

Nutrient scarcity as a selective pressure for mast seeding

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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 of the continents, we tested whether masting behaviour appears predominantly in species with low foliar nitrogen and phosphorus 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 in those with 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.

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 scenarios.

The most widely accepted hypotheses explaining the selective advantages of masting are all related to economies of scale^{5,6}. Briefly, these hypotheses state that, in terms of fitness, it is more efficient for plants to produce a large number of seeds every few to several years than to produce a constant number every year. This general mechanism includes the predator satiation hypothesis^{7,8–9}, 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^{5,10,11}, which states 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 to ensure pollination. Given that masting is present in only a modest percentage of plant species¹², such economies of scale are apparently advantageous only under certain circumstances. What those circumstances are remains, so far, under debate.

The environmental stress hypothesis¹³ 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^{3,11,14}. 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^{15,16}. 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 reproduction¹⁵. 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 regularly. In contrast, weather variability has been found to be a key factor driving interannual variability in fruit production in many plant species^{11,17–20}. Therefore, temporal patterns in weather events (that is, temporal variability and autocorrelation) could potentially shape the temporal patterns of fruit production²¹.

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^{22–24}. Together with carbon, they are the basis of ecological stoichiometry^{25,26} and are fundamental parts of the elementome or the biogeochemical niche²⁷, useful for inferring ecological traits from the elemental composition of organisms²⁸. N and P, as well as carbon (C), have been suggested to be potential resources determining seed production and masting behaviour^{14,29–31}, because seeds and fruits are enriched with N and P compared with vegetative tissues³².

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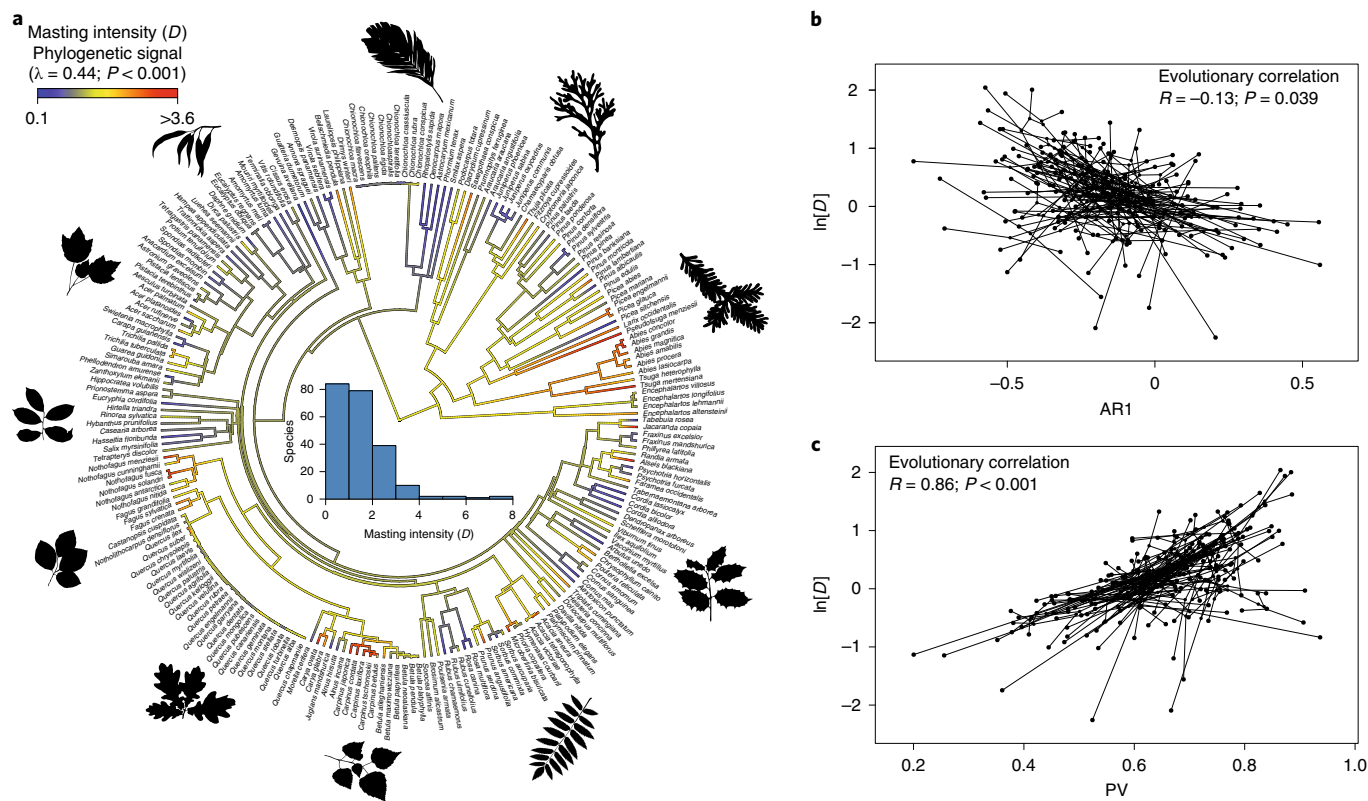


Fig. 1 | Masting behaviour intensity per species and its relationship with potential resource depletion (negative AR1) and temporal variability (PV) of reproductive effort. **a**, Reconstructed evolution of masting intensity based on the disparity (D) index (using continuous character mapping; see Methods) and 219 species ($n = 219$ biologically independent samples). Inset: distribution of values of masting intensity. Phylogenetic signal was estimated using Pagel's lambda (λ). **b, c**, Phylomorphospace plots showing the evolutionary Pearson's correlation for masting intensity (natural logarithm of disparity ($\ln[D]$)) versus potential resource depletion (AR1; negative values indicate that resource depletion may happen) (**b**) and temporal variability (PV) (**c**). In **b** and **c**, t -values of the correlations were -2.08 and 25.19 (217 degrees of freedom (DF)), respectively. The plant silhouettes in **a** were drawn by F.S. and are available at PhyloPic (<http://phylopic.org>).

