

**Editor summary:**

Mast seeding is a reproductive trait of some perennial plants that display synchronous highly variable annual production of fruit. The drivers of mast seeding are not well understood. Here the authors reported a global scale investigation of masting behaviour and revealed a link with nutrient economy.

**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.

**1. Extended Data**

<b>Figure #</b>	<b>Figure title</b> One sentence only	<b>Filename</b> This should be the name the file is saved as when it is uploaded to our system. Please include the file extension. i.e.: <i>Smith_ED_Fig1.jpg</i>	<b>Figure Legend</b> If you are citing a reference for the first time in these legends, please include all new references in the Online Methods References section, and carry on the numbering from the main References section of the paper.
<b>Extended Data Figure 1</b>	Evolutionary relationship between potential resource depletion coefficient (AR1) and temporal variability (PV) in seed production	EDF1.pdf	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 <i>Pagel's lambda</i> ( $\lambda$ ). Potential resource depletion and variability in seed production were not evolutionary correlated. Negative values of AR1 indicate that potential resource depletion may happen, see <b>Methods</b> . N=219 species. <i>t</i> -value of the Pearson's correlation was 1.95 (218 DF).

<p><b>Extended Data Figure 2</b></p>	<p>Mean differences (<math>\Delta AICc</math>, second-order Akaike information criterion) between each of the model's <math>AICc</math> and the model with the lowest <math>AICc</math>.</p>	<p>EDF2.pdf</p>	<p>Mean differences (<math>\Delta AICc</math>, second-order Akaike information criterion) between each of the model's <math>AICc</math> and the model with the lowest <math>AICc</math>. 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 <math>AICc</math> 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</p>
--------------------------------------	--	-----------------	--

			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 $\Delta AICc$ lower than 2 (indicating equal performance) were highlighted. See <b>Methods</b> for further information.
<b>Extended Data Figure 3</b>	Phylogenetic tree including the subset of low (non-masting) and high masting intensity (masting) species used to perform the generalised Ornstein-Uhlenbeck model results.	EDF3.pdf	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 (20 <sup>th</sup> – 80 <sup>th</sup> percentile thresholds for non-masting and masting species, <b>Figure 3, Extended Data Figure 2 and Extended Data Figure 4</b> ). 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 <b>Methods</b> for further information).
<b>Extended Data Figure 4</b>	Estimated foliar nitrogen (N) and phosphorus (P) concentrations, N:P and N×P (overall nutrient availability) optimal values for masting and non-masting species	EDF4.pdf	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 <b>Methods</b> for further information about the models), chosen based on the lowest $\Delta AICc$ estimating different state means for masting and non-masting species ( <b>Extended Data Figure 2</b> ). Masting and non-masting species were classified depending on the percentile of masting intensity (e.g., 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. $\Delta M-N$ , 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. $\Delta M-N\%$ , followed by s.e.m., indicates the average percentual difference (geometric, paired differences) in mean optimal values between masting and non-masting species.
<b>Extended Data Figure 5</b>	Evolutionary relationship between foliar N and P shown in a continuous trait phylogenetic reconstruction (a) and a phylomorphospace plot (b).	EDF5.pdf	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 <i>Pagel's lambda</i> ( $\lambda$ ). Foliar N and P concentrations were evolutionary correlated. N=168 species. $t$ -value of the Pearson's correlation was 5.38 (166 DF).
<b>Extended Data Figure 6</b>	Map showing interannual variability (PV index) in mean annual precipitation (MAP) and site of origin of our fruit production data (blue dots).	EDF6.pdf	Map showing interannual variability (PV index) in mean annual precipitation (MAP) and site of origin of our fruit production data (blue dots).

# 1 **Nutrient scarcity as a selective pressure for mast seeding**

2 **Authors:** M. Fernández-Martínez<sup>\*1</sup>, I. Pearse<sup>2</sup>, J. Sardans<sup>3,4</sup>, F. Sayol<sup>5,6</sup>, W.D. Koenig<sup>7</sup>, J.M.  
3 LaMontagne<sup>8</sup>, M. Bogdziewicz<sup>9</sup>, A. Collalti<sup>10,11</sup>, A. Hacket-Pain<sup>12</sup>, G. Vacchiano<sup>13</sup>, J.M. Espelta<sup>4</sup>,  
4 J. Peñuelas<sup>3,4</sup>, I.A. Janssens<sup>1</sup>

## 5 **Affiliations:**

6 <sup>1</sup> Centre of Excellence PLECO (Plants and Ecosystems), Department of Biology, University of  
7 Antwerp, 2610 Wilrijk, Belgium.

8 <sup>2</sup> U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado 80526 USA

9 <sup>3</sup> CSIC, Global Ecology Unit, CREAM-CSIC-UAB, Bellaterra 08193 Barcelona, Catalonia, Spain

10 <sup>4</sup> CREAM, Cerdanyola del Vallès, 08193 Barcelona, Catalonia, Spain

11 <sup>5</sup> Department of Biological and Environmental Sciences, University of Gothenburg, SE 405 30  
12 Gothenburg, Sweden

13 <sup>6</sup> Gothenburg Global Biodiversity Centre, SE 405 30 Gothenburg, Sweden

14 <sup>7</sup> Lab of Ornithology, Cornell University, Ithaca, NY, USA

15 <sup>8</sup> Department of Biological Sciences, DePaul University, Chicago, IL, USA

16 <sup>9</sup> Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University in Poznań,  
17 Poland

18 <sup>10</sup> Institute for Agriculture and Forestry Systems in the Mediterranean, National Research  
19 Council of Italy (CNR-ISAFOM), 87036, Rende (CS), Italy

20 <sup>11</sup> Department of Innovation in Biological, Agro-food and Forest Systems, University of  
21 Tuscia, 01100 Viterbo, Italy

22 <sup>12</sup> Department of Geography and Planning, School of Environmental Sciences, University of  
23 Liverpool, Liverpool, UK

24 <sup>13</sup> Università di Milano, DISAA. Via Celoria 2, 20133, Milan - Italy

25 \* **Correspondence to:** M. Fernández-Martínez, marcos.fernandez-martinez@uantwerpen.be

26 **Length of the main text:** 2488 words

27 **Length of the methods:** 2367 words

28 **Figures and tables:** 3 figures, 1 table

29 **Length of the captions:** 511 words

30 **References:** 56 (+17 from Methods)

## 31 **Abstract**

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

## 44 **Main text**

45 Mast seeding, often called *masting*, has long intrigued biologists as one of the most  
46 bizarre reproductive behaviours found in nature<sup>1,2</sup>. This behaviour consists of the  
47 synchronous production of highly variable seed crops over time<sup>3</sup>. Masting has often  
48 been considered an evolutionary paradox because organisms that skip reproductive  
49 attempts should have lower fitness than those that reproduce at every opportunity<sup>4</sup>.  
50 Nonetheless, the fact that this reproductive behaviour is found in different lineages  
51 suggests that masting behaviour should be beneficial, at least under certain scenarios<sup>5</sup>.

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

57 years of null or low reproduction and satiated during high reproduction *mast* years,  
58 leaving large numbers of seeds intact. Another example is the *pollination efficiency*  
59 hypothesis<sup>6,11,12</sup>, stating that, particularly for wind-pollinated plants, saturating the  
60 atmosphere with pollen in a given year is more efficient than producing regular  
61 amounts of pollen each year in order to ensure pollination. Given that masting is  
62 present in only a modest percentage of plant species<sup>13</sup>, such economies of scale are  
63 apparently advantageous only under certain circumstances. What those circumstances  
64 are remains, so far, under debate.

65 The environmental stress hypothesis<sup>14</sup> suggests that masting behaviour should be  
66 stronger under unfavourable growing conditions or limitation of resources, conditions  
67 under which *economies of scale* should be more beneficial<sup>3,12,15</sup>. This is because plants  
68 growing in unfavourable environments presumably experience more difficulties in  
69 acquiring the required resources to reproduce, as suggested by the *resource*  
70 *accumulation* hypothesis<sup>16,17</sup>. According to this hypothesis, plants growing under  
71 favourable conditions will be able to accumulate the required amount of resources  
72 every year and, therefore, present a regular pattern in seed production, without  
73 exhibiting any underlying negative temporal autocorrelation that could indicate resource  
74 depletion after reproduction<sup>16</sup>. The opposite is true for plants growing in unfavourable  
75 conditions, which will exhibit high interannual variability and negative temporal  
76 autocorrelation in seed production due to potential resource depletion after seeding.  
77 However, there is no current empirical evidence suggesting that species with higher  
78 interannual variability in fruit production are more likely to exhibit negative temporal  
79 autocorrelation than species that produce seeds more regularly<sup>5</sup>. On the other hand,  
80 weather variability has been found to be a key factor driving interannual variability in  
81 fruit production in many plant species<sup>12,18–21</sup>. Temporal patterns in weather events (i.e.,  
82 temporal variability and autocorrelation) could, therefore, potentially shape the temporal  
83 patterns of fruit production<sup>22</sup>.

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<sup>23-25</sup>. Together with carbon, they are the basis of ecological  
87 stoichiometry<sup>26,27</sup> and are fundamental parts of the *elementome* or the *biogeochemical*  
88 *niche*<sup>28</sup>, useful for inferring ecological traits from the elemental composition of  
89 organisms<sup>29</sup>. Carbon (C), and especially N and P have been suggested to be potential  
90 resources determining seed production and masting behaviour<sup>15,30-32</sup> because seeds  
91 and fruits are enriched with N and P compared to vegetative tissues<sup>33</sup>. Low foliar  
92 concentrations of N and P would imply lower photosynthetic rates<sup>23</sup> 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<sup>34-36</sup>. 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<sup>37-40</sup> and to relate to reproductive effort<sup>36</sup> and ecological  
101 strategies<sup>28</sup>. The lower N:P ratio of seeds compared to vegetative tissues suggest that  
102 nutrient imbalances may constrain reproduction more than growth<sup>38</sup>. Previous studies  
103 have reported that plants and shoots producing flowers often exhibit lower N:P ratios  
104 than those that do not<sup>38,41</sup>, 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)<sup>5</sup>. 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<sup>42,43</sup>, 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<sup>44</sup> PV, see **Methods**) in seed production is evolutionary conserved  
126 (**Extended Data Figure 1a**), showing a strong phylogenetic signal<sup>45</sup>. In contrast, lag-1  
127 temporal autocorrelation (AR1, indicating potential resource depletion when it takes  
128 negative values) is not phylogenetically conserved. Additionally, temporal variability  
129 and autocorrelation are not evolutionary correlated. Hence, species exhibiting higher  
130 temporal variability do not necessarily exhibit any particular pattern of temporal  
131 autocorrelation (**Extended Data Figure 1b**). Masting intensity, defined as D in this  
132 study (see **Methods**), accounted for both features of masting behaviour (**Figure 1**),  
133 temporal variability and potential resource depletion (negative AR1 coefficients), hence  
134 defining masting behaviour more broadly than the coefficient of variation (CV) alone, as  
135 it is typically assessed<sup>42</sup>. Masting intensity was also preserved phylogenetically (**Figure**  
136 **1**). 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**).

