.3%	1000	OUMV
N:P	10.57	11.15	11.44	10.46	10.79	11.28	83.5%	0.31	0.01	<0.001	2.9%	0.1%	903	OUMV
N×P	0.26	0.31	0.38	0.33	0.42	0.50	9.3%	-0.10	0.00	<0.001	-24.3%	0.7%	1000	OUMV
25 - 75%														
N	1.57	1.73	1.91	1.74	1.94	2.11	11.5%	-0.20	0.01	<0.001	-10.5%	0.3%	1000	OUM
P	0.14	0.16	0.18	0.17	0.19	0.22	10.1%	-0.03	0.00	<0.001	-15.4%	0.4%	1000	OUM
N:P	10.77	11.38	11.93	10.43	10.79	11.17	92.4%	0.58	0.01	<0.001	5.3%	0.1%	906	OUMV
N×P	0.23	0.31	0.39	0.33	0.42	0.51	9.9%	-0.11	0.00	<0.001	-27.2%	0.8%	1000	OUM
20 - 80%														
N	1.55	1.76	2.02	1.68	1.97	2.18	23.3%	-0.19	0.01	<0.001	-9.5%	0.4%	1000	OUM
P	0.14	0.16	0.19	0.18	0.20	0.23	9.0%	-0.04	0.00	<0.001	-18.3%	0.5%	1000	OUM
N:P	10.85	11.74	12.53	10.06	10.51	10.88	97.7%	1.20	0.02	<0.001	11.4%	0.2%	927	OUMV
N×P	0.22	0.32	0.42	0.33	0.45	0.54	11.9%	-0.13	0.00	<0.001	-28.7%	1.0%	1000	OUM
15 - 85%														
N	1.54	1.71	1.95	1.77	2.03	2.22	10.00%	-0.29	0.01	<0.001	-14.3%	0.4%	1000	OUM
P	0.14	0.16	0.18	0.20	0.22	0.24	0.9%	-0.06	0.00	<0.001	-26.1%	0.3%	998	OUMV
N:P	10.44	11.88	12.80	9.28	9.71	9.99	99.7%	2.12	0.02	<0.001	21.7%	0.2%	890	OUMV
N×P	0.21	0.30	0.41	0.38	0.49	0.59	3.80%	-0.19	0.00	<0.001	-38.7%	1.0%	1000	OUM
10 - 80%														
N	1.67	1.87	2.05	1.64	1.85	2.05	54.2%	0.02	0.01	<0.001	1.3%	0.4%	999	OUM
P	0.14	0.18	0.21	0.18	0.20	0.24	12.0%	-0.03	0.00	<0.001	-14.8%	0.5%	999	OUM
N:P	9.90	12.52	13.96	9.49	9.85	10.22	96.6%	2.46	0.04	<0.001	24.5%	0.3%	914	OUMV
N×P	0.23	0.36	0.48	0.33	0.45	0.56	20.6%	-0.09	0.00	<0.001	-22.2%	2.0%	1000	OUM