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 time[3]. Masting has often been considered an evolutionary paradox because organisms that skip reproductive attempts should have lower fitness than those that reproduce at every opportunity[4]. Nonetheless, the fact that this reproductive behaviour is found in different lineages suggests that masting behaviour should be beneficial, at least under certain scenarios[5].

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 species[13], such economies of scale are apparently advantageous only under certain circumstances. What those circumstances are remains, so far, under debate.

The environmental stress hypothesis[14] 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 reproduction[16]. 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[5]. 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 production[22].

84   Foliar nutrient concentrations play a key role in plant ecophysiology and ecosystem

85   functioning: photosynthetic rates are linked to foliar nitrogen (N) and phosphorus (P)

86   concentrations[23–25]. Together with carbon, they are the basis of ecological

87   stoichiometry[26,27] and are fundamental parts of the *elementome* or the *biogeochemical*

88   *niche*[28], useful for inferring ecological traits from the elemental composition of

89   organisms[29]. Carbon (C), and especially N and P have been suggested to be potential

90   resources determining seed production and masting behaviour[15,30–32] because seeds

91   and fruits are enriched with N and P compared to vegetative tissues[33]. Low foliar

92   concentrations of N and P would imply lower photosynthetic rates[23] that would in turn

93   result in reduced accumulation of C, in addition to low accumulation of N and P. Thus,

94   based on the *resource budget* model, plant species with low foliar N and P

95   concentrations would be expected to exhibit stronger masting behaviour in terms of

96   variability and negative temporal autocorrelation.

97   Both foliar N and P have been reported to be positively correlated with investment in

98   plant reproduction[34–36]. Additionally, the interaction between foliar N and P, (i.e., the

99   N:P ratio) has been suggested to be an important indicator of plant nutritional status, to

100   promote vegetative productivity[37–40] and to relate to reproductive effort[36] and ecological

101   strategies[28]. The lower N:P ratio of seeds compared to vegetative tissues suggest that

102   nutrient imbalances may constrain reproduction more than growth[38]. Previous studies

103   have reported that plants and shoots producing flowers often exhibit lower N:P values

104   than those that do not[38,41], highlighting the role of nutrient imbalances in plant

105   reproduction. However, no study has yet been focused on the evolutionary linkage

106   between plant reproduction and foliar nutrient stoichiometry over a large set of species.

107   Here we hypothesize that mast seeding behaviour evolved predominantly in plant

108   species with low foliar N and P concentrations and high N:P ratios. To test this

109   hypothesis, we first explored the relationship between temporal variability and

110   autocorrelation in reproductive effort using a global dataset of 219 plant species from

111 all the continents to see if higher variability in seed production is related to higher

112 potential resource depletion (negative temporal autocorrelation)[5]. We then fitted

113 phylogenetic linear models to test whether masting intensity, here defined as the

114 combination of temporal variability and autocorrelation using the consecutive disparity

115 (D) index[42,43], was related to foliar N, P and N:P ratio, while controlling for the

116 evolutionary history of the species and other potentially influencing factors such as

117 local climate and productivity of the regions where species were sampled. Finally, we

118 tested the model of evolution of masting behaviour by means of ancestral character

119 reconstructions and explored whether it has evolved in concert with foliar N and P

120 economies.

121 **Results**

122 *Redefining masting intensity: temporal variability, potential resource depletion and their*

123 *evolutionary relationships*

124 Our results indicated that temporal variability (here calculated as the proportional

125 variability index[44] PV, see **Methods**) in seed production is evolutionary conserved

126 (**Figure S1a**), showing a strong phylogenetic signal[45]. In contrast, lag-1 temporal

127 autocorrelation (AR1, indicating potential resource depletion when it takes negative

128 values) is not phylogenetically conserved. Additionally, temporal variability and

129 autocorrelation are not evolutionary correlated. Hence, species exhibiting higher

130 temporal variability do not necessarily exhibit any particular pattern of temporal

131 autocorrelation (**Figure S1b**). Masting intensity, defined as D in this study (see

132 **Methods**), accounted for both features of masting behaviour (**Figure 1**), temporal

133 variability and potential resource depletion (negative AR1 coefficients), hence defining

134 masting behaviour more broadly than the coefficient of variation (CV) alone, as it is

135 typically assessed[42]. Masting intensity was also preserved phylogenetically (**Figure 1**).

136 Our results suggest that most species exhibit low or intermediate masting intensity,

137 while only a few exhibit strong masting behaviour (see histogram in **Figure 1a**).

139   Phylogenetic models indicated a statistically significant negative interaction between

140   foliar N and P explaining variability in masting intensity across species (**Table 1, Figure**

141   **2**). Model results indicated that when foliar P is low, increasing foliar N increases

142   masting intensity as N:P increases. The inverse situation (high masting intensity at very

143   low N:P ratios) is also possible according to model results, despite being a less likely

144   scenario (we only had 19 species with N:P < 8 in our dataset). The highest masting

145   intensity was found in species with high N:P while the lowest was found in species with

146   high foliar N and P concentrations. Species with low foliar N and P concentrations

147   showed intermediate values of masting intensity. Temporal variability of the local

148   climate or productivity of the region from where species were sampled did not explain

149   variation in masting intensity. Mean annual precipitation, however, was positively

150   related to masting intensity (**Table 1**). Temporal variability in seed production was

151   negatively related to mean annual temperature and positively related to temporal

152   variability of annual precipitation. Additionally, species with higher foliar P exhibited

153   lower temporal variability. When assessing temporal variability using the CV, we found

154   that species from regions with higher temporal variability in productivity also presented

155   higher CV of seed production (β=0.22 ± 0.08, *P*=0.004, λ=0.58). Potential resource

156   depletion was more likely to occur in species living in climates exhibiting negative

157   temporal autocorrelation in annual precipitation (**Table 1**). Interestingly, the model also

158   showed a positive interaction between foliar N and P, indicating that potential resource

159   depletion after seeding was more likely to occur in species with low foliar N and P.

160   Our analyses also revealed the evolutionary processes linking masting behaviour and

161   foliar nutrient concentrations (**Table S1**). We found that adaptive processes - Ornstein-

162   Uhlenbeck (OU) models based on ancestral character reconstructions (**Figure S2**) -

163   are the models that better explain current patterns in masting intensity, linked to foliar

164   nutrient concentrations. Adaptive OU models explaining evolutionary history of masting

165   intensity with N, P and N×P (a measure of total N and P foliar concentration) assumed

166   that species evolved toward different optimum values depending on whether they

167   present high or low masting intensity (masting and non-masting species) (OUM model).