138 *Estimating controls and the mode of evolution of masting behaviour*

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 ( $\beta=0.22 \pm 0.08$ ,  $t=2.96$ ,  $P=0.004$ ,  $\lambda=0.58$ ,  $N=168$   
156 species). Potential resource depletion was more likely to occur in species living in  
157 climates exhibiting negative temporal autocorrelation in annual precipitation (**Table 1**).  
158 Interestingly, the model also showed a positive interaction between foliar N and P,  
159 indicating that potential resource depletion after seeding was more likely to occur in  
160 species with low foliar N and P.

161 Our analyses also revealed the evolutionary processes linking masting behaviour and  
162 foliar nutrient concentrations (**Extended Data Figure 2**). We found that adaptive  
163 processes - Ornstein-Uhlenbeck (OU) models based on ancestral character  
164 reconstructions (**Extended Data Figure 3**) - are the models that better explain current

165 patterns in masting intensity, linked to foliar nutrient concentrations. Adaptive OU  
166 models explaining evolutionary history of masting intensity with N, P and N×P (a  
167 measure of total N and P foliar concentration) assumed that species evolved toward  
168 different optimum values depending on whether they present high or low masting  
169 intensity (masting and non-masting species) (OUM model). However, a single optimum  
170 for all species was equally likely for foliar N, P and N×P (less than 2 units of AICc  
171 between models were found, OU1, see **Methods**). Nonetheless, given that OUM  
172 models with different optimum values performed equally well for foliar N, P and N×P  
173 (**Extended Data Figure 2**), OUM models are used to illustrate our results. The model  
174 that best fitted the data for foliar N:P was an adaptive OU model with different optimum  
175 and phenotypic variation for high and low masting intensity species (OUMV model).

176 Results from OU models indicated that masting species had, on average,  $9.5 \pm 0.4\%$   
177 and  $18.3 \pm 0.5\%$  lower foliar N and P concentrations, respectively, than non-masting  
178 species (**Figure 3, Extended Data Figure 4**). Foliar N:P ratio was  $11.4 \pm 0.2\%$  (mean  
179  $\pm$  standard error of the mean) higher in masting species, while N×P, combined  
180 availability of N and P, was  $28.7 \pm 1.0\%$  lower than in non-masting species. These  
181 results were consistent when using five different thresholds of masting intensity (see  
182 **Methods**) to classify species as masting or non-masting species (**Extended Data**  
183 **Figure 4**). Like masting intensity, both foliar N and P concentrations were preserved  
184 throughout the phylogeny (**Extended Data Figure 5**).

## 185 **Discussion**

### 186 *The role of foliar nutrients in seed production*

187 Our results suggest that masting intensity co-evolved with species-specific optimal  
188 foliar N and P concentrations and that species with lower N and especially lower P, and  
189 therefore high N:P, exhibit higher masting intensity (**Figure 3**). Hence, our analyses  
190 supported our initial hypothesis stating that masting behaviour evolved predominantly

191 in plant species with low foliar N and P concentrations and high N:P ratios. This  
192 observed evolutionary pattern may have originated because of different underlying  
193 mechanisms driven by environmental and physiological constraints. One potential  
194 mechanism explaining these findings could be the physiological role of foliar N and P  
195 concentrations in plants. Foliar N is well known for being the primary limiting nutrient for  
196 reproduction<sup>34,35</sup> and vegetative growth<sup>46,47</sup>. Elevated foliar P concentrations, and low  
197 N:P ratios, have been shown to allow larger seed crops in multiple species<sup>15,36,41,48</sup>,  
198 coinciding with fast growing species according to the *growth rate* hypothesis<sup>26</sup>. P is also  
199 essential to maintain water-use efficiency and growth, particularly during drought  
200 conditions<sup>49</sup>. Both nutrients are essential elements of ribosomes and, therefore, play a  
201 major role in organismal metabolism<sup>50</sup>. The production of seeds, which are structures  
202 enriched with N and P<sup>33</sup>, may potentially benefit from high concentrations of nutrients  
203 even more than vegetative tissues.

204 Low foliar N and P concentrations and high N:P imbalance are often indicative of  
205 unfavourable environments for plant growth<sup>15,51,52</sup>, such as infertile soils. These poor  
206 growing conditions are often related to dry or cold climates where decomposition of  
207 organic matter is constrained, rates of nutrient mineralisation and weathering are  
208 low<sup>49,53</sup>, or disturbances (e.g., wildfires) are frequent<sup>54</sup>. However, differences in foliar N  
209 and P concentrations may not always reflect differences in nutrient availability across  
210 species, as coexisting species may have different elemental compositions (the  
211 *biogeochemical niche* hypothesis<sup>28</sup>). Nonetheless, plants with high foliar N and P  
212 concentrations must either be growing in environments without nutrient limitations or  
213 have developed mechanisms that allow them to sustain high foliar nutrient  
214 concentrations even if they are growing under unfavourable conditions. In any case,  
215 these higher concentrations of nutrients should confer a competitive advantage in  
216 terms of C acquisition, because higher N and P concentrations are, on average, linked  
217 to higher photosynthetic rates<sup>23</sup>.

218 *Evolutionary history of masting intensity and foliar nutrients*

219 Being capable to invest more in reproduction does not explain masting behaviour by  
220 itself, because equal average seed crops over time could lead to different reproductive  
221 behaviours<sup>15</sup>. The necessary link between the ecological stoichiometry and masting  
222 theoretical backgrounds lies in the *resource accumulation* hypothesis<sup>16,17</sup>. Plant species  
223 with lower or imbalanced availability of N and P may present more difficulties in  
224 acquiring the necessary amount of C, N and P to successfully produce seeds regularly,  
225 thereby mechanistically producing a reproductive behaviour aligned with high masting  
226 intensity: high interannual variability and negative temporal autocorrelation (i.e.,  
227 potential resource depletion). The combination of low and imbalanced nutrient  
228 availability, causing high variability in seed production and potential resource depletion  
229 after crops, and environmental variability that synchronises the reproduction of  
230 individuals through weather cues<sup>7,19</sup> would finally shape the reproductive behaviour of  
231 masting species. In fact, our results also revealed that mean annual precipitation, and  
232 its temporal variability and autocorrelation, are related to the reproductive behaviour of  
233 plant species (**Table 1**). These results indicate that even nutrient-rich species can  
234 present masting behaviour if they grow under climates with highly fluctuating weather  
235 conditions. Therefore, we suggest that the interaction between weather conditions and  
236 the availability of nutrients, both conditioning photosynthetic rates, are the triggering  
237 factor of the common nonlinear (often exponential-like) response<sup>22</sup> between seed  
238 production and weather variability in masting species<sup>8,18,21</sup>.

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

245 nutrient-poor or nutrient-imbalanced species, the pressure to exhibit more cost-efficient  
246 reproduction may have selected such species to produce fewer but larger reproductive  
247 events in order to take advantage of one or more *economies of scale*<sup>6,7,11</sup>. As a side  
248 effect of these massive reproductive events, negative temporal autocorrelation would  
249 also have appeared in masting species because of potential resource depletion  
250 (**Extended Data Figure 1**). Hence, these particular traits would have been preserved  
251 throughout evolutionary history (**Figure 1**) because foliar functional traits and masting  
252 intensity have co-evolved (**Figure 3, Extended Data Figure 4**). Nonetheless, our  
253 results do not discard other potential selective pressures that may have triggered the  
254 evolution of masting behaviour. Some species may have been selected to mast to  
255 improve their pollination efficiency<sup>55</sup>, to escape seed predation from voracious  
256 predators<sup>8,9</sup> or because of interspecific competition in different ways (e.g., seedling  
257 establishment). Also, a selective pressure towards reproducing more constantly could  
258 happen in animal-pollinated species, where a more constant production of flowers  
259 would favour populations of pollinators and, hence, pollination. Further research on  
260 reproductive behaviour of early plants, such as bryophytes<sup>56</sup>, and taxa from different  
261 realms using concepts from the masting literature may facilitate better understanding of  
262 the evolution of different reproductive behaviours in nature.

## 263 **Methods**

### 264 Datasets

#### 265 *Masting database*

266 Data on interannual reproductive effort (seed or fruit production) were compiled from  
267 Web of Science searches, scanning the literature cited of published papers to look for  
268 more records of reproductive effort, contacting managers of wildlife surveys, forestry  
269 districts, and regional seed surveys, and soliciting datasets in the Ecolog listserv

270 (<https://listserv.umd.edu/archives/ecolog-l.html>). See Pearse et al.<sup>14</sup> for more  
271 information on data collection methods and characteristics of the dataset.

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

281 Overall, the reproductive effort dataset contained 1084 records of reproductive effort  
282 including 363 plant species (trees, shrubs, vines, grasses and herbs) from 205 studies,  
283 ranging from 1900 to 2014 and covering the six majorly vegetated continents (Africa  
284 (17), North America (466), Europe (280), Japan (68), New Zealand (67), Central  
285 America (118) and other regions (68)). On average, records were 11.9 years long,  
286 although 131 studies had more than 20 years of data<sup>14</sup>.

287 For each site and species, we calculated the proportional variability index in seed  
288 production (PV)<sup>44</sup> as a measure of temporal variability. The PV index overcomes  
289 several statistical and mathematical issues of the CV index<sup>44</sup>. The PV index was  
290 calculated, for each time series, as:

$$291 \quad PPPP = \frac{2 \sum zz}{n(n-1)}$$

292 Where z is calculated as:

$$293 \quad zz = 1 - \frac{\min(z_i, z_j)}{\max(z_i, z_j)}$$

294 Where “z” represents the list of individual values (seed production per year), from each  
 295 time series, from which to calculate the pairwise comparisons and “n” indicates the  
 296 number of values in a time series. We also calculated the lag-1 temporal  
 297 autocorrelation (AR1) as a measure of potential resource depletion using the *acf*  
 298 function in R, and the consecutive disparity index (D)<sup>42,43</sup> as a measure of masting  
 299 intensity. We defined masting intensity as D because, like the PV index, this index also  
 300 overcomes several statistical and mathematical limitations of the coefficient of variation  
 301 (CV = standard deviation × mean<sup>-1</sup>), including dependence on the mean, dependence  
 302 on the length of the time series, and bias associated with non-Gaussian data  
 303 commonly used to describe masting<sup>13,14</sup>. More importantly, we used D because it  
 304 combines two of the main features describing masting behaviour: temporal variability  
 305 and lag-1 autocorrelation (AR1) in seed production<sup>42</sup>. D is defined as:

$$306 \quad D = \frac{1}{n-1} \sum_{i=1}^{n-1} \ln \frac{p_{i+1} + k}{p_i + k}$$

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

319 *Climate, productivity and foliar nutrients*



320 We extracted mean annual temperature (MAT, °C) and precipitation (MAP, mm yr<sup>-1</sup>)  
321 and their seasonality (MAT<sub>s</sub> [standard deviation of monthly values × 100] and MAP<sub>s</sub>  
322 [CV]) for each location in our masting database from the WorldClim2 database<sup>57</sup>. The  
323 climate database contains long-term means (1950-2000), calculated on a 30 arc-  
324 second grid. Data for variability and autocorrelation for temperature and precipitation  
325 was extracted from the CRU TS v3.25 dataset<sup>58</sup>. To estimate site productivity we used  
326 a remotely-sensed gross primary production (GPP) database<sup>59</sup>. For annual  
327 temperature and precipitation of the CRU TS and the GPP global databases we  
328 calculated D, PV and AR1 indices for each pixel. We then extracted climate (i.e.,  
329 MAT<sub>D</sub>, MAP<sub>D</sub>, MAT<sub>PV</sub>, MAP<sub>PV</sub>, MAT<sub>AR1</sub> and MAP<sub>AR1</sub>) and productivity (i.e., GPP<sub>D</sub>,  
330 GPP<sub>PV</sub> and GPP<sub>AR1</sub>) data for each site and species in our masting database and  
331 calculated the average per species (**Extended Data Figure 6**). We used these  
332 variables in our statistical analyses to control for site-specific differences in temporal  
333 variability and autocorrelation patterns of climate and productivity.