Low foliar concentrations of N and P would imply lower photosynthetic rates²² 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.

Foliar N and P have both been reported to be positively correlated with investment in plant reproduction^{33–35}. Additionally, the interaction between foliar N and P (that is, the N/P ratio) has been suggested to be an important indicator of plant nutritional status, to promote vegetative productivity^{36–39} and to relate to reproductive effort³⁵ and ecological strategies²⁷. The lower N/P ratio of seeds compared with vegetative tissues suggests that nutrient imbalances may constrain reproduction more than growth³⁷. Previous studies have reported that plants and shoots producing flowers often exhibit lower N/P ratios than those that do not^{37,40}, 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 of the continents, to investigate whether higher variability in seed production is related to higher potential resource depletion (negative temporal autocorrelation). 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^{41,42}—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 the 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

Temporal variability, potential resource depletion and their evolutionary relationships. Our results indicated that temporal variability (here, calculated as the proportional variability index⁴³ (PV); see Methods) in seed production is evolutionarily conserved (Extended Data Fig. 1a), showing a strong phylogenetic signal⁴⁴. 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 evolutionarily correlated. Hence, species exhibiting higher temporal variability do not necessarily exhibit any particular pattern of temporal autocorrelation (Extended Data Fig. 1b). Masting intensity, defined as D in this study (see Methods), accounted for both features of masting behaviour (Fig. 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 assessed⁴¹.

Table 1 | Model summary of the phylogenetic linear models based on 168 species

| | β | s.e.m. | t | P | λ |
|---|---------|--------|-------|-------|-----------|
| Masting intensity (D) | | | | | |
| MAP | 0.22 | 0.09 | 2.44 | 0.016 | |
| N | 0.04 | 0.10 | 0.38 | 0.708 | |
| P | −0.04 | 0.10 | −0.42 | 0.674 | |
| N × P | −0.19 | 0.07 | −2.76 | 0.007 | 0.47 |
| Temporal variability (PV) | | | | | |
| MAP _{PV} | 0.16 | 0.08 | 2.05 | 0.042 | |
| MAT | −0.18 | 0.09 | −2.07 | 0.040 | |
| P | −0.16 | 0.08 | −2.03 | 0.044 | 0.41 |
| Potential resource depletion (AR1) | | | | | |
| MAP _{AR1} | 0.27 | 0.08 | 3.42 | 0.001 | |
| N | −0.09 | 0.10 | −0.85 | 0.001 | |
| P | −0.05 | 0.10 | −0.45 | 0.008 | |
| N × P | 0.22 | 0.07 | 3.19 | 0.002 | 0 |

Masting intensity was also preserved phylogenetically (Fig. 1). Our results suggest that most species exhibit low or intermediate masting intensity, while only a few exhibit strong masting behaviour (see histogram in Fig. 1a).

Estimating controls and the mode of evolution of masting behaviour. Phylogenetic models indicated a statistically significant negative interaction between foliar N and P, explaining variability in masting intensity across species (Table 1 and Fig. 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 which species were sampled did not explain variation in masting intensity. However, mean annual precipitation (MAP) was positively related to masting intensity (Table 1). Temporal variability in seed production was negatively related to mean annual temperature (MAT) 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 a higher CV of seed production (standardized model coefficient, $\beta = 0.22 \pm 0.08$; $t = 2.96$; $P = 0.004$; phylogenetic signal, $\lambda = 0.58$; $n = 168$ species). 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 (Extended Data Fig. 2). We found that adaptive processes—Ornstein–Uhlenbeck models based on ancestral character reconstructions (Extended Data Fig. 3)—are the models that better explain current patterns in masting intensity linked to foliar nutrient concentrations. Adaptive Ornstein–Uhlenbeck models explaining

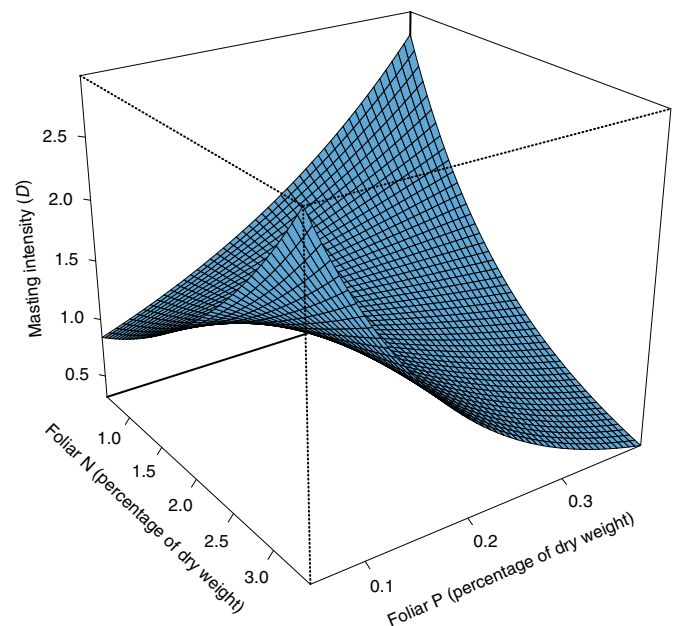


Fig. 2 | 3D graph showing the interaction between foliar N and P and masting intensity. Combined high foliar N and P concentrations decreased the masting intensity, although the highest masting intensity was found in species with the highest N/P imbalances. The response surface of the negative interaction between N and P (see Table 1 for statistics) was estimated from a phylogenetic linear model based on 168 species ($n = 168$ biologically independent samples). See Methods for further information on the models.

the evolutionary history of masting intensity with N, P and $N \times P$ (a measure of the total N and P foliar concentration) assume that species evolved towards 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 $N \times P$ (< 2 units of second-order Akaike information criterion (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 $N \times P$ (Extended Data Fig. 2), OUM models are used to illustrate our results. The model that best fitted the data for foliar N/P was an adaptive Ornstein–Uhlenbeck model with different optimum and phenotypic variation for high and low masting intensity species (the OUMV model).