168   However, a single optimum for all species was equally likely for foliar N, P and N×P

169   (less than 2 units of AICc between models were found, OU1, see **Methods**).

170   Nonetheless, given that OUM models with different optimum values performed equally

171   well for foliar N, P and N×P (**Table S1**), OUM models are used to illustrate our results.

172   The model that best fitted the data for foliar N:P was an adaptive OU model with

173   different optimum and phenotypic variation for high and low masting intensity species

174   (OUMV model).

175   Results from OU models indicated that masting species had, on average, 9.5 ± 0.4%

176   and 18.3 ± 0.5% lower foliar N and P concentrations, respectively, than non-masting

177   species (**Figure 3**, **Table S2**). Foliar N:P ratio was 11.4 ± 0.2% (mean ± standard error

178   of the mean) higher in masting species, while N×P, combined availability of N and P,

179   was 28.7 ± 1.0% lower than in non-masting species. These results were consistent

180   when using five different thresholds of masting intensity (see **Methods**) to classify

181   species as masting or non-masting species (**Table S2**). Like masting intensity, both

182   foliar N and P concentrations were preserved throughout the phylogeny (**Figure S3**).

183   **Discussion**

184   *The role of foliar nutrients in seed production*

185   Our results suggest that masting intensity co-evolved with species-specific optimal

186   foliar N and P concentrations and that species with lower N and especially lower P, and

187   therefore high N:P, exhibit higher masting intensity (**Figure 3**). Hence, our analyses

188   supported our initial hypothesis stating that masting behaviour evolved predominantly

189   in plant species with low foliar N and P concentrations and high N:P ratios. This

190   observed evolutionary pattern may have originated because of different underlying

191 mechanisms driven by environmental and physiological constraints. One potential

192 mechanism explaining these findings could be the physiological role of foliar N and P

193 concentrations in plants. Foliar N is well known for being the primary limiting nutrient for

194 reproduction[34,35] and vegetative growth[46,47]. Elevated foliar P concentrations, and low

195 N:P ratios, have been shown to allow larger seed crops in multiple species[15,36,41,48],

196 coinciding with fast growing species according to the *growth rate* hypothesis[26]. P is also

197 essential to maintain water-use efficiency and growth, particularly during drought

198 conditions[49]. Both nutrients are essential elements of ribosomes and, therefore, play a

199 major role in organismal metabolism[50]. The production of seeds, which are structures

200 enriched with N and P[33], may potentially benefit from high concentrations of nutrients

201 even more than vegetative tissues.

202 Low foliar N and P concentrations and high N:P imbalance are often indicative of

203 unfavourable environments for plant growth[15,51,52], such as infertile soils. These poor

204 growing conditions are often related to dry or cold climates where decomposition of

205 organic matter is constrained, rates of nutrient mineralisation and weathering are

206 low[49,53], or disturbances (e.g., wildfires) are frequent[54]. However, differences in foliar N

207 and P concentrations may not always reflect differences in nutrient availability across

208 species, as coexisting species may have different elemental compositions (the

209 *biogeochemical niche* hypothesis[28]). Nonetheless, plants with high foliar N and P

210 concentrations must either be growing in environments without nutrient limitations or

211 have developed mechanisms that allow them to sustain high foliar nutrient

212 concentrations even if they are growing under unfavourable conditions. In any case,

213 these higher concentrations of nutrients should confer a competitive advantage in

214 terms of C acquisition, because higher N and P concentrations are, on average, linked

215 to higher photosynthetic rates[23].

216 *Evolutionary history of masting intensity and foliar nutrients*

217 Being capable to invest more in reproduction does not explain masting behaviour by

218 itself, because equal average seed crops over time could lead to different reproductive

219 behaviours[15]. The necessary link between the ecological stoichiometry and masting

220 theoretical backgrounds lies in the *resource accumulation* hypothesis[16,17]. Plant species

221 with lower or imbalanced availability of N and P may present more difficulties in

222 acquiring the necessary amount of C, N and P to successfully produce seeds regularly,

223 thereby mechanistically producing a reproductive behaviour aligned with high masting

224 intensity: high interannual variability and negative temporal autocorrelation (i.e.,

225 potential resource depletion). The combination of low and imbalanced nutrient

226 availability, causing high variability in seed production and potential resource depletion

227 after crops, and environmental variability that synchronises the reproduction of

228 individuals through weather cues[7,19] would finally shape the reproductive behaviour of

229 masting species. In fact, our results also revealed that mean annual precipitation, and

230 its temporal variability and autocorrelation, are related to the reproductive behaviour of

231 plant species (**Table 1**). These results indicate that even nutrient-rich species can

232 present masting behaviour if they grow under climates with highly fluctuating weather

233 conditions. Therefore, we suggest that the interaction between weather conditions and

234 the availability of nutrients, both conditioning photosynthetic rates, are the triggering

235 factor of the common nonlinear (often exponential-like) response[22] between seed

236 production and weather variability in masting species[8,18,21].

237 As a result of the environmental and physiological constraints, species may have been

238 selected to exhibit distinctive reproductive behaviours in order to increase their fitness.

239 Nutrient-rich species may not have developed a resource-conservative masting-like

240 reproduction strategy because of their capacity to produce abundant seeds with

241 regularity, avoiding losing reproduction attempts. Instead, because the investment in

242 reproduction in terms of C and nutrients should be proportionally more expensive for

243 nutrient-poor or nutrient-imbalanced species, the pressure to exhibit more cost-efficient

244 reproduction may have selected such species to produce fewer but larger reproductive

245 events in order to take advantage of one or more *economies of scale*[6,7,11]. As a side

246 effect of these massive reproductive events, negative temporal autocorrelation would

247 also have appeared in masting species because of potential resource depletion

248 (**Figure S1**). Hence, these particular traits would have been preserved throughout

249 evolutionary history (**Figure 1**) because foliar functional traits and masting intensity

250 have co-evolved (**Figure 3, Table S2**). Nonetheless, our results do not discard other

251 potential selective pressures that may have triggered the evolution of masting

252 behaviour. Some species may have been selected to mast to improve their pollination

253 efficiency[55], to escape seed predation from voracious predators[8,9] or because of

254 interspecific competition in different ways (e.g., seedling establishment). Also, a

255 selective pressure towards reproducing more constantly could happen in animal-

256 pollinated species, where a more constant production of flowers would favour

257 populations of pollinators and, hence, pollination. Further research on reproductive

258 behaviour of early plants, such as bryophytes, and taxa from different realms using

259 concepts from the masting literature may facilitate better understanding of the evolution

260 of different reproductive behaviours in nature.