334 Data for foliar concentration of N and P for the species in our database were gathered  
335 from the TRY trait database (<https://www.try-db.org/TryWeb/Home.php>)<sup>60</sup>, the BIEN  
336 database (<http://bien.nceas.ucsb.edu/bien/>)<sup>61</sup>, the ICP Forests database on foliar  
337 elemental concentration<sup>62</sup> ([www.icp-forests.net](http://www.icp-forests.net)), and the Catalan Forest Inventory  
338 (<http://www.creaf.uab.cat/iefc/>). To estimate an average value per species, we first  
339 calculated the mean value per species and database. We then merged all databases  
340 and calculated the mean values per species. Species names in our database were  
341 checked and corrected using The Plant List database in the R package *Taxonstand*<sup>63</sup>.  
342 Phylogenetic analyses were performed using the plant phylogeny provided by Qian &  
343 Jin (2016). Out of the 363 species in the masting database, 219 species (~60%) names  
344 matched those in the phylogenetic tree, and therefore, only those were used for further  
345 analyses. Analyses using foliar N and P data were restricted to the 168 species (~46%)  
346 for which we could find data.

347 Data analyses

348 *Evolutionary link between masting intensity, temporal variability and autocorrelation*

349 To explore how well the phylogenetic ancestry can explain masting behaviour, we first  
350 estimated the phylogenetic signal (i.e. tendency for related species to resemble each  
351 other more than they resemble species drawn at random from the phylogenetic tree) of  
352 masting intensity (D) , PV and AR1 using the *phylosig* function in the R<sup>65</sup> package  
353 *phytools*<sup>66</sup>. Phylogenetic signal was assessed by the lambda ( $\lambda$ ) metric, which varies  
354 from 0 (where phylogenetic and trait similarity are totally independent) to 1 (where the  
355 traits are completely explained by shared ancestry). We then used continuous mapped  
356 phylogenetic trees (*contMap* function in R package *phytools*) to visualise their  
357 phylogenetic signal. Finally, we explored the evolutionary relationship between  
358 temporal variability, temporal autocorrelation and masting intensity using pairwise  
359 correlations correcting for the phylogeny. Relationships were shown using  
360 phylomorphospace plots<sup>66</sup>, which depicts each species as a data point in a trait space,  
361 together with the phylogenetic relationship of each species-point.

362 *Controls of masting intensity and its mode of evolution*

363 We first tested whether masting intensity (D) was related to climate, productivity, foliar  
364 N and P concentrations and their interaction. To do so, we fitted phylogenetic linear  
365 models in which the response variable was masting intensity (D) and the predictors  
366 were foliar N and P concentrations and their interaction, MAT, MAP, MAT<sub>s</sub>, MAP<sub>s</sub>,  
367 MAT<sub>D</sub> and MAP<sub>D</sub> for climate and GPP and GPP<sub>D</sub> for productivity. Phylogenetic models  
368 were fitted optimising lambda (i.e., the strength of phylogenetic signal) and using the  
369 *phylolm* function in the R *phylolm* package<sup>67</sup>. The final model was achieved by  
370 removing the least significant terms from the full model, in a step-by-step process, until  
371 all variable estimates were significant. The same models were fitted for the PV and  
372 AR1, but changing the predictors from D to PV or AR1 respectively (e.g., MAT<sub>PV</sub>

373 instead of  $MAT_D$  when predicting PV). Because the CV has been widely used to  
374 assess temporal variability, we also fitted a model using CV as the predictor variable to  
375 compare its results with those of the model using the PV index. Masting intensity and  
376 PV were transformed to natural logarithms to normalise model residuals. We used the  
377 package *visreg*<sup>68</sup> to visualise model results.

### 378 *Evolution of masting intensity and foliar N and P and their interaction*

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

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

397 To reconstruct ancestral states of masting behaviour, for each of the five classifications  
398 we performed stochastic character mappings<sup>69</sup>, which reconstructs the state of the

399 ancestors of a phylogeny based on the observed traits of the current species and the  
400 phylogenetic structure. Ancestral reconstructions were performed using the  
401 *make.simmap* function in the *phytools* R package<sup>66</sup>, simulating 1000 stochastic  
402 ancestral reconstructions, specifying equal rates of transition amongst the character  
403 states and using the “*mcmc*” method.

404 Once we had the 1000 stochastic character mappings for each masting classification,  
405 we performed generalised Ornstein–Uhlenbeck Hansen models to test whether the  
406 inferred evolutionary trajectories in foliar concentrations of N, P, N:P and N×P  
407 (hereafter “continuous traits”) were associated with the two alternative masting  
408 behaviour strategies (hereafter “ancestral states”) and whether they followed an  
409 adaptive (Ornstein–Uhlenbeck: OU) or random (Brownian motion—BM) model of  
410 evolution<sup>70–72</sup>. To do so, we used the OU function from *OUIwie* R package<sup>73</sup>. We fitted  
411 five different models using the 1000 ancestral reconstructions mentioned above for  
412 each classification. The five different models represent different types of underlying  
413 evolutionary processes, being: i) single-state BM models (BM1), where evolutionary  
414 rates for the continuous traits are equal for all ancestral states, ii) BM models with  
415 different evolutionary rates for each ancestral state (BMS), iii) OU models with a single  
416 optimal value for the continuous traits for all ancestral states (OU1), iv) OU models with  
417 different optimal values but a single alpha (the strength of the pull towards the optimal  
418 values of the trait) and single theta (the rate of phenotypic variation around the optimal  
419 value) for each state (OUM), and v) OU models that assumed different optimal values  
420 with multiple rates of phenotypic evolution (theta) for each state (OUMV).

421 Models containing negative eigenvalues (non-sound models) were deleted when  
422 summarising our results<sup>29</sup>. Different evolutionary models were compared using second-  
423 order Akaike information criterion (AICc) amongst all sound models. Those models with  
424 the lowest AICc were considered to be those that fitted the data best. For models  
425 assuming different optimal values of foliar N, P, N:P and N×P for masting and non-

426 masting species (i.e., OUM and OUMV models) we calculated the geometric mean of  
427 the percentage differences of each model. Statistical differences in optimal values  
428 estimated between subsets of masting and non-masting species by the OU models  
429 with different state means (OUM and OUMV) were tested using paired *t*-tests. Given  
430 that results pointed out to the same direction (see **Extended data**) for all masting  
431 intensity thresholds, we only show those from the intermediate (0% to 20% for non-  
432 masting and 80% to 100% for masting). These analyses used the 168 species for  
433 which we had data for masting intensity and foliar N and P concentrations. All statistical  
434 analyses were performed with R statistical software version 3.5.1<sup>65</sup>.

#### 435 **Data availability**

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

440

441 **References:**

- 442 1. Salisbury, E. *The reproductive capacity of plants*. (Bell, 1942).
- 443 2. Silvertown, J. W. The evolutionary ecology of mast seeding in trees. *Biol. J. Linn.*  
444 *Soc.* **14**, 235–250 (1980).
- 445 3. Kelly, D. & Sork, V. L. Mast seeding in perennial plants: why, how, where? *Annu.*  
446 *Rev. Ecol. Syst.* **33**, 427–447 (2002).
- 447 4. Waller, D. M. Models of mast fruiting in trees. *J. Theor. Biol.* **80**, 223–232 (1979).
- 448 5. Pearse, I. S., LaMontagne, J. M., Lordon, M. & Koenig, W. D. Biogeography and  
449 phylogeny of masting: Do global patterns fit functional hypotheses? *J. Ecol.*
- 450 6. Norton, D. A. & Kelly, D. Mast Seeding Over 33 Years by *Dacrydium*  
451 *cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: The Importance of  
452 Economies of Scale. *Funct. Ecol.* **2**, 399–408 (1988).
- 453 7. Pearse, I. S., Koenig, W. D. & Kelly, D. Mechanisms of mast seeding: resources,  
454 weather, cues, and selection. *New Phytol.* **212**, 546–562 (2016).
- 455 8. Espelta, J. M., Cortés, P., Molowny-horas, R., Sánchez-humanes, B. & Retana,  
456 J. Masting Mediated by Summer Drought Reduces Acorn Predation in  
457 Mediterranean Oak Forests. *Ecology* **89**, 805–817 (2008).
- 458 9. Espelta, J. M. *et al.* Beyond predator satiation: Masting but also the effects of  
459 rainfall stochasticity on weevils drive acorn predation. *Ecosphere* **8**, e01836  
460 (2017).
- 461 10. Donaldson, J. S. Mast-seeding in the cycad genus *Encephalartos*: a test of the  
462 predator satiation hypothesis. *Oecologia* **94**, 262–271 (1993).
- 463 11. Smith, C. C., Hamrick, J. L. & Kramer, C. L. The Advantage of Mast Years for  
464 Wind Pollination. *The American Naturalist* **136**, 154 (1990).
- 465 12. Fernández-Martínez, M., Belmonte, J., Maria Espelta, J. & Espelta, J. M.  
466 Masting in oaks: Disentangling the effect of flowering phenology, airborne pollen  
467 load and drought. *Acta Oecologica* **43**, 51–59 (2012).
- 468 13. Herrera, C., Jordano, P., Guitián, J. & Traveset, A. Annual variability in seed  
469 production by woody plants and the masting concept: reassessment of principles  
470 and relationship to pollination and seed dispersal. *Am. Nat.* **152**, 576–594  
471 (1998).