Results from Ornstein–Uhlenbeck models indicated that masting species had, on average, 9.5 ± 0.4 and $18.3 \pm 0.5\%$ lower foliar N and P concentrations, respectively, than non-masting species (Fig. 3 and Extended Data Fig. 4). The foliar N/P ratio was $11.4 \pm 0.2\%$ (mean \pm s.e.m.) higher in masting species, while $N \times P$ (the 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 (Extended Data Fig. 4). Like masting intensity, foliar N and P concentrations were both preserved throughout the phylogeny (Extended Data Fig. 5).

Discussion

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 (Fig. 3). Hence, our analyses supported our initial hypothesis stating that masting behaviour evolved predominantly

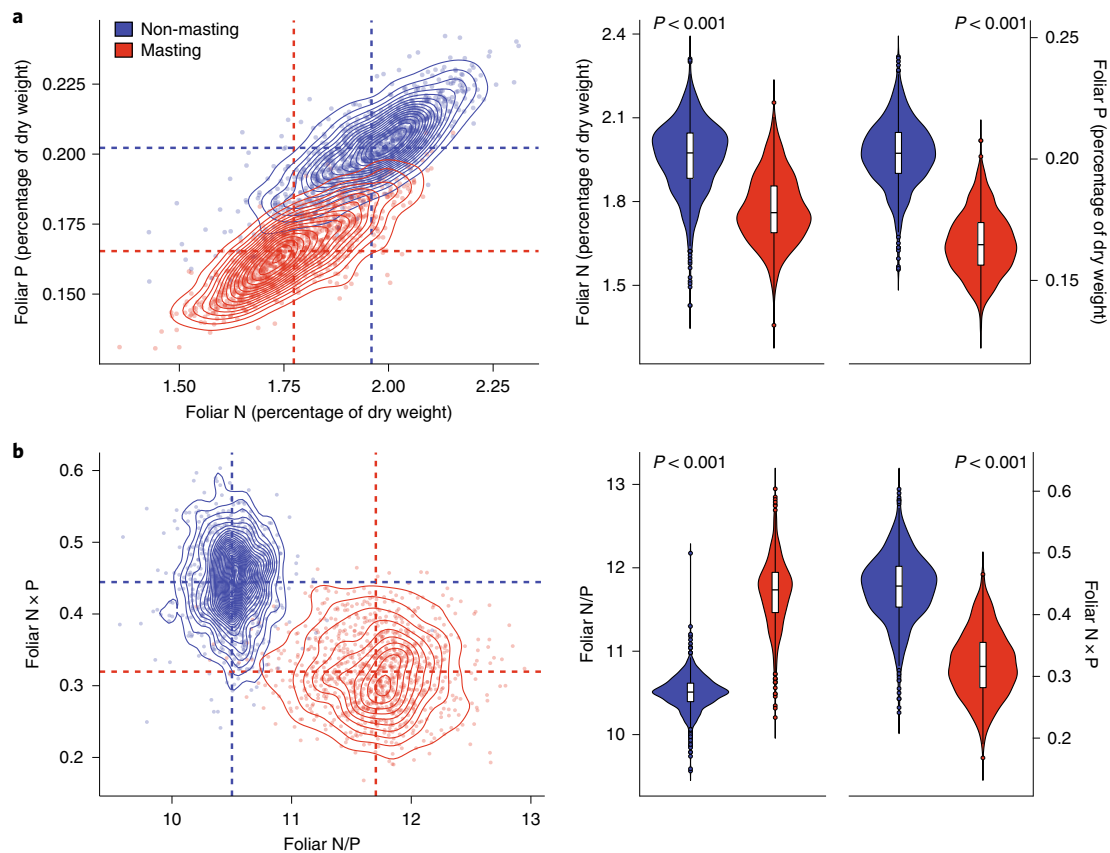


Fig. 3 | Different optimum values of foliar N and P for subsets of masting and non-masting species. a, Model results for foliar N and P concentrations for a subset of species identified as masting (high masting intensity) and non-masting based on the 20th and 80th percentiles of the *D* distribution (see Methods). **b,** Model results for foliar N/P and N x P (overall nutrient availability) for masting and non-masting species. In **a** and **b**, $n=1,000$ and 927 independent stochastic character mapping simulations were used, respectively (see Extended Data Fig. 4). For foliar N/P, the results from OUMV models were used, while for N, P and N x P, OUM models were used (see Extended Data Figs. 2 and 4). Differences between groups were calculated based on two-sided paired *t*-tests (*t*-values were -24.34 , -47.44 (both on 999 DF), 66.05 and -39.24 (both for 926 DF) for N, P, N/P and N x P, respectively). Dashed lines indicate the mean *x* and *y* values for the different groups. Violin plots represent density distributions of the data. Boxplots show the median (centre line), 25th and 75th quartiles (hinges), 1.5 times the interquartile range from the hinges (whiskers) and values outside 1.5 times the interquartile range (points). See Methods for further information.

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^{33,34} and vegetative growth^{45,46}. Elevated foliar P concentrations and low N/P ratios have been shown to allow larger seed crops in multiple species^{14,35,40,47}, coinciding with fast-growing species according to the growth rate hypothesis²⁵. P is also essential to maintain water-use efficiency and growth, particularly during drought conditions⁴⁸. Both nutrients are essential elements of ribosomes and therefore play a major role in organismal metabolism⁴⁹. The production of seeds, which are structures enriched with N and P³², 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^{14,50,51}, 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 mineralization and weathering are low^{48,52}, or disturbances (for example, wildfires) are frequent⁵³. 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 hypothesis²⁷). 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 rates²².

Evolutionary history of masting intensity and foliar nutrients. Being capable of investing more in reproduction does not explain masting behaviour by itself, because equal average seed crops over time could lead to different reproductive behaviours¹⁴. The necessary link between the ecological stoichiometry and masting theoretical backgrounds lies in the resource accumulation hypothesis^{15,16}. Plant species with lower or imbalanced availability of N and P may present more difficulties in acquiring the necessary amounts 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 (that is, 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 (which synchronizes the reproduction of individuals through weather cues^{6,18}) would finally shape the reproductive behaviour of masting species. In fact, our results also revealed that MAP, its temporal variability and its 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 of which condition photosynthetic rates) is the triggering factor of the common nonlinear (often exponential-like) response²¹ between seed production and weather variability in masting species^{7,17,20}.