261 **Methods**

262 *Datasets*

263 *Masting database*

264 Data on interannual reproductive effort (seed or fruit production) were compiled from

265 Web of Science searches, scanning the literature cited of published papers to look for

266 more records of reproductive effort, contacting managers of wildlife surveys, forestry

267 districts, and regional seed surveys, and soliciting datasets in the Ecolog listserv

268 (https://listserv.umd.edu/archives/ecolog-l.html). See Pearse et al.[14] for more

269 information on data collection methods and characteristics of the dataset.

270   We only included records when: i) data were available for more than four consecutive

271   years per species at a given site (with clear geographical coordinates), ii) records could

272   be clearly assigned to plants of a particular species, iii) records were not measured in

273   such an indirect way their accuracy could be jeopardised (e.g., anticipated correlations

274   with gamete abundance), iv) data represented seed or fruit production, or inflorescence

275   set only for those cases where inflorescences are strongly linked to seed or fruit

276   production, and v) records from iteroparous perennial plants whose seed set could not

277   be explained by changes in population size. We did not include records of pollen

278   production nor from records from agricultural settings.

279   Overall, the reproductive effort dataset contained 1084 records of reproductive effort

280   including 363 plant species (trees, shrubs, vines, grasses and herbs) from 205 studies,

281   ranging from 1900 to 2014 and covering the six majorly vegetated continents (Africa

282   (17), North America (466), Europe (280), Japan (68), New Zealand (67), Central

283   America (118) and other regions (68)). On average, records were 11.9 years long,

284   although 131 studies had more than 20 years of data[14].

285   For each site and species, we calculated the proportional variability index in seed

286   production (PV)[44] as a measure of temporal variability. The PV index overcomes

287   several statistical and mathematical issues of the CV index[44]. The PV index was

288   calculated as:

289
$$PV = \frac{2 \sum z}{n(n-1)}$$

290   Where z is calculated as:

291
$$z = 1 - \frac{\min(z_i, z_j)}{\max(z_i, z_j)}$$

292   Where "z" represents the list of individual values (seed production per year) from which

293   to calculate the pairwise comparisons and "n" indicates the number of values in a

294   variable. We also calculated the lag-1 temporal autocorrelation (AR1) as a measure of

295   potential resource depletion using the *acf* function in R, and the consecutive disparity

296   index (D)[42,43] as a measure of masting intensity. We defined masting intensity as D

297   because, like the PV index, this index also overcomes several statistical and

298   mathematical limitations of the coefficient of variation (CV = standard deviation × mean^{-}

299   ^{1}), including dependence on the mean, dependence on the length of the time series,

300   and bias associated with non-Gaussian data commonly used to describe masting[13,14].

301   More importantly, we used D because it combines two of the main features describing

302   masting behaviour: temporal variability and lag-1 autocorrelation (AR1) in seed

303   production[42]. D is defined as:

304

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

305   Where p_i is the series value (seed production in our case) at time i, n is the series

306   length and k is a constant (often one unit) to avoid numerical indetermination in time

307   series with 0 values. D is high when temporal variability is high and lag-1 temporal

308   autocorrelation is negative (i.e., strong masting behaviour, showing potential resource

309   depletion after large seed crops[20,31]). Conversely, D is low when temporal variability is

310   low and temporal autocorrelation is close to zero or positive (i.e., describing a constant

311   pattern of seed production and hence, no masting behaviour). Given that the CV is still

312   the most widely used index to assess temporal variability in masting studies, we also

313   calculated the CV of seed production per species and site to compare its results with

314   those shown by the PV index. When multiple records from the same species were

315   available, we calculated the average masting intensity (D), temporal variability (PV and

316   CV) and the potential resource depletion coefficient (AR1) per species.

317   *Climate, productivity and foliar nutrients*

318   We extracted mean annual temperature (MAT, °C) and precipitation (MAP, mm yr^{-1})

319   and their seasonality (MAT$_s$ [standard deviation of monthly values × 100] and MAP$_s$

320   [CV]) for each location in our masting database from the WorldClim2 database[56]. The

321   climate database contains long-term means (1950-2000), calculated on a 30 arc-

322   second grid. Data for variability and autocorrelation for temperature and precipitation

323   was extracted from the CRU TS v3.25 dataset[57]. To estimate site productivity we used

324   a remotely-sensed gross primary production (GPP) database[58]. For annual

325   temperature and precipitation of the CRU TS and the GPP global databases we

326   calculated D, PV and AR1 indices for each pixel. We then extracted climate (i.e., MAT$_D$,

327   MAP$_D$, MAT$_{PV}$, MAP$_{PV}$, MAT$_{AR1}$ and MAP$_{AR1}$) and productivity (i.e., GPP$_D$, GPP$_{PV}$ and

328   GPP$_{AR1}$) data for each site and species in our masting database and calculated the

329   average per species. We used these variables in our statistical analyses to control for

330   site-specific differences in temporal variability and autocorrelation patterns of climate

331   and productivity.

332   Data for foliar concentration of N and P for the species in our database were gathered

333   from the TRY trait database (https://www.try-db.org/TryWeb/Home.php)[59], the BIEN

334   database (http://bien.nceas.ucsb.edu/bien/)[60], the ICP Forests database on foliar

335   elemental concentration[61] (www.icp-forests.net), and the Catalan Forest Inventory

336   (http://www.creaf.uab.cat/iefc/). To estimate an average value per species, we first

337   calculated the mean value per species and database. We then merged all databases

338   and calculated the mean values per species. Species names in our database were

339   checked and corrected using The Plant List database in the R package *Taxonstand*[62].

340   Phylogenetic analyses were performed using the plant phylogeny provided by Qian &

341   Jin (2016). Out of the 363 species in the masting database, 219 species (~60%) names

342   matched those in the phylogenetic tree, and therefore, only those were used for further

343   analyses. Analyses using foliar N and P data were restricted to the 168 species (~46%)

344   for which we could find data.