- 472 14. Pearse, I. S., LaMontagne, J. M. & Koenig, W. D. Inter-annual variation in seed  
473 production has increased over time (1900–2014). *Proc. R. Soc. B Biol. Sci.* **284**,  
474 20171666 (2017).
- 475 15. Fernández-Martínez, M., Vicca, S., Janssens, I. A., Espelta, J. M. & Peñuelas, J.  
476 The role of nutrients, productivity and climate in determining tree fruit production  
477 in European forests. *New Phytol.* **213**, 669–679 (2016).
- 478 16. Isagi, Y., Sugimura, K., Sumida, a. & Ito, H. How Does Masting Happen and  
479 Synchronize? *J. Theor. Biol.* **187**, 231–239 (1997).
- 480 17. Ye, X. & Sakai, K. A new modified resource budget model for nonlinear  
481 dynamics in citrus production. *Chaos, Solitons & Fractals* **87**, 51–60 (2016).
- 482 18. Pérez-Ramos, I. M., Ourcival, J. M., Limousin, J. M. & Rambal, S. Mast seeding  
483 under increasing drought: results from a long-term data set and from a rainfall  
484 exclusion experiment. *Ecology* **91**, 3057–68 (2010).
- 485 19. Fernández-Martínez, M., Vicca, S., Janssens, I. A., Espelta, J. M. & Peñuelas, J.  
486 The North Atlantic Oscillation synchronises fruit production in western European  
487 forests. *Ecography (Cop.)*. **39**, 864–874 (2016).
- 488 20. Sork, V. L., Bramble, J. & Sexton, O. Ecology of mast-fruiting in three species of  
489 North American deciduous oaks. *Ecology* **74**, 528–541 (1993).
- 490 21. Perez-Ramos, I. M., Padilla-Díaz, C. M., Koenig, W. D. & Marañón, T.  
491 Environmental drivers of mast-seeding in Mediterranean oak species: Does leaf  
492 habit matter? *J. Ecol.* **103**, 691–700 (2015).
- 493 22. Fernández-Martínez, M., Bogdziewicz, M., Espelta, J. M. & Peñuelas, J. Nature  
494 beyond Linearity: Meteorological Variability and Jensen's Inequality Can Explain  
495 Mast Seeding Behavior. *Front. Ecol. Evol.* **5**, 1–8 (2017).
- 496 23. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–7  
497 (2004).
- 498 24. Domingues, T. F. *et al.* Co-limitation of photosynthetic capacity by nitrogen and  
499 phosphorus in West Africa woodlands. *Plant, Cell Environ.* **33**, 959–980 (2010).
- 500 25. Field, C., Merino, J. & Mooney, H. a. Compromises between water-use efficiency  
501 and nitrogen-use efficiency in five species of California evergreens. *Oecologia*  
502 **60**, 384–389 (1983).
- 503 26. Elser, J. J. *et al.* Nutritional constraints in terrestrial and freshwater food webs.

- 504 *Nature* **408**, 578–580 (2000).
- 505 27. Sardans, J. *et al.* Factors influencing the foliar elemental composition and  
506 stoichiometry in forest trees in Spain. *Perspect. Plant Ecol. , Evol. Syst.* **18**, 52–  
507 69 (2016).
- 508 28. Peñuelas, J. *et al.* The bioelements, the elementome, and the biogeochemical  
509 niche. *Ecology* **100**, e02652 (2019).
- 510 29. Fernández-Martínez, M. *et al.* Nutrient-rich plants emit a less intense blend of  
511 volatile isoprenoids. *New Phytol.* **220**, 773–784 (2018).
- 512 30. Camarero, J. J., Albuixech, J., López-Lozano, R., Casterad, M. A. & Montserrat-  
513 Martí, G. An increase in canopy cover leads to masting in *Quercus ilex*. *Trees*  
514 **24**, 909–918 (2010).
- 515 31. Fernández-Martínez, M., Garbulsky, M., Peñuelas, J., Peguero, G. & Espelta, J.  
516 M. Temporal trends in the enhanced vegetation index and spring weather predict  
517 seed production in Mediterranean oaks. *Plant Ecol.* **216**, 1061–1072 (2015).
- 518 32. Sala, A., Hopping, K., McIntire, E. J. B., Delzon, S. & Crone, E. E. Masting in  
519 whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytol.* **196**,  
520 189–99 (2012).
- 521 33. Reekie, E. G. & Bazzaz, F. A. Reproductive effort in plants. II Does carbon  
522 reflect the allocation of other resources? *Am. Nat.* **129**, 897–906 (1987).
- 523 34. Miyazaki, Y. *et al.* Nitrogen as a key regulator of flowering in *Fagus crenata*:  
524 understanding the physiological mechanism of masting by gene expression  
525 analysis. *Ecol. Lett.* **17**, 1299–1309 (2014).
- 526 35. Han, Q., Kabeya, D., Iio, A., Inagaki, Y. & Kakubari, Y. Nitrogen storage  
527 dynamics are affected by masting events in *Fagus crenata*. *Oecologia* **174**, 679–  
528 687 (2013).
- 529 36. Fujita, Y. *et al.* Low investment in sexual reproduction threatens plants adapted  
530 to phosphorus limitation. *Nature* **505**, 82–6 (2014).
- 531 37. Sardans, J., Rivas-Ubach, A. & Peñuelas, J. The C:N:P stoichiometry of  
532 organisms and ecosystems in a changing world: A review and perspectives.  
533 *Perspect. Plant Ecol. Evol. Syst.* **14**, 33–47 (2012).
- 534 38. Güsewell, S. N:P ratios in terrestrial plants: Variation and functional significance.  
535 *New Phytologist* **164**, 243–266 (2004).



- 536 39. McGroddy, M. E., Daufresne, T. & Hedin, O. L. Scaling of C : N : P Stoichiometry  
537 in Forests Worldwide : Implications of Terrestrial Redfield- Type Ratios. *Ecology*  
538 **85**, 2390–2401 (2004).
- 539 40. Sardans, J. *et al.* Foliar and soil concentrations and stoichiometry of nitrogen  
540 and phosphorous across European *Pinus sylvestris* forests: relationships with  
541 climate, N deposition and tree growth. *Funct. Ecol.* **30**, 676–689 (2016).
- 542 41. Eckstein, R. L. & Karlsson, P. S. Above-ground growth and nutrient use by  
543 plants in a subarctic environment: effects of habitat, life-form and species. *Oikos*  
544 **79**, 311–324 (1997).
- 545 42. Fernández-Martínez, M., Vicca, S., Janssens, I. A., Martín-Vide, J. & Peñuelas,  
546 J. The consecutive disparity index, D, as measure of temporal variability in  
547 ecological studies. *Ecosphere* **9**, e02527 (2018).
- 548 43. Martín-Vide, J. Notes per a la definició d'un índex de «desordre» en  
549 pluviometria. *Soc. Catalana Geogr.* **7**, 89–96 (1986).
- 550 44. Heath, J. P. Quantifying temporal variability in population abundances. *Oikos*  
551 **115**, 573–581 (2006).
- 552 45. Losos, J. B. Phylogenetic niche conservatism, phylogenetic signal and the  
553 relationship between phylogenetic relatedness and ecological similarity among  
554 species. *Ecol. Lett.* **11**, 995–1003 (2008).
- 555 46. Elser, J. J. *et al.* Global analysis of nitrogen and phosphorus limitation of primary  
556 producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **10**, 1135–  
557 42 (2007).
- 558 47. LeBauer, D. S. & Treseder, K. K. Nitrogen limitation of net primary productivity in  
559 terrestrial ecosystems is globally distributed. *Ecology* **89**, 371–379 (2008).
- 560 48. Erel, R. Flowering and fruit set of olive trees. *Am. Soc.* **133**, 639–647 (2008).
- 561 49. Sardans, J. & Peñuelas, J. Drought changes phosphorus and potassium  
562 accumulation patterns in an evergreen Mediterranean forest. *Funct. Ecol.* **21**,  
563 191–201 (2007).
- 564 50. Elser, J. J. *et al.* Growth rate-stoichiometry couplings in diverse biota. *Ecol. Lett.*  
565 **6**, 936–943 (2003).
- 566 51. Fernández-Martínez, M. *et al.* Nutrient availability as the key regulator of global  
567 forest carbon balance. *Nat. Clim. Chang.* **4**, 471–476 (2014).

- 568 52. Nogueira, C. *et al.* Leaf nutrients, not specific leaf area, are consistent indicators  
569 of elevated nutrient inputs. *Nat. Ecol. Evol.* **3**, 400–406 (2019).
- 570 53. Smaill, S. J., Clinton, P. W., Allen, R. B. & Davis, M. R. Climate cues and  
571 resources interact to determine seed production by a masting species. *J. Ecol.*  
572 **99**, 870–877 (2011).
- 573 54. Saura-Mas, S. & Lloret, F. Linking post-fire regenerative strategy and leaf  
574 nutrient content in Mediterranean woody plants. *Perspect. Plant Ecol. Evol. Syst.*  
575 **11**, 219–229 (2009).
- 576 55. Kelly, D., Hart, D. & Allen, R. B. Evaluating the wind pollination benefits of mast  
577 seeding. *Ecology* **82**, 117–126 (2001).
- 578 56. Fernández-Martínez, M. *et al.* Towards a moss sclerophylly continuum:  
579 evolutionary history, water chemistry and climate control traits of hygrophytic  
580 mosses. *Funct. Ecol.* 1365-2435.13443 (2019). doi:10.1111/1365-2435.13443
- 581 57. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate  
582 surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
- 583 58. Harris, I., Jones, P. D. D., Osborn, T. J. J. & Lister, D. H. H. Updated high-  
584 resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *Int.*  
585 *J. Climatol.* **34**, 623 – 642 (2013).
- 586 59. Zhang, Y. *et al.* A global moderate resolution dataset of gross primary production  
587 of vegetation for 2000–2016. *Sci. Data* **4**, 170165 (2017).
- 588 60. Kattge, J. *et al.* TRY - a global database of plant traits. *Glob. Chang. Biol.* **17**,  
589 2905–2935 (2011).
- 590 61. Maitner, B. S. *et al.* The `bien` package: A tool to access the  
591 Botanical Information and Ecology Network (BIEN) database. *Methods Ecol.*  
592 *Evol.* **2017**, 1–7 (2017).
- 593 62. Rautio, P., Fürst, A., Stefan, K., Raitio, H. & Bartels, U. Sampling and Analysis of  
594 Needles and Leaves. *ICP Forests Manual XII*, 19 (2010).
- 595 63. Cayuela, L. & Oksanen, J. Taxonstand: Taxonomic Standardization of Plant  
596 Species Names. (2016).
- 597 64. Qian, H. & Jin, Y. An updated megaphylogeny of plants, a tool for generating  
598 plant phylogenies and an analysis of phylogenetic community structure. *J. Plant*  
599 *Ecol.* **9**, 233–239 (2016).