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, to take advantage of one or more economies of scale^{5,6,10}. As a side effect of these massive reproductive events, negative temporal autocorrelation would also have appeared in masting species because of potential resource depletion (Extended Data Fig. 1). Hence, these particular traits would have been preserved throughout evolutionary history (Fig. 1) because foliar functional traits and masting intensity have co-evolved (Fig. 3 and Extended Data Fig. 4). 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 efficiency^{5,4}, to escape seed predation from voracious predators^{7,8} or because of interspecific competition in different ways (for example, seedling establishment). Also, a selective pressure towards reproducing more constantly could occur in animal-pollinated species, where a more constant production of flowers would favour populations of pollinators and, hence, pollination. Further research on the reproductive behaviours of early plants such as bryophytes⁵⁵ and taxa from different realms, using concepts from the masting literature, may facilitate a 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 by searching the Web of Science, scanning literature citations in 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. See Pearse et al.¹³ for more information on the data collection methods and characteristics of the dataset.

We only included records when: (1) data were available for more than four consecutive years per species at a given site (with clear geographical coordinates); (2) records could be assigned clearly to plants of a particular species; (3) records were not measured in such an indirect way that their accuracy could be jeopardized (for example, anticipated correlations with gamete abundance); (4) data represented seed or fruit production, or inflorescence set only for those cases where inflorescences were strongly linked to seed or fruit production; and (5) records were 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 records from agricultural settings.

Overall, the reproductive effort dataset contained 1,084 records of reproductive effort, including 363 plant species (trees, shrubs, vines, grasses and herbs) from 205 studies, ranging from 1900–2014 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 data¹³.

For each site and species, we calculated the proportional variability index in seed production (PV)⁴³ as a measure of temporal variability. The PV index

overcomes several statistical and mathematical issues of the CV index⁴³.

The PV index was calculated, for each time series, as:

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

where z was 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 each time series, from which to calculate the pairwise comparisons, and n indicates the number of values in a time series. 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)^{41,42} 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 ($CV = \text{standard deviation} \times \text{mean}^{-1}$, commonly used to describe masting^{12,13}), including dependence on the mean, dependence on the length of the time series and bias associated with non-Gaussian data. 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 production⁴¹. D was 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 (that is, strong masting behaviour, showing potential resource depletion after large seed crops^{19,20}). Conversely, D is low when temporal variability is low and temporal autocorrelation is close to zero or positive (that is, describing a constant pattern of seed production and, hence, no masting behaviour). Given that the CV is still the most widely used index for assessing 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 potential resource depletion coefficient (AR1) per species.

Climate, productivity and foliar nutrients. We extracted MAT (°C) and MAP (mm yr⁻¹) and their seasonality (MAT, (standard deviation of monthly values $\times 100$) and MAP_s (CV)) for each location in our masting database from the WorldClim 2 database⁵⁶. The climate database contains long-term means (1950–2000), calculated on a 30 arcsec grid. Data (for variability) and autocorrelation (for temperature and precipitation) were extracted from the CRU TS version 3.25 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 GPP global databases, we calculated D , PV and AR1 indices for each pixel. We then extracted climate (that is, MAT_D, MAP_D, MAT_{PV}, MAP_{PV}, MAT_{AR1} and MAP_{AR1}) and productivity (that is, GPP_D, GPP_{PV} and GPP_{AR1}) data for each site and species in our masting database and calculated the average per species (Extended Data Fig. 6). We used these variables in our statistical analyses to control for site-specific differences in temporal variability, as well as autocorrelation patterns of climate and productivity.

Data on the foliar concentration of N and P for the species in our database were gathered from the TRY Plant Trait Database (<https://www.try-db.org/TryWeb/Home.php>)⁵⁹, BIEN database (<http://bien.nceas.ucsb.edu/bien/>)⁶⁰, ICP Forests database on foliar elemental concentration⁶¹ (www.icp-forests.net) and Catalan Forest Inventory (<http://www.creaf.uab.cat/iecf/>). 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 Taxonstand⁶². Phylogenetic analyses were performed using the plant phylogeny provided by Qian and Jin⁶³. Of the 363 species in the masting database, 219 species names (~60%) matched those in the phylogenetic tree; therefore, only these were used for further analyses. Analyses using foliar N and P data were restricted to the 168 species (~46%) for which we could find data⁶³.

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 (that is, the 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 phyttools⁶⁵. The phylogenetic signal was assessed by the 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 the R package phytools) to visualize 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 depict 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_p, MAP_p, MAT_p and MAP_p for climate; and GPP and GPP_p for productivity. Phylogenetic models were fitted optimizing λ (that is, 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 ARI, but changing the predictors from D to PV or ARI, respectively (for example, MAT_{PV} instead of MAT_D when predicting PV). Because 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 normalize model residuals. We used the package visreg⁶⁷ to visualize the 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 a three-step analysis: (1) we classified species as masting and non-masting; (2) we reconstructed the ancestral state between the two types of reproducing behaviour; and (3) we fitted different evolutionary models to test whether foliar concentrations of N, P and N/P ratio and N × 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 the 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 five 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: (1) from 0–33% non-masting ($n = 38$ species) and from 66–100% masting ($n = 58$); (2) from 0–25% non-masting ($n = 32$) and from 75–100% masting ($n = 43$); (3) from 0–20% non-masting ($n = 27$) and from 80–100% masting ($n = 34$); (4) from 0–15% non-masting ($n = 22$) and from 85–100% masting ($n = 26$); and (5) from 0–10% non-masting ($n = 16$) and from 90–100% masting ($n = 17$).

To reconstruct ancestral states of masting behaviour, for each of the five classifications, we performed stochastic character mappings⁶⁸, which reconstruct 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 1,000 stochastic ancestral reconstructions, specifying equal rates of transition among the character states and using the Markov chain Monte Carlo method.