Data analyses

Evolutionary link between masting intensity, temporal variability and autocorrelation

347 To explore how well the phylogenetic ancestry can explain masting behaviour, we first

348 estimated the phylogenetic signal (i.e. tendency for related species to resemble each

349 other more than they resemble species drawn at random from the phylogenetic tree) of

350 masting intensity (D) , PV and AR1 using the *phylosig* function in the R[64] package

351 *phytools*[65]. Phylogenetic signal was assessed by the lambda (λ) metric, which varies

352 from 0 (where phylogenetic and trait similarity are totally independent) to 1 (where the

353 traits are completely explained by shared ancestry). We then used continuous mapped

354 phylogenetic trees (*contMap* function in R package *phytools*) to visualise their

355 phylogenetic signal. Finally, we explored the evolutionary relationship between

356 temporal variability, temporal autocorrelation and masting intensity using pairwise

357 correlations correcting for the phylogeny. Relationships were shown using

358 phylomorphospace plots [65], which depicts each species as a data point in a trait space,

359 together with the phylogenetic relationship of each species-point.

Controls of masting intensity and its mode of evolution

361 We first tested whether masting intensity (D) was related to climate, productivity, foliar

362 N and P concentrations and their interaction. To do so, we fitted phylogenetic linear

363 models in which the response variable was masting intensity (D) and the predictors

364 were foliar N and P concentrations and their interaction, MAT, MAP, MAT_s, MAP_s,

365 MAT_D and MAP_D for climate and GPP and GPP_D for productivity. Phylogenetic models

366 were fitted optimising lambda (i.e., the strength of phylogenetic signal) and using the

367 *phylolm* function in the R *phylolm* package[66]. The final model was achieved by

368 removing the least significant terms from the full model, in a step-by-step process, until

369 all variable estimates were significant. The same models were fitted for the PV and

370 AR1, but changing the predictors from D to PV or AR1 respectively (e.g., MAT_{PV}

371   instead of MAT_D when predicting PV). Because the CV has been widely used to assess

372   temporal variability, we also fitted a model using CV as the predictor variable to

373   compare its results with those of the model using the PV index. Masting intensity and

374   PV were transformed to natural logarithms to normalise model residuals. We used the

375   package *visreg*[67] to visualise model results.

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

377   To test the hypothesis that masting behaviour has evolved as an adaptation to nutrient

378   imbalances and low foliar N and P concentrations, we performed three step analysis.

379   First, we classified species as masting and non-masting. Second, we reconstructed the

380   ancestral state between the two types of reproducing behaviour, and third, we fitted

381   different evolutionary models to test whether foliar concentrations of N, P and N:P ratio

382   and N×P (N times P, as a measure of the overall availability of nutrients) evolved under

383   the reconstructed discrete selective regimes (masting or non-masting).

384   To define masting behaviour, and as a test for robustness of our results, we classified

385   species as subsets that represent masting (high temporal variability and strong

386   potential resource depletion) or non-masting (low temporal variability and no resource

387   depletion) behaviours based on 5 different thresholds of masting intensity (D), selecting

388   only the lower and upper bounds for the analyses and discarding the intermediate

389   species. The selected percentile thresholds were: i) from 0% to 33% non-masting

390   (N=38 species) and from 66% to 100% masting (N=58); ii) from 0% to 25% non-

391   masting (N=32) and from 75% to 100% masting (N=43); iii) from 0% to 20% non-

392   masting (N=27) and from 80% to 100% masting (N=34); iv) from 0% to 15% non-

393   masting (N=22) and from 85% to 100% masting (N=26) and v) from 0% to 10% non-

394   masting (N=16) and from 90% to 100% masting (N=17).

395   To reconstruct ancestral states of masting behaviour, for each of the five classifications

396   we performed stochastic character mappings[68], which reconstructs the state of the

397 ancestors of a phylogeny based on the observed traits of the current species and the

398 phylogenetic structure. Ancestral reconstructions were performed using the

399 *make.simmap* function in the *phytools* R package[65], simulating 1000 stochastic

400 ancestral reconstructions, specifying equal rates of transition amongst the character

401 states and using the "*mcmc*" method.

402 Once we had the 1000 stochastic character mappings for each masting classification,

403 we performed generalised Ornstein–Uhlenbeck Hansen models to test whether the

404 inferred evolutionary trajectories in foliar concentrations of N, P, N:P and N×P

405 (hereafter "continuous traits") were associated with the two alternative masting

406 behaviour strategies (hereafter "ancestral states") and whether they followed an

407 adaptive (Ornstein–Uhlenbeck: OU) or random (Brownian motion—BM) model of

408 evolution[69–71]. To do so, we used the OU function from *OUwie* R package[72]. We fitted

409 five different models using the 1000 ancestral reconstructions mentioned above for

410 each classification. The five different models represent different types of underlying

411 evolutionary processes, being: i) single-state BM models (BM1), where evolutionary

412 rates for the continuous traits are equal for all ancestral states, ii) BM models with

413 different evolutionary rates for each ancestral state (BMS), iii) OU models with a single

414 optimal value for the continuous traits for all ancestral states (OU1), iv) OU models with

415 different optimal values but a single alpha (the strength of the pull towards the optimal

416 values of the trait) and single theta (the rate of phenotypic variation around the optimal

417 value) for each state (OUM), and v) OU models that assumed different optimal values

418 with multiple rates of phenotypic evolution (theta) for each state (OUMV).

419 Models containing negative eigenvalues (non-sound models) were deleted when

420 summarising our results[29]. Different evolutionary models were compared using second-

421 order Akaike information criterion (AICc) amongst all sound models. Those models with

422 the lowest AICc were considered to be those that fitted the data best. For models

423 assuming different optimal values of foliar N, P, N:P and N×P for masting and non-

masting species (i.e., 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 OU models with different state means (OUM and OUMV) were tested using paired *t*-tests. Given that results pointed out to the same direction (see **Supplementary Information**) for all masting intensity thresholds, we only show those from the intermediate (0% to 20% for non-masting and 80% to 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 perform with R statistical software version 3.5.1[64].