- 600 65. R Core Team. R: A Language and Environment for Stasitical Computing. (2018).
- 601 66. Revell, L. J. phytools: An R package for phylogenetic comparative biology (and  
602 other things). *Methods Ecol. Evol.* **3**, 217–223 (2012).
- 603 67. Tung Ho, L. S. & Ané, C. A linear-time algorithm for gaussian and non-gaussian  
604 trait evolution models. *Syst. Biol.* **63**, 397–408 (2014).
- 605 68. Breheny, P. & Burchett, W. Visualization of Regression Models Using visreg, R  
606 package version 2.2-0. (2015).
- 607 69. Bollback, J. P. SIMMAP: Stochastic character mapping of discrete traits on  
608 phylogenies. *BMC Bioinformatics* **7**, 1–7 (2006).
- 609 70. O’Meara, B. C., Ané, C., Sanderson, M. J. & Wainwright, P. C. Testing for  
610 different rates of continuous trait evolution using likelihood. *Evolution (N. Y.)*. **60**,  
611 922–933 (2006).
- 612 71. Thomas, G. H., Freckleton, R. P. & Székely, T. Comparative analyses of the  
613 influence of developmental mode on phenotypic diversification rates in  
614 shorebirds. *Proc. R. Soc. London B* **273**, 1619–24 (2006).
- 615 72. Beaulieu, J. M., Jhwueng, D. C., Boettiger, C. & O’Meara, B. C. Modeling  
616 stabilizing selection: Expanding the Ornstein-Uhlenbeck model of adaptive  
617 evolution. *Evolution (N. Y.)*. **66**, 2369–2383 (2012).
- 618 73. Beaulieu, J. M. & O’Meara, B. OUwie: Analysis of Evolutionary Rates in an OU  
619 Framework. (2016).
- 620

621 **Correspondence and requests for materials should be addressed to:**

622 Marcos Fernández-Martínez: marcos.fernandez-martinez@uantwerpen.be

623 **Acknowledgements**

624 This research was supported by the Spanish Government project CGL2016-79835-P  
625 (FERTWARM), the European Research Council Synergy grant ERC-2013-726 SyG-  
626 610028 IMBALANCE-P, and the Catalan Government project SGR 2017-1005.  
627 M.F.M. is a postdoctoral fellow of the Research Foundation – Flanders (FWO). MB was  
628 supported by (Polish) NSF grants Sonatina 2017/24/C/NZ8/00151 and Uwertura  
629 2018/28/U/NZ8/00003. The research was also supported by NSF grant DEB-1745496  
630 to J.M.L. and DEB-1256394 to W.D.K.

631

632 **Author Contributions**

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

636 **Competing interests**

637 The authors declare no competing interests.

638 **Figure captions**

639 **Figure 1: Masting behaviour intensity per species and its relationship with**  
640 **potential resource depletion (negative AR1) and temporal variability (PV) of**  
641 **reproductive effort.** Panel (a) shows the reconstructed evolution of masting intensity  
642 based on the disparity (D) index (using continuous character mapping, see **Methods**)  
643 and 219 species (n=219 biologically independent samples). The inset graph shows the  
644 distribution of values of masting intensity. Phylogenetic signal was estimated using  
645 *Pagel's lambda* ( $\lambda$ ). Panels (b) and (c) are phylomorphospace plots showing the  
646 evolutionary Pearson's correlation between masting intensity ( $\ln(D)$ , natural logarithm  
647 of disparity), potential resource depletion (AR1, negative values indicate potential  
648 resource depletion may happen) and temporal variability (PV). *t*-values of the  
649 correlations were -2.08 and 25.19 (217 degrees of freedom), for panels b and c,  
650 respectively. Plant silhouettes in panel (a) were drawn by FS and are available at  
651 PhyloPic (<http://phylopic.org>).

652 **Figure 2: 3D graph showing the interaction between foliar N and P on masting**  
653 **intensity.** Combined high foliar N and P concentrations decreased masting intensity,  
654 although the highest masting intensity was found in species with the highest N to P  
655 imbalances. Response surface of the negative interaction between N and P (see **Table**  
656 **1** for statistics) was estimated from a phylogenetic linear model based on 168 species  
657 (n=168 biologically independent samples). See **Methods** for further information about  
658 the models.

659 **Figure 3: Different optimum values of foliar N and P for subsets of masting and**  
660 **non-masting species.** Panel a shows model results for foliar N and P concentrations  
661 for a subset of species identified as masting (high masting intensity) and non-masting  
662 based on percentiles 20<sup>th</sup> and 80<sup>th</sup> of the D distribution (see **Methods**). Panel b shows  
663 model results for foliar N:P and N×P (overall nutrient availability) for masting and non-  
664 masting species. For panels a and b, 1000 and 927 (n=1000 and 927 independent

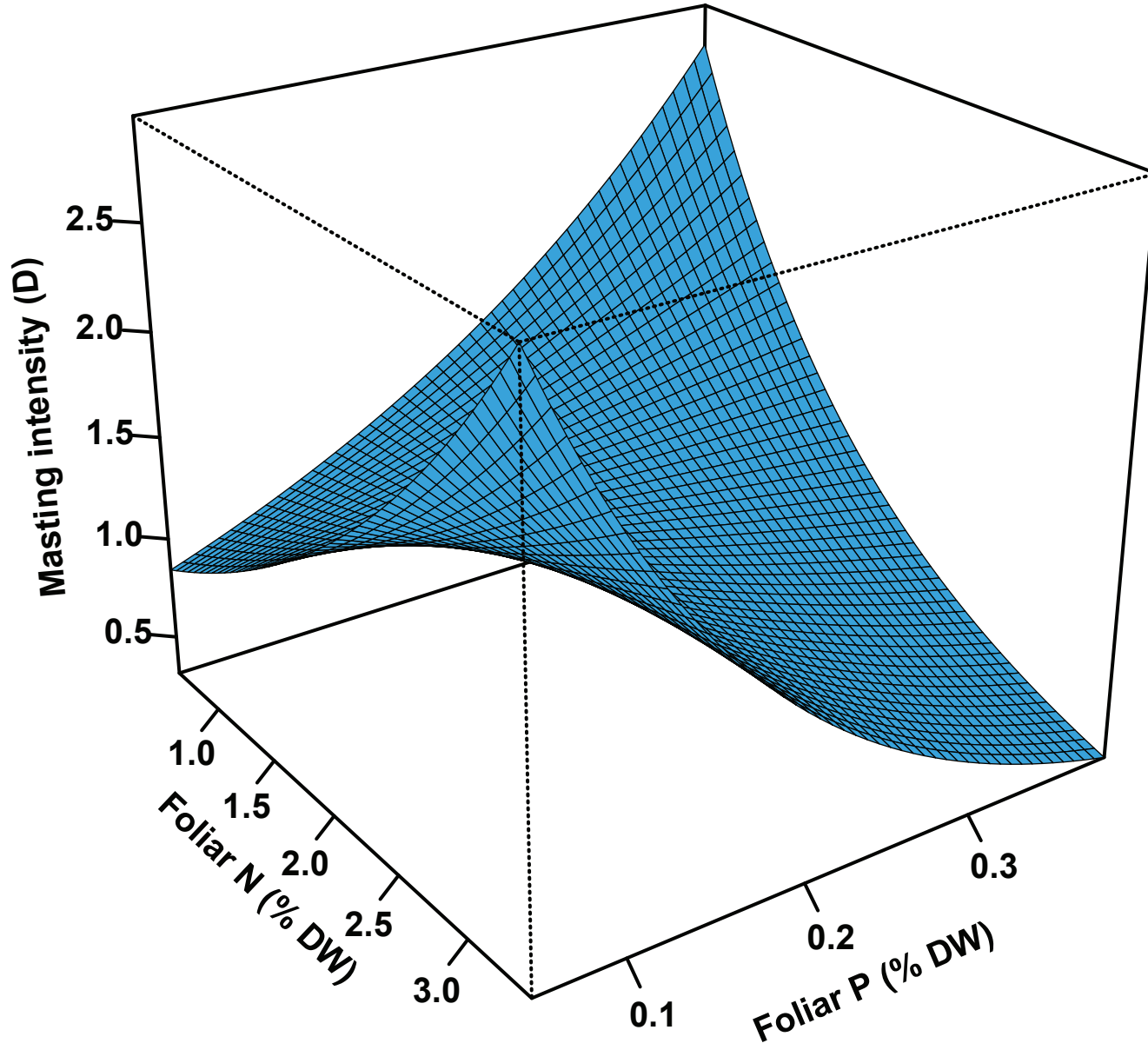
665 simulations) stochastic character mapping simulations were respectively used (see  
666 **Extended Data Figure 4**). For foliar N:P results from OUMV models were used, while  
667 for N, P and N×P, OUM models were used (see **Extended Data Figure 2** and  
668 **Extended Data Figure 4**). Differences between groups were calculated based on two-  
669 sided paired t-tests (t-values were -24.34, -47.44 [both on 999 DF], 66.05, and -39.24  
670 [both for 926 DF] for N, P, N:P and NxP respectively). Violin plots represent density  
671 distributions of the data. Boxplots indicate the median (centre line), hinges indicate 25<sup>th</sup>  
672 and 75<sup>th</sup> quartiles, whiskers indicate 1.5 times the inter-quartile range from the hinges,  
673 and points indicate values outside 1.5 times the inter-quartile range. See **Methods** for  
674 further information.

675 **Table 1: Model summary of the phylogenetic linear models based on 168**  
676 **species.** Masting intensity was defined as the D index, PV indicates temporal  
677 variability and AR1 potential resource depletion coefficient (i.e., negative values  
678 indicate potential resource depletion). Beta ( $\beta$ ) shows the standardised model  
679 coefficients, followed by the standard error of the mean (s.e.m), t-value ( $t$ ), the two-  
680 sided  $P$ -value ( $P$ ) and lambda ( $\lambda$ ) indicating the phylogenetic signal in the models  
681 (n=168 biologically independent samples). See **Methods** for further information.  
682 **Acronyms:** mean annual precipitation (MAP), foliar nitrogen (N), foliar phosphorus (P),  
683 mean annual temperature (MAT), temporal autocorrelation at lag 1 (AR1).