Once we had the 1,000 stochastic character mappings for each masting classification, we performed generalized 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) or random (Brownian motion) model of evolution^{69–71}. To do so, we used the Ornstein–Uhlenbeck function from the OUwie R package⁷². We fitted five different models using the 1,000 ancestral reconstructions mentioned above for each classification. The five different models represent different types of underlying evolutionary processes, being: (1) single-state Brownian motion models (BM1), where evolutionary rates for the continuous traits are equal for all ancestral states; (2) Brownian motion models with different evolutionary rates for each ancestral state (BMS); (3) Ornstein–Uhlenbeck models with a single optimal value for the continuous traits for all ancestral states (OU1); (4) Ornstein–Uhlenbeck models with different optimal values but a single α (the strength of the pull towards the optimal values of the trait) and single θ (the rate of phenotypic variation around the optimal value) for each state (OUM); and (5) Ornstein–Uhlenbeck models that assumed different optimal values with multiple rates of phenotypic evolution (θ) for each state (OUMV).

Models containing negative eigenvalues (non-sound models) were deleted when summarizing our results³⁸. Different evolutionary models were compared using AICc among all sound models. Those models with the lowest AICc were considered to fit the data best. For models assuming different optimal values of foliar N, P, N/P and N × P for masting and non-masting species (that is, the OUM and OUMV models), we calculated the geometric mean of the percentage differences of each model. Statistical differences in optimal values estimated between subsets of masting and non-masting species by the Ornstein–Uhlenbeck models with different state means (OUM and OUMV) were tested using paired t -tests. Given that the results pointed out in the same direction (see Extended

Data Fig. 4) for all masting intensity thresholds, we only show those from the intermediate threshold (0–20% for non-masting and 80–100% for masting). These analyses used the 168 species for which we had data for masting intensity and foliar N and P concentrations. All statistical analyses were performed with R statistical software version 3.5.1 (ref. ⁶⁹).

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

Data availability

Data supporting the findings of this study can be found at <https://doi.org/10.6084/m9.figshare.9863006.v1> and <https://www.sciencebase.gov/catalog/item/5d9f7f49e4b036616294495d>. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Received: 8 April 2019; Accepted: 8 October 2019;

Published online: 02 December 2019

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Acknowledgements

This research was supported by the Spanish Government project CGL2016-79835-P (FERTWARM), European Research Council Synergy Grant ERC-2013-726 SyG-610028 IMBALANCE-P and Catalan Government project SGR 2017-1005. M.F.-M. is a postdoctoral fellow of the Research Foundation – Flanders (FWO). M.B. was supported by (Polish) NSF grants Sonata 2017/24/C/NZ8/00151 and Uwertura 2018/28/U/NZ8/00003. This research was also supported by NSF grants DEB-1745496 630 to J.M.L. and DEB-1256394 to W.D.K.

Author contributions

M.F.-M., I.P. and I.A.J. conceived the paper. M.F.-M. and F.S. analysed the data. M.F.-M., J.S., J.P., I.P., W.D.K. and J.M.L. provided the data. All authors, including M.B., A.C., A.H.-P., G.V. and J.M.E. contributed substantially to the writing and discussion of the paper.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41477-019-0549-y>.

Supplementary information is available for this paper at <https://doi.org/10.1038/s41477-019-0549-y>.

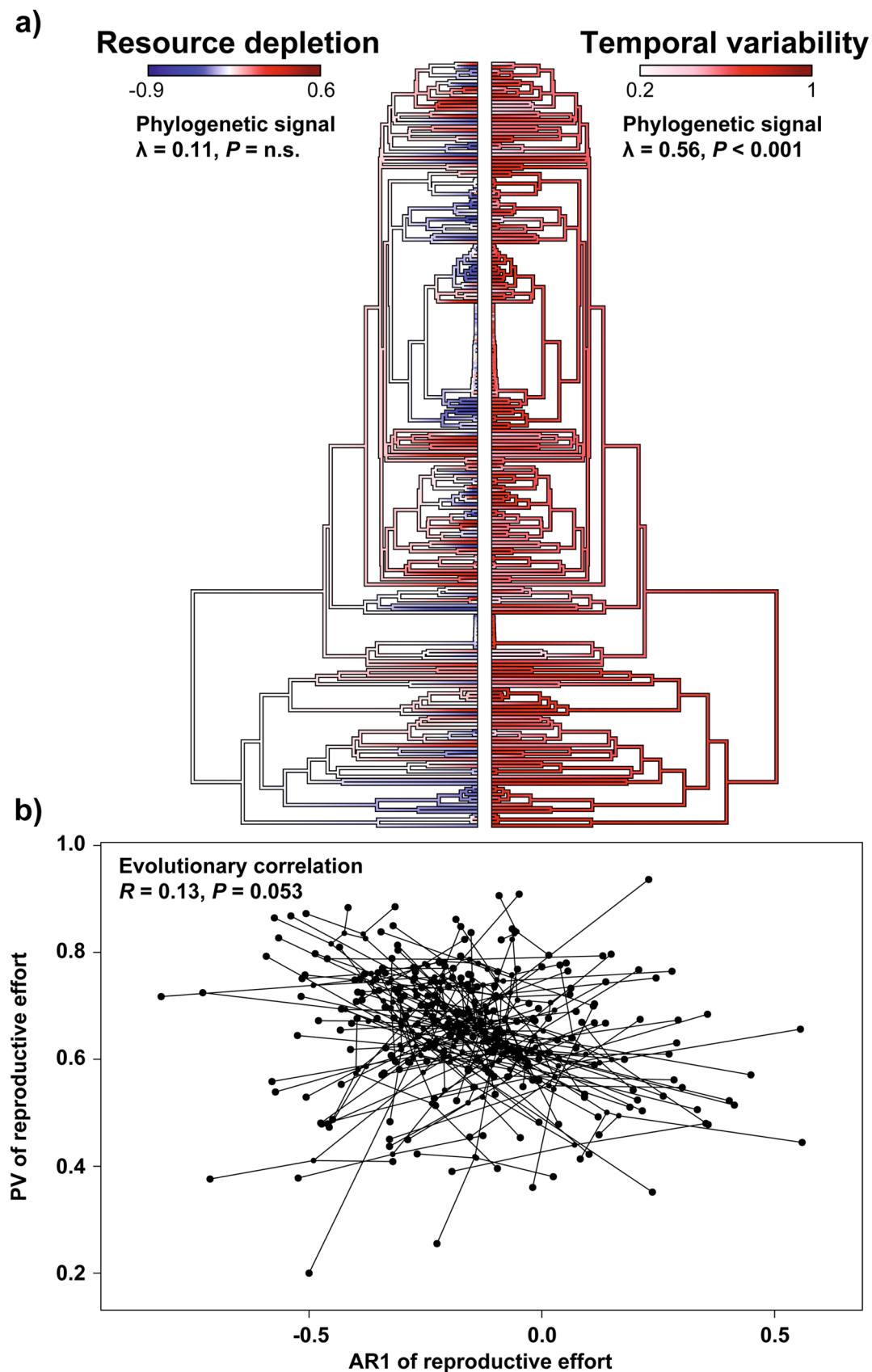
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Peer review information *Nature Plants* thanks Shuli Niu, Ignacio Perez Ramos and the other, anonymous, reviewer for their contribution to the peer review of this work.