Data availability

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

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616

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619 **Acknowledgements**

627

628 **Author Contributions**

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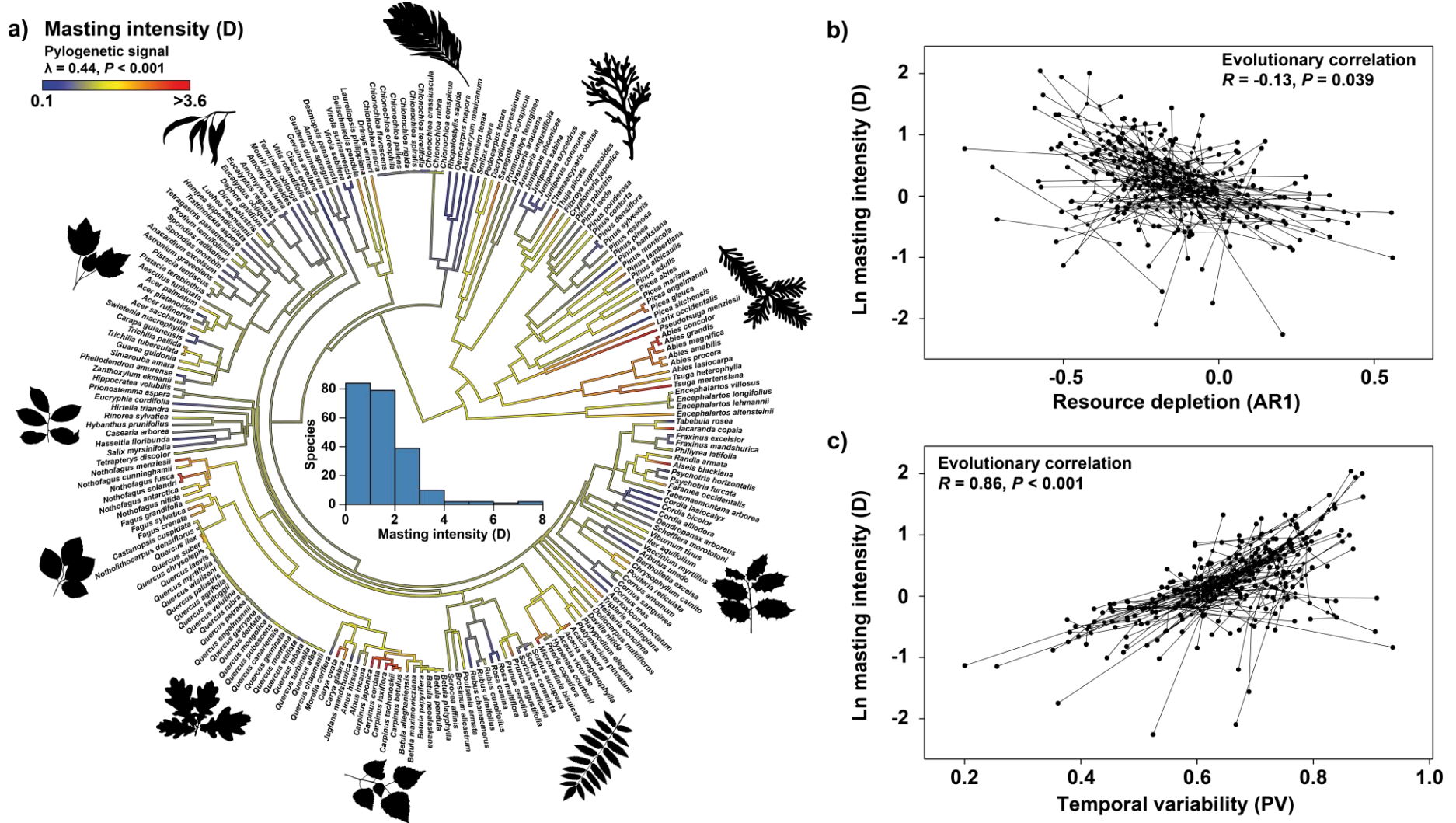631 to the writing and discussion of the paper.

632

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.

659 **Table 1: Model summary of the phylogenetic linear models based on 168**

660 **species.** Masting intensity was defined as the D index, PV indicates temporal

661 variability and AR1 <mark>potential</mark> resource depletion coefficient (i.e., negative values

662 indicate <mark>potential</mark> resource depletion). Beta (β) shows the standardised model

663 coefficients, followed by the standard error of the mean (s.e.m), the *P*-value (*P*) and

664 lambda (λ) indicating the phylogenetic signal in the models. See **Methods** for further

665 information. **Acronyms:** mean annual precipitation (MAP), foliar nitrogen (N), foliar

666 phosphorus (P), mean annual temperature (MAT), temporal autocorrelation at lag 1

667 (AR1).

668

669   **Figure 1**

a) **Masting intensity (D)**

Pylogenetic signal
λ = 0.44, *P* < 0.001

0.1   >3.6

b) Evolutionary correlation
R = -0.13, *P* = 0.039

Ln masting intensity (D)

Resource depletion (AR1)

c) Evolutionary correlation
R = 0.86, *P* < 0.001

Ln masting intensity (D)

Temporal variability (PV)