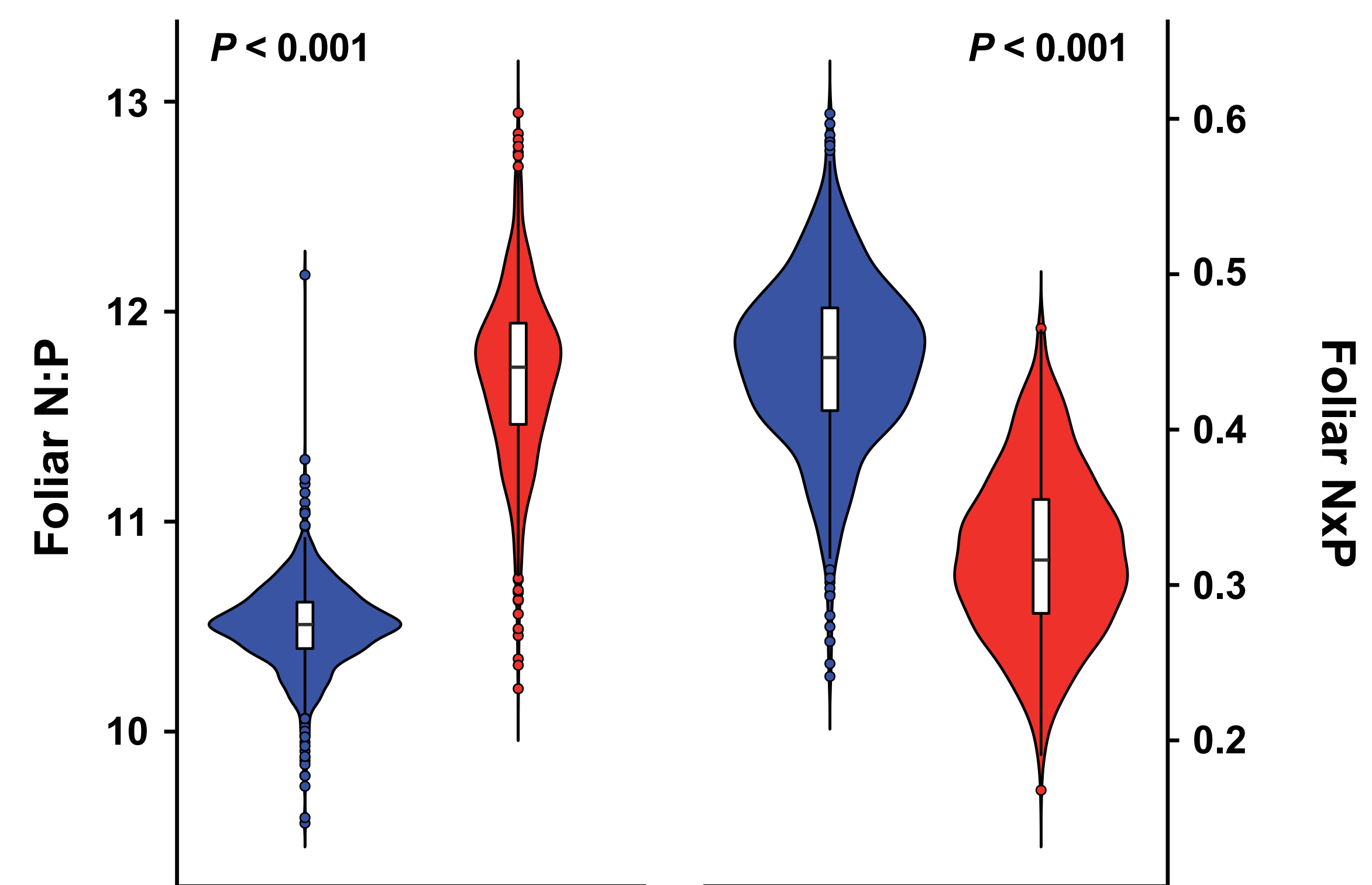
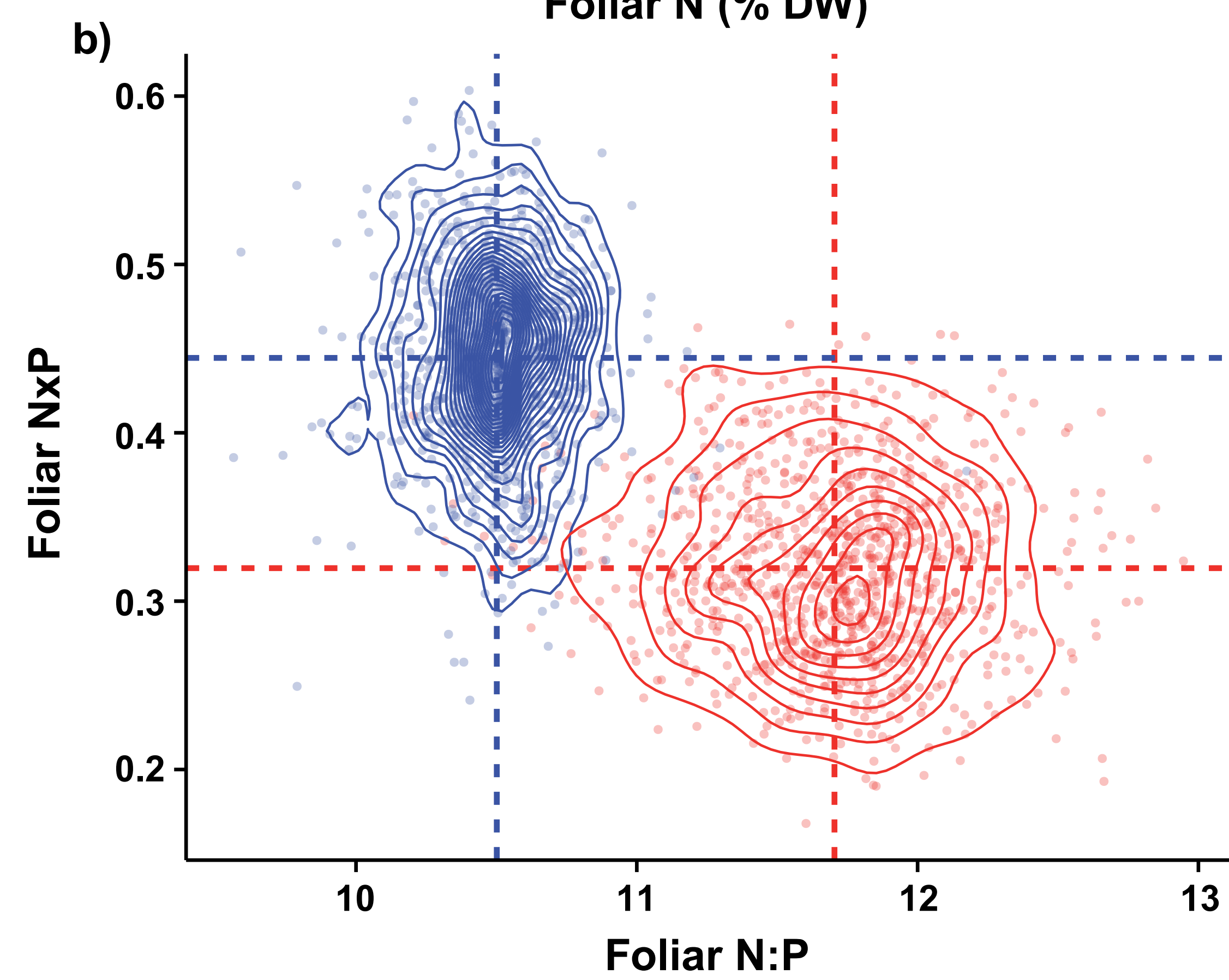
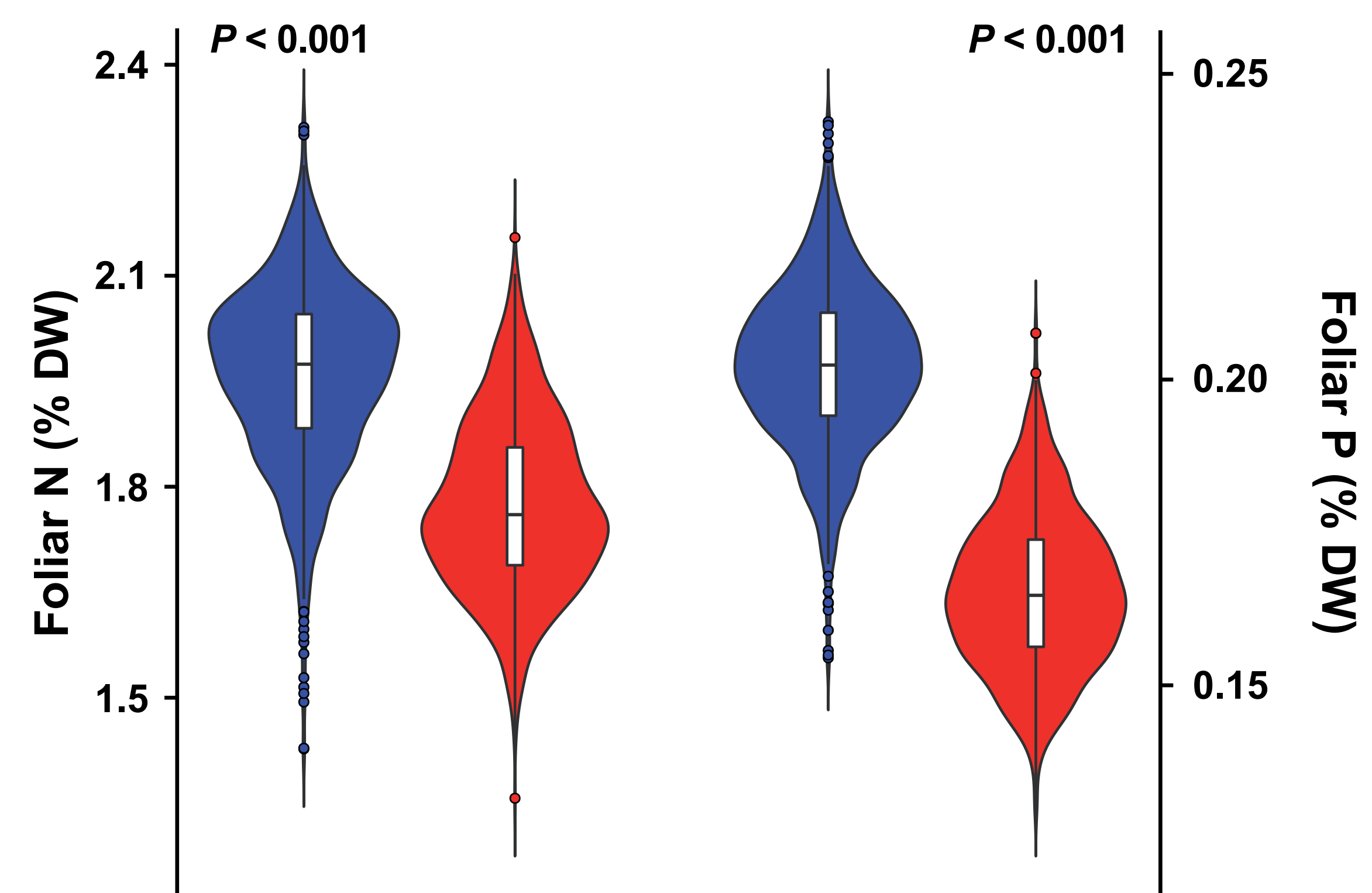
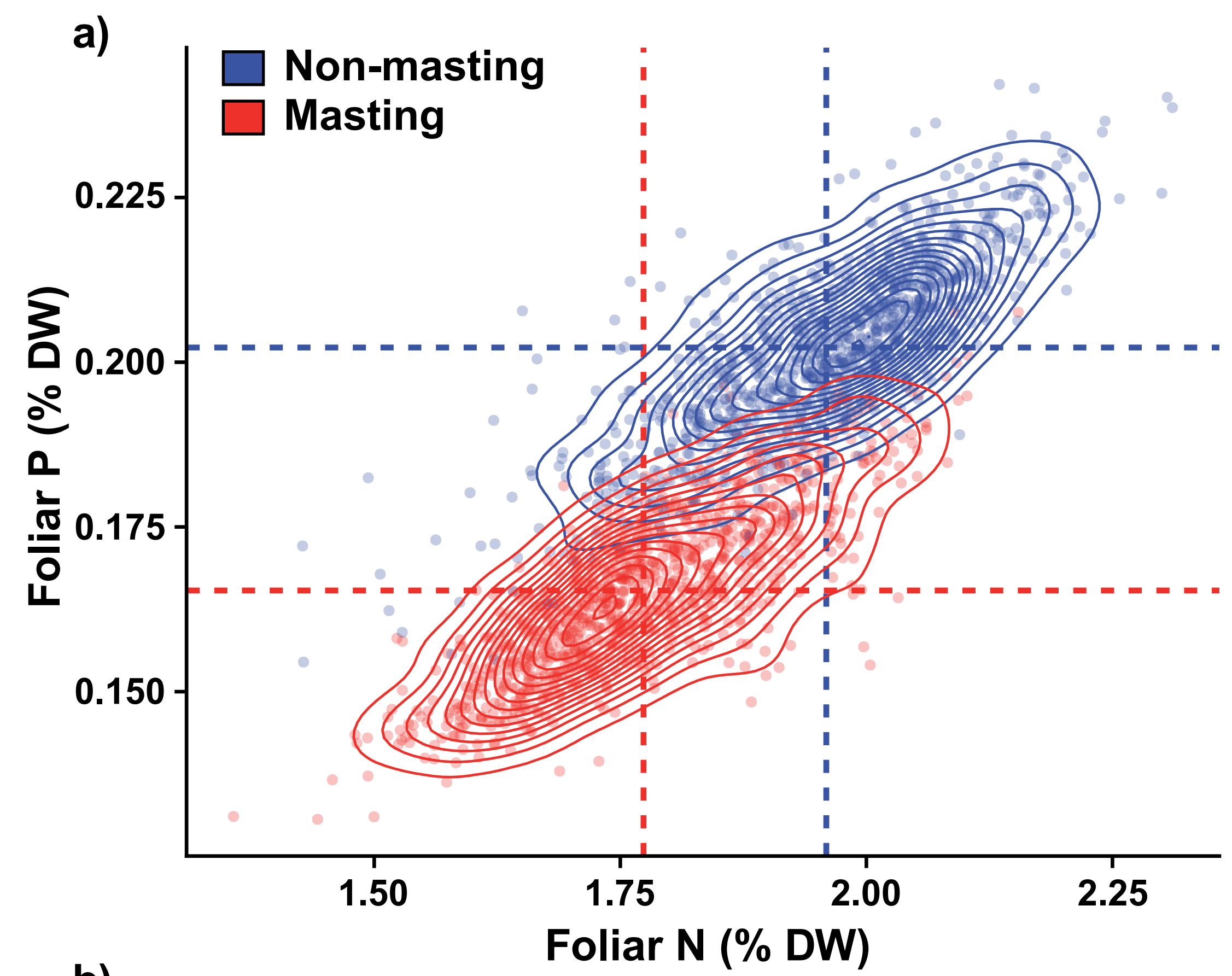