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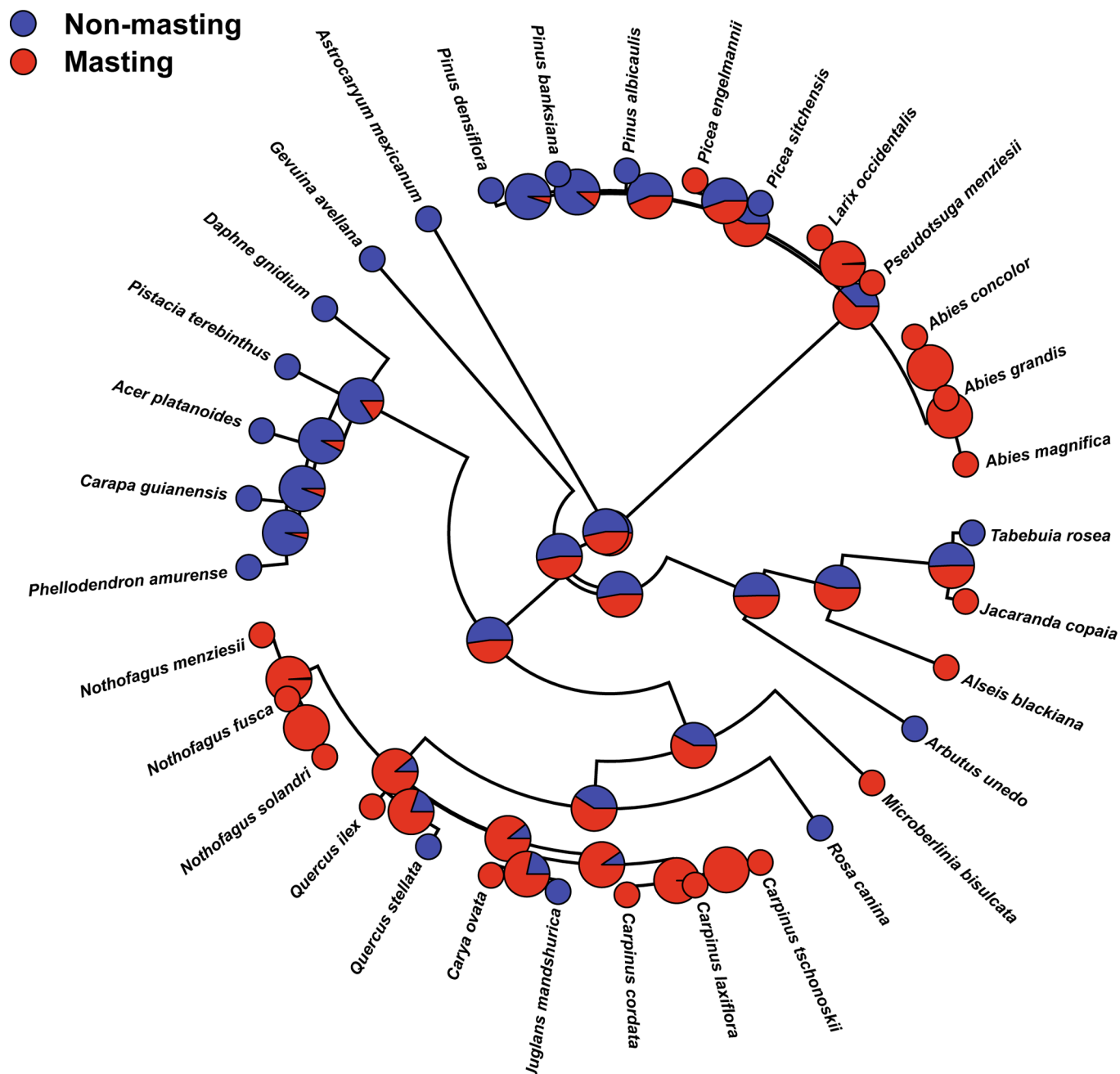
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Extended Data Fig. 1 | Evolutionary relationship between potential resource depletion coefficient (AR1) and temporal variability (PV) in seed production. Evolutionary relationship between potential resource depletion coefficient (AR1) and temporal variability (PV) in seed production shown in a continuous trait phylogenetic reconstruction (**a**) and a phylomorphospace plot (**b**). Phylogenetic signal was estimated using *Pagel's lambda* (λ). 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. *t*-value of the Pearson's correlation was 1.95 (218 DF).