670

671   **Figure 2**

672

Figure 3

674

675

676   **Table 1**
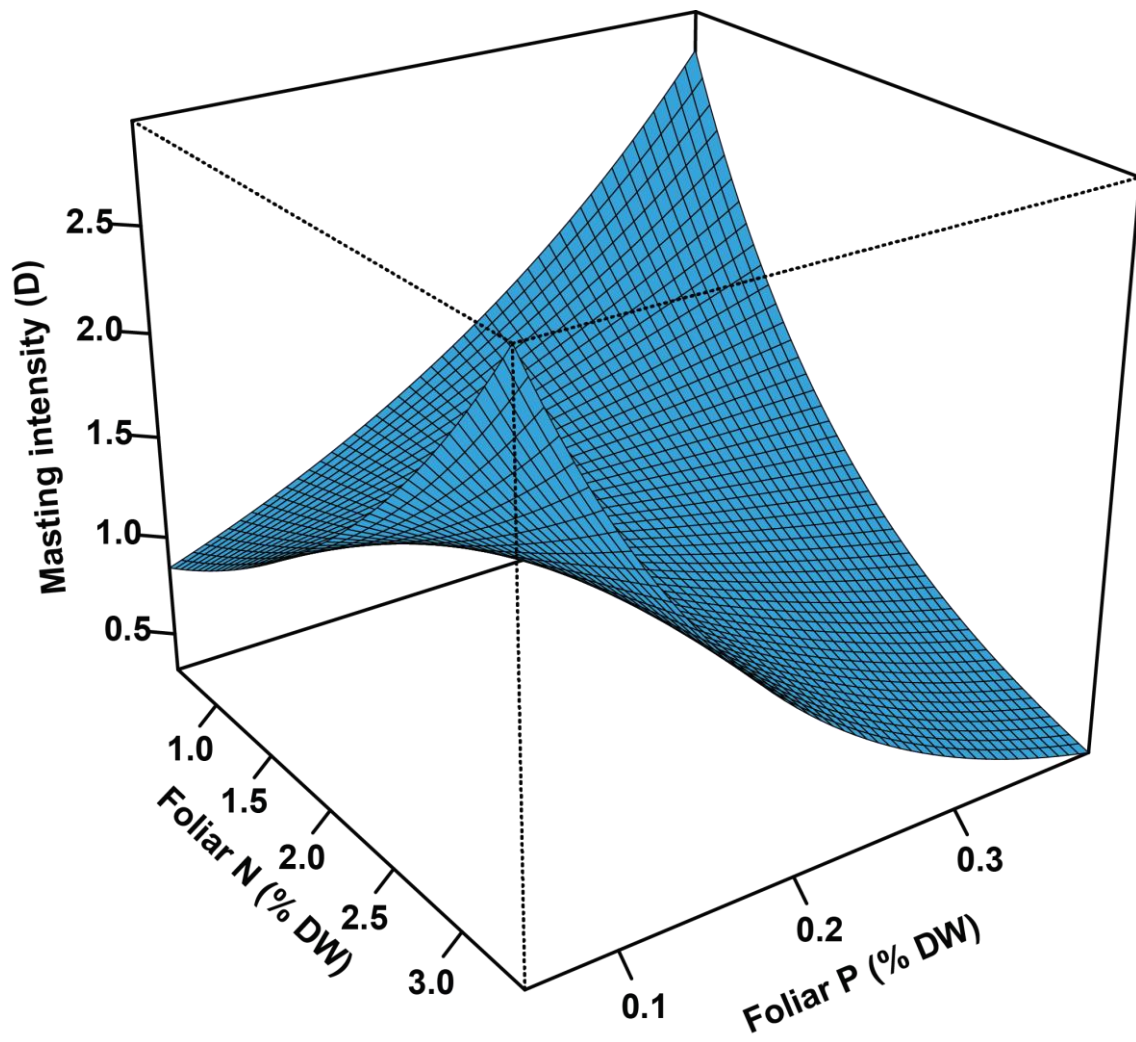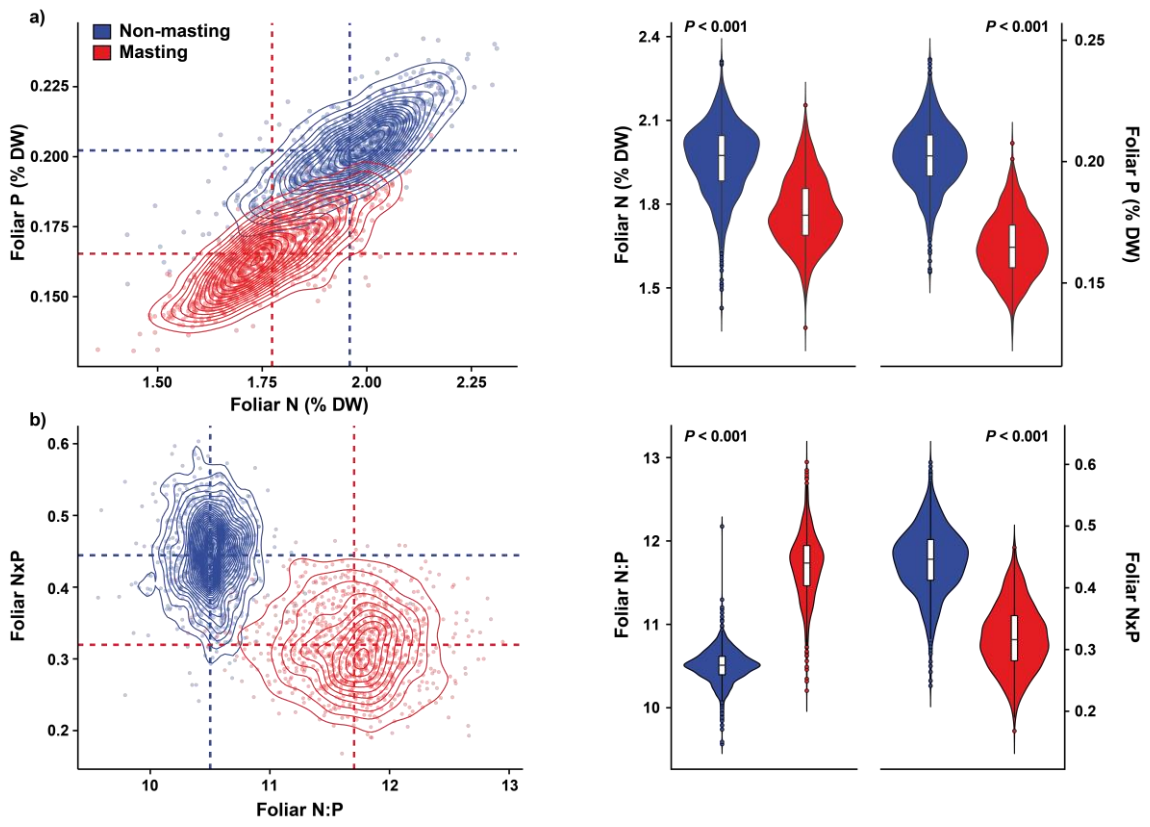
	β	s.e.m	*P*	λ
Masting intensity (D)				
MAP	0.22	0.09	0.016	
N	0.04	0.10	0.708	
P	-0.04	0.10	0.674	
N×P	-0.19	0.07	0.007	0.47
Temporal variability (PV)				
MAP$_{PV}$	0.16	0.08	0.042	
MAT	-0.18	0.09	0.040	
P	-0.16	0.08	0.044	0.41
Potential resource depletion (AR1)				
MAP$_{AR1}$	0.27	0.08	0.001	
N	-0.09	0.10	0.001	
P	-0.05	0.10	0.008	
N×P	0.22	0.07	0.002	0.00

677

678　**Supplementary Material**

679　**Figure S1**: Evolutionary relationship between <mark>potential</mark> resource depletion coefficient

680　(AR1) and temporal variability (PV) in seed production shown in a continuous trait

681　phylogenetic reconstruction (a) and a phylomorphospace plot (b). <mark>Potential</mark> resource

682　depletion and variability in seed production were not evolutionary correlated. Negative

683　values of AR1 indicate that <mark>potential</mark> resource depletion may happen, see **Methods**.