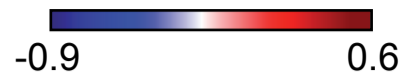


**Table 1**

	<b><math>\beta</math></b>	<b>s.e.m</b>	<b>t</b>	<b>P</b>	<b><math>\lambda</math></b>
<b><i>Masting intensity (D)</i></b>					
<b>MAP</b>	0.22	0.09	2.44	0.016	
<b>N</b>	0.04	0.10	0.38	0.708	
<b>P</b>	-0.04	0.10	-0.42	0.674	
<b>N×P</b>	-0.19	0.07	-2.76	0.007	0.47
<b><i>Temporal variability (PV)</i></b>					
<b>MAP<sub>PV</sub></b>	0.16	0.08	2.05	0.042	
<b>MAT</b>	-0.18	0.09	-2.07	0.040	
<b>P</b>	-0.16	0.08	-2.03	0.044	0.41
<b><i>Potential resource depletion (AR1)</i></b>					
<b>MAP<sub>AR1</sub></b>	0.27	0.08	3.42	0.001	
<b>N</b>	-0.09	0.10	-0.85	0.001	
<b>P</b>	-0.05	0.10	-0.45	0.008	
<b>N×P</b>	0.22	0.07	3.19	0.002	0.00

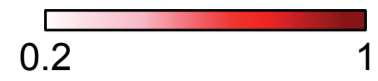
a)