| | 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 | | |

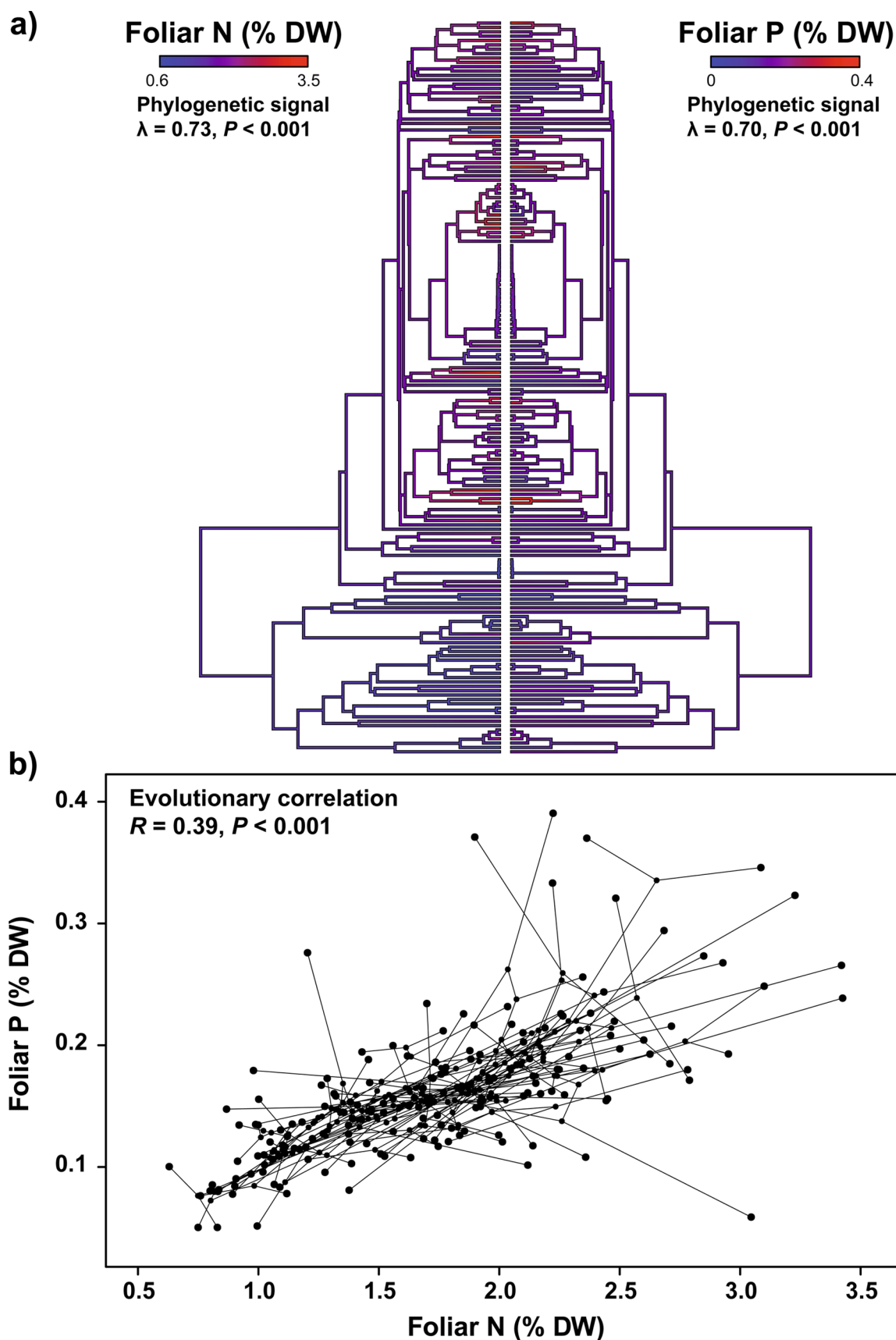
Extended Data Fig. 2 | Mean differences (ΔAICc , second-order Akaike information criterion) between each of the model's AICc and the model with the lowest AICc . Mean differences (ΔAICc , second-order Akaike information criterion) between each of the model's AICc and the model with the lowest AICc . 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, n column: samples, independent simulations). 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 (that is, higher than for example, 33%) and masting (that is, lower than for example, 66%). Models with ΔAICc lower than 2 (indicating equal performance) were highlighted. See Methods for further information.



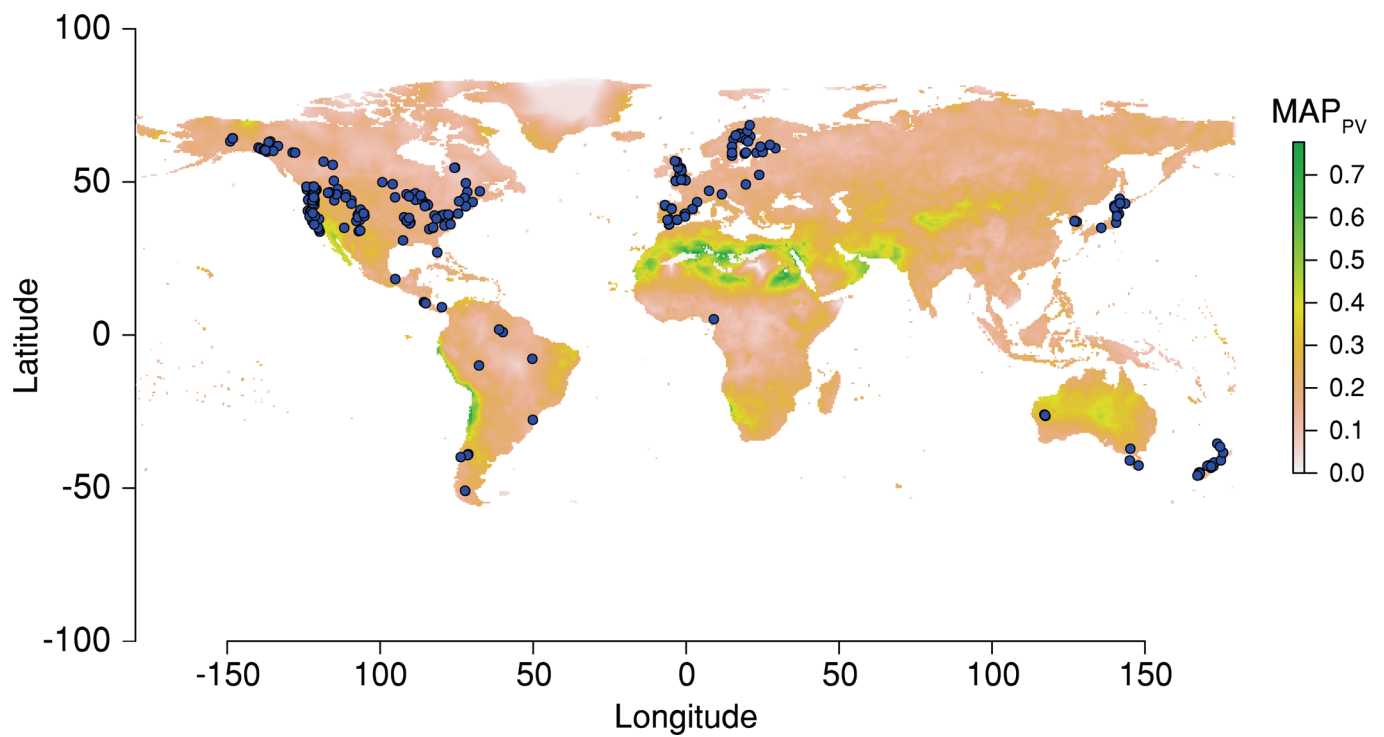
Extended Data Fig. 3 | Phylogenetic tree including the subset of low (non-masting) and high masting intensity (masting) species used to perform the generalised Ornstein-Uhlenbeck model results. Phylogenetic tree including the subset of low (non-masting) and high masting intensity (masting) species used to perform the generalised Ornstein-Uhlenbeck model results presented in the main text (20th – 80th percentile thresholds for non-masting and masting species, Fig. 3, Extended Data Fig. 2 and Extended Data Fig. 4). 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).