684　N=219 species.

685
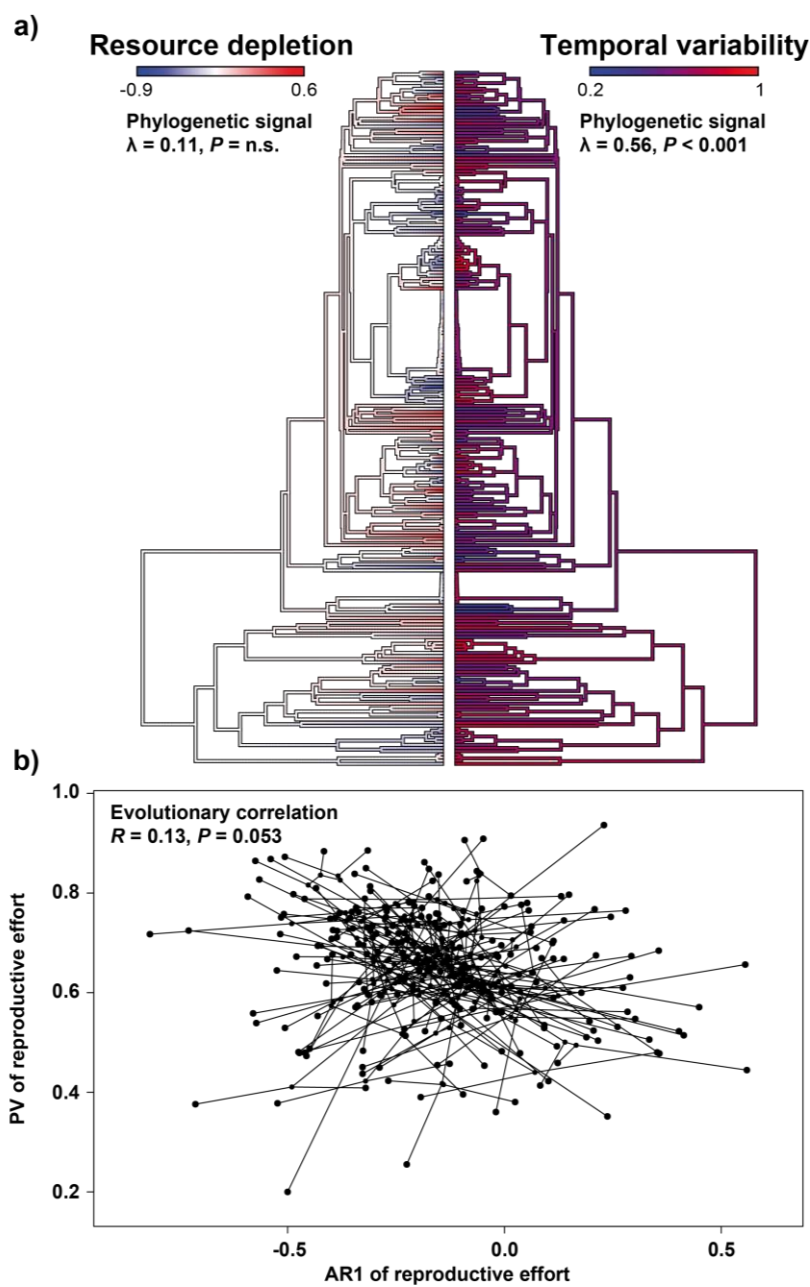
Figure S2: Phylogenetic tree including the subset of low (non-masting) and high

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).
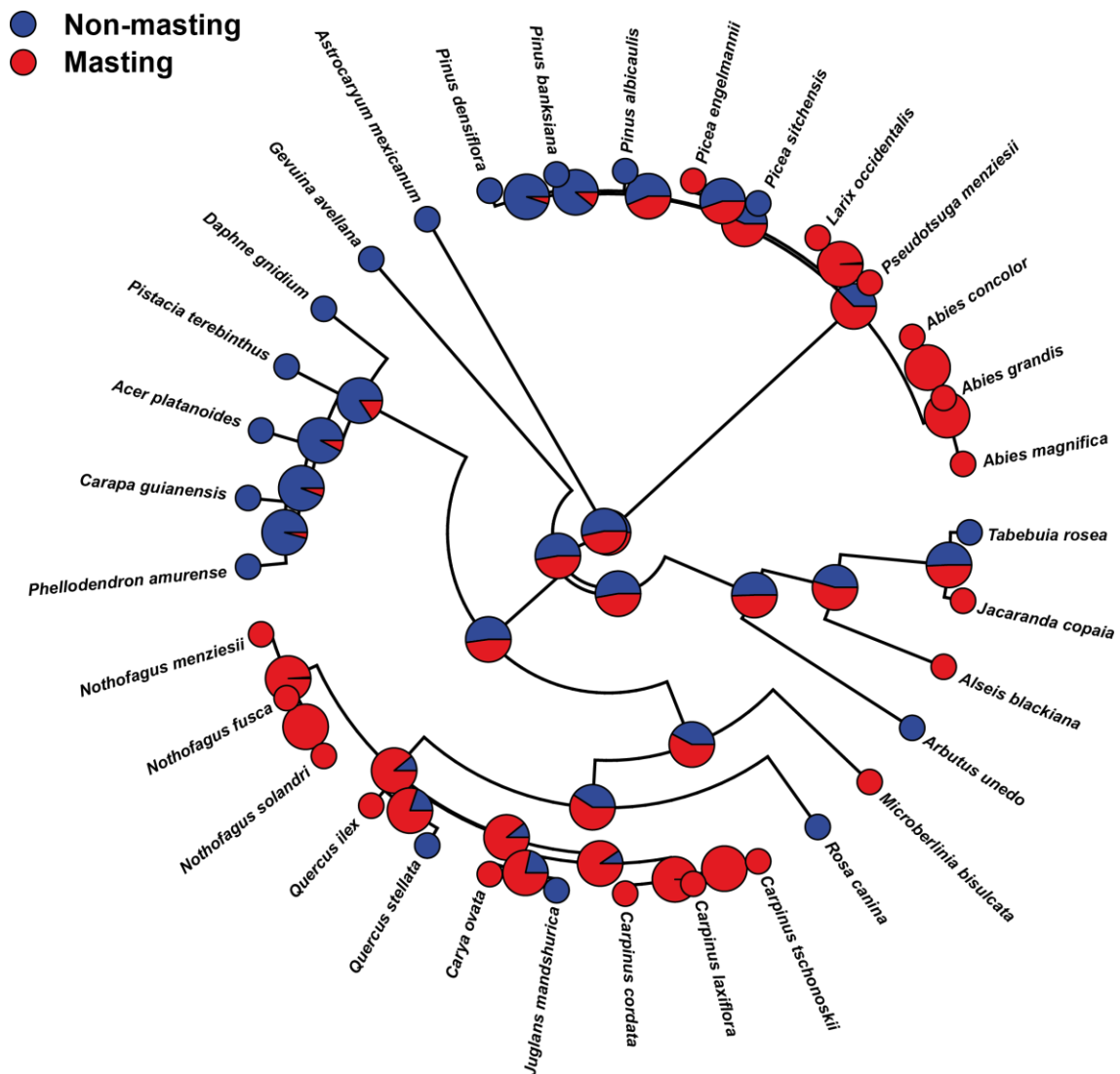
696 **Figure S3**: Evolutionary relationship between foliar N and P shown in a continuous trait