Resource depletion

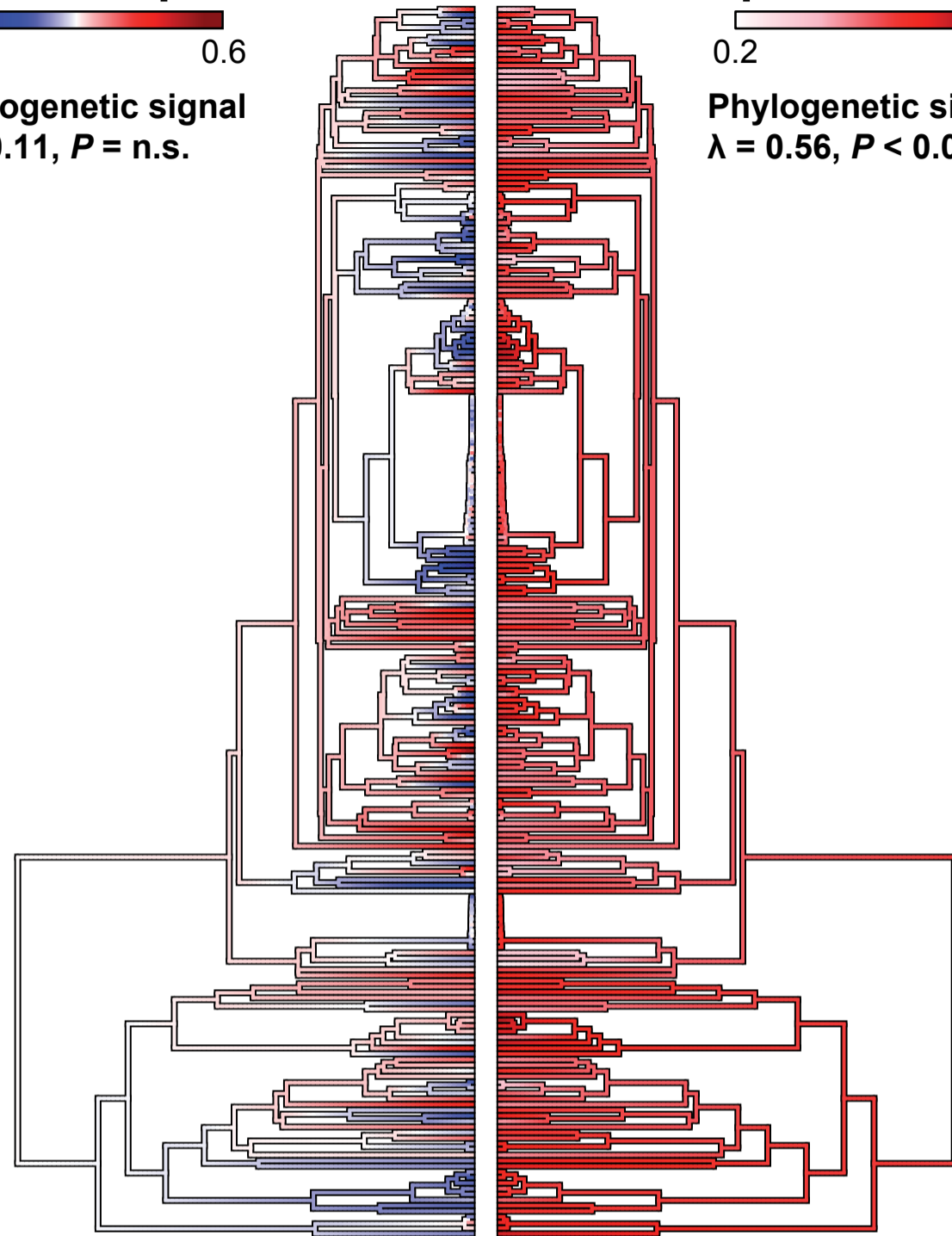


Phylogenetic signal  
 $\lambda = 0.11, P = \text{n.s.}$

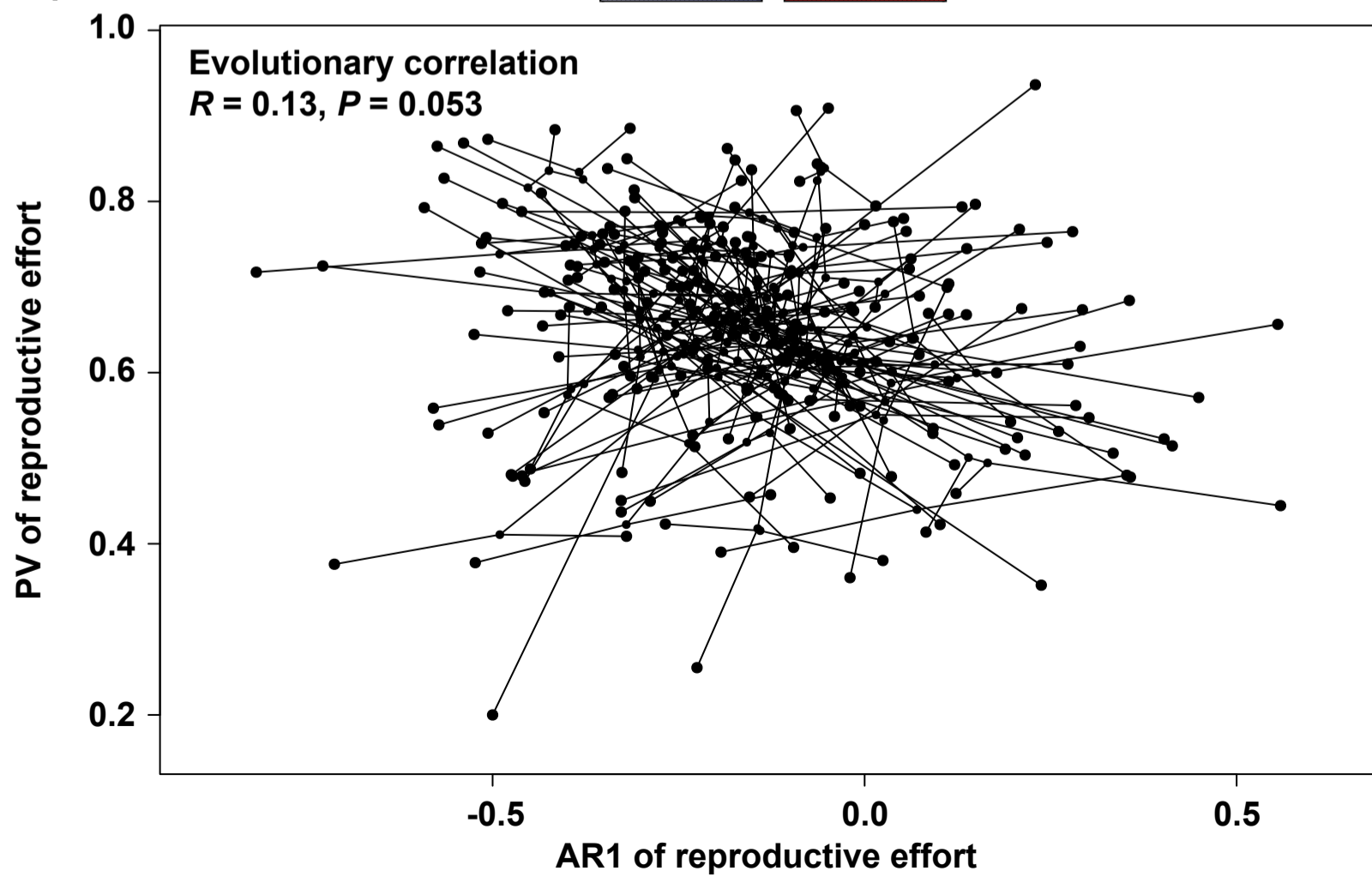
Temporal variability



Phylogenetic signal  
 $\lambda = 0.56, P < 0.001$

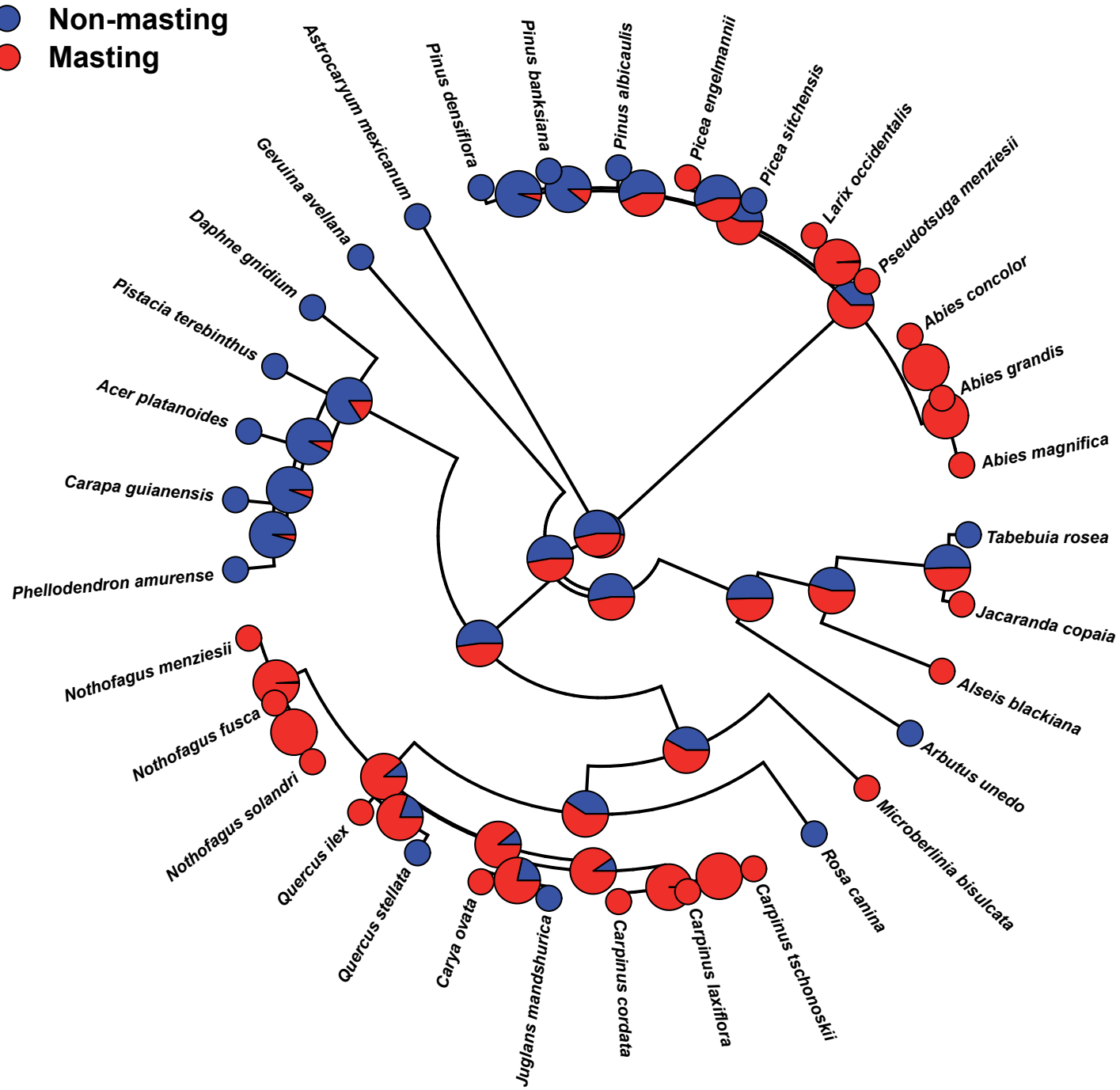


b)



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

● Non-masting  
● Masting



	Masting			Non-masting			M>N%	$\Delta M-N$	s.e.m	P (t-test)	$\Delta M-N\%$	s.e.m	n	Model
	2.5%	50%	97.5%	2.5%	50%	97.5%								
<b>33 - 66%</b>														
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
NxP	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
<b>25 - 75%</b>														
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%	<b>1000</b>	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%	<b>1000</b>	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%	<b>906</b>	OUMV
NxP	0.23	0.31	0.39	0.33	0.42	0.51	9.9%	-0.11	0.00	<0.001	-27.2%	0.8%	<b>1000</b>	OUM
<b>20 - 80%</b>														
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%	<b>1000</b>	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%	<b>1000</b>	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%	<b>927</b>	OUMV
NxP	0.22	0.32	0.42	0.33	0.45	0.54	11.9%	-0.13	0.00	<0.001	-28.7%	1.0%	<b>1000</b>	OUM
<b>15 - 85%</b>														
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%	<b>1000</b>	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%	<b>998</b>	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%	<b>890</b>	OUMV
NxP	0.21	0.30	0.41	0.38	0.49	0.59	3.80%	-0.19	0.00	<0.001	-38.7%	1.0%	<b>1000</b>	OUM
<b>10 - 80%</b>														
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%	<b>999</b>	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%	<b>999</b>	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%	<b>914</b>	OUMV
NxP	0.23	0.36	0.48	0.33	0.45	0.56	20.6%	-0.09	0.00	<0.001	-22.2%	2.0%	<b>1000</b>	OUM



a)

Foliar N (% DW)

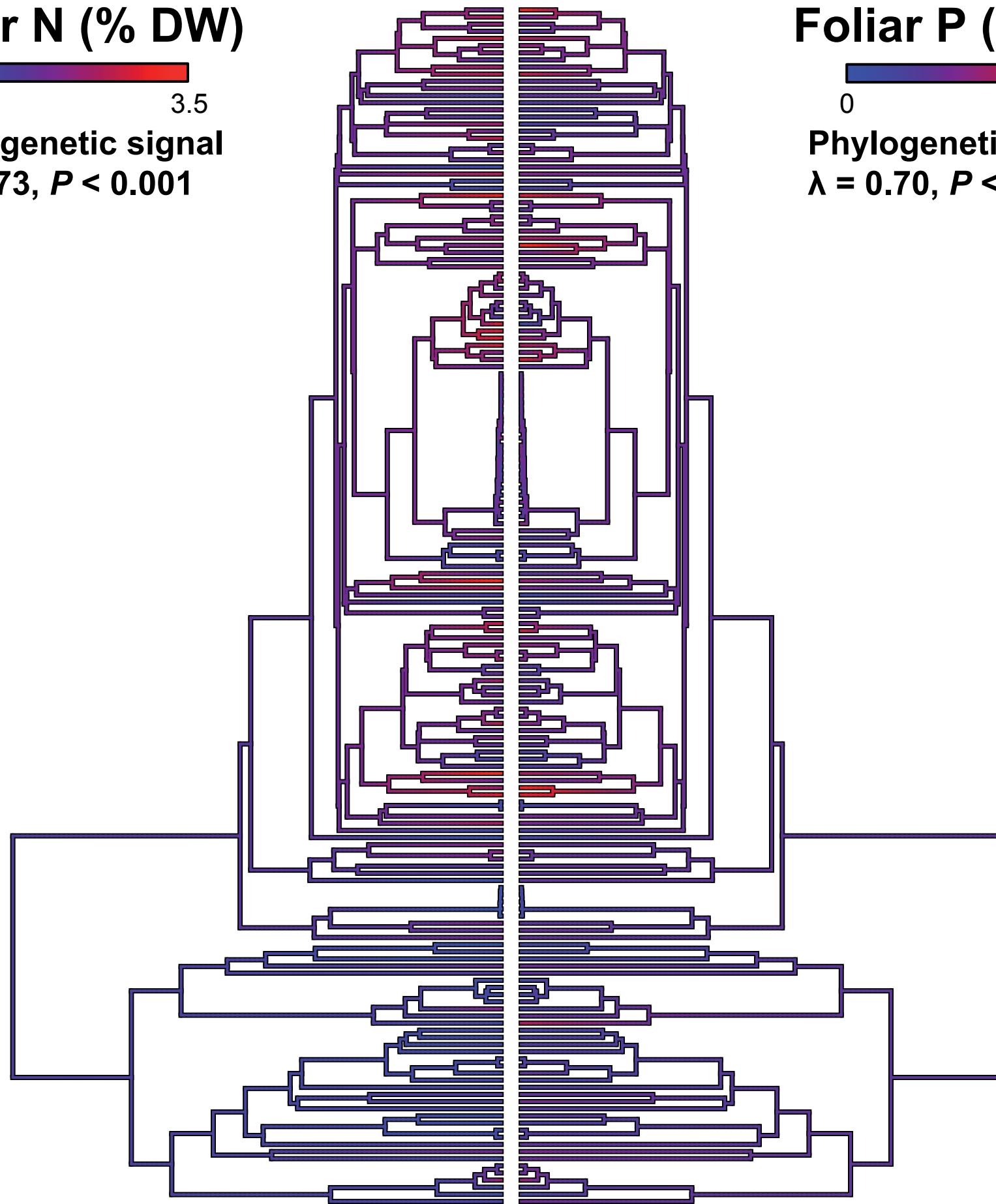


Phylogenetic signal  
 $\lambda = 0.73, P < 0.001$

Foliar P (% DW)



Phylogenetic signal  
 $\lambda = 0.70, P < 0.001$



b)