| | 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 |

Extended Data Fig. 4 | Estimated foliar nitrogen (N) and phosphorus (P) concentrations, N:P and N×P (overall nutrient availability) optimal values for masting and non-masting species. Estimated foliar nitrogen (N) and phosphorus (P) concentrations, N:P and N×P (overall nutrient availability) optimal values for masting and non-masting species using OUMV and OUM models (see **Methods** for further information about the models), chosen based on the lowest ΔAICc estimating different state means for masting and non-masting species (Extended Data Fig. 2). Masting and non-masting species were classified depending on the percentile of masting intensity (for example, masting for higher than 66%, non-masting for lower than 33%, see subheaders 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 the sound models (without negative eigenvalues, n column: samples, independent simulations) used. M>N% indicate the percentage of models in which masting species presented average higher N, P, N:P or N×P optimal values than non-masting species. ΔM-N, followed by s.e.m (standard error of the mean), indicate the paired (across simulations) difference between optimal values in masting and non-masting species. P (two-sided t-test) shows the P-value of the paired t-test testing for differences in the mean optimal values of masting and non-masting species. ΔM-N%, followed by s.e.m., indicates the average percentual difference (geometric, paired differences) in mean optimal values between masting and non-masting species.



Extended Data Fig. 5 | Evolutionary relationship between foliar N and P shown in a continuous trait phylogenetic reconstruction (a) and a phylomorphospace plot (b). Evolutionary relationship between foliar N and P shown in a continuous trait phylogenetic reconstruction (a) and a phylomorphospace plot (b). Phylogenetic signal was estimated using *Pagel's lambda* (λ). Foliar N and P concentrations were evolutionarily correlated. N=168 species. *t*-value of the Pearson's correlation was 5.38 (166 DF).



Extended Data Fig. 6 | Map showing interannual variability (PV index) in mean annual precipitation (MAP) and site of origin of our fruit production data (blue dots). Map showing interannual variability (PV index) in mean annual precipitation (MAP) and site of origin of our fruit production data (blue dots).

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Software and code

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Data collection

Data was collected through literature review and previously published databases (e.g., TRY, ICP Forests). The origin of all the data used is stated in the Methods section of the paper.

Data analysis

We used R statistical software (v. 3.5.1) to analyse our data. All statistical methods and packages used are stated in the Methods.

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| | |
|-----------------------------------|---|
| Study description | We tested whether foliar nutrient concentrations was related to masting behaviour using a global dataset containing foliar nutrient concentrations and seed production for 219 plant species. |
| Research sample | Our research sample were 219 plant species distributed across the globe. This data was previously used in a publication: Pearse et al., 2017. We also used foliar concentrations of N and P coming from the TRY database, the ICP forests, the Catalan Forest Inventory and amongst other smaller databases and from literature reviews carried out by coauthors. |
| Sampling strategy | This is paper uses data collected from published literature on seed and fruit production and the elemental composition of leaves (from databases such as TRY and BIEN). 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 Methods for more information. We collected all available data. |
| Data collection | <p>Data was collected from pre-existing databases (TRY, BIEN) and from a literature review (explained above). Compilation of seed and fruit production was carried on by Drs. Pearse, LaMontagne and Koenig. They cleaned the database to include only records that matched certain characteristics (see Data exclusions).</p> <p>Drs. Sardans, Peñuelas, Fernández-Martínez collected foliar nutrient concentrations (from TRY and BIEN databases). TRY and BIEN databases are already curated. We downloaded the complete databases and merged it with the species for which we had fruit production data.</p> |
| Timing and spatial scale | Records of seed production were irregularly comprised between the years 1900-2014. The spatial scale of this dataset is global (see figure ED6). |
| Data exclusions | We pre-established several criteria to include records in our dataset. We only included records when: i) data was available for more than four consecutive years per species at a given site (with clear 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 game 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. |
| Reproducibility | No experiments were performed. Reproducibility is ensured by providing the collected dataset, for which anyone will be able to check values of seed production and average plant foliar N and P concentrations. |
| Randomization | We did not perform any experiment, therefore, randomization was not necessary. |
| Blinding | We did not run any experiment, so no blinding was performed. |
| Did the study involve field work? | <input type="checkbox"/> Yes <input checked="" type="checkbox"/> No |

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