697 phylogenetic reconstruction (a) and a phylomorphospace plot (b). Foliar N and P

698 concentrations were evolutionary correlated. N=168 species.

699
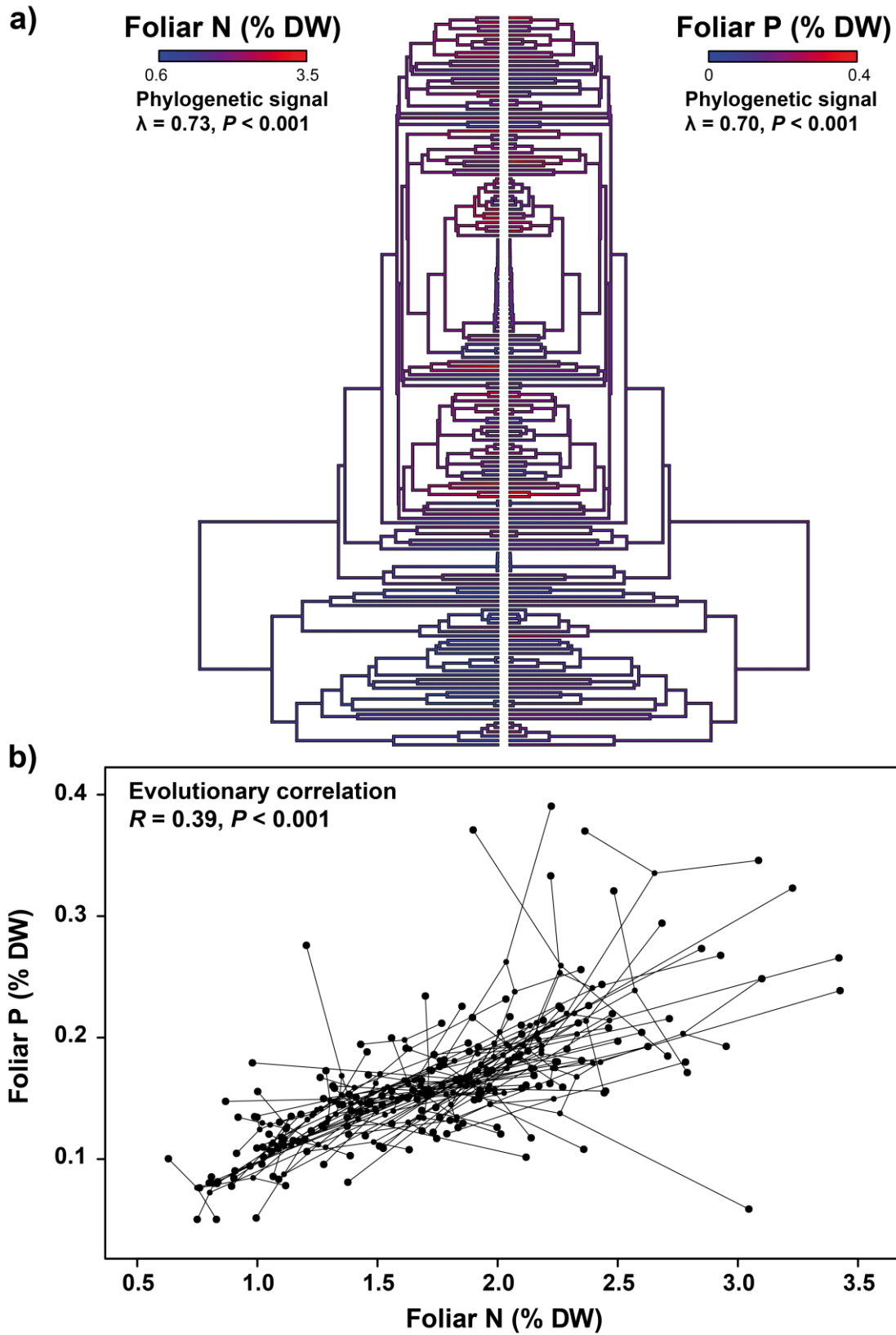
Table S1: Mean differences (ΔAICc, second-order Akaike information criterion)
between each of the model's AICc and the model with the lowest AICc. Evolutionary
models were Brownian motion (BM1, BMS) and generalised Ornstein-Uhlenbeck-
based Hansen (OU1, OUM, OUMV), fitting "masting" and "non-masting" 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		

712 **Table S2**: Estimated foliar nitrogen (N) and phosphorus (P) concentrations, N:P and N×P (overall nutrient availability) optimal values for

713 masting and non-masting species using OUMV and OUM models (see **Methods** for further information about the models), chosen based on the

714 lowest ΔAICc estimating different state means for masting and non-masting species (**Table S1**). Masting and non-masting species were

715 classified depending on the percentile of masting intensity (e.g., masting for higher than 66%, non-masting for lower than 33%, see subheaders

716 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

717 the sound models (without negative eigenvalues, N column) used. M>N% indicate the percentage of models in which masting species

718 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),

719 indicate the paired (across simulations) difference between optimal values in masting and non-masting species. *P* (*t*-test) shows the *P*-value of

720 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

721 the average percentual difference (geometric, paired differences) in mean optimal values between masting and non-masting species.

722

723 **Table S2:**

	Masting			Non-masting			M>N%	ΔM-N	s.e.m	P (t-test)	ΔM-N%	s.e.m	N	Model
	2.5%	50%	97.5%	2.5%	50%	97.5%								
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

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