

This is the **accepted version** of the article:

Veresoglou, Stavros; Peñuelas, Josep. Variance in biomass-allocation fractions is explained by distribution in European trees. DOI 10.1111/nph.15686

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1 **Variance in biomass-allocation fractions is explained by distribution**
2 **in European trees**

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16 Summary

- 17 • Intraspecific variability in ecological traits confers the ability of a species to adapt to an
18 ever-changing environment. Fractions of biomass allocation in plants (BAFs) represent
19 both ecological traits and direct expressions of investment strategies and so have
20 important implications on plant fitness particularly under current global change.
- 21 • We combined data on BAFs of trees in more than 10000 forest plots with their
22 distributions in Europe. We aimed to test whether plant species with wider distributions
23 have more or less variable intraspecific variance of BAFs foliage-woody biomass and
24 shoot-root ratios than species with limited distribution.
- 25 • Irrespective of corrections for tree age and phylogenetic relatedness, the standard
26 deviation in BAFs was up to three times higher in species with most extensive
27 distributions than in those with least extensive distribution due to a higher genetic
28 diversity. Variance in BAFs also increased with latitude.
- 29 • We show that a combination of 36% tree genetic diversity and 64% environmental
30 variability explains variance in BAFs and imply that changes in genetic diversity occur
31 quickly. Genetic diversity should thus play a key role in regulating species responses to
32 future climate change. Loss of habitat, even if transient, could induce a loss of genetic
33 diversity and hinder species survival.

34

35 Key-words: allometry; effective population size; extinction; genetic diversity; plant allometry;
36 plant morphology; woody plants

37

38

39 Introduction

40

41 The strategies of fitness and growth of sessile organisms are largely determined by biomass
42 allocation (Hodge, 2004; Poorter *et al.*, 2012; Veresoglou *et al.*, 2017), which in turn determines
43 the long-term morphology of the individual. The morphology of sessile organisms has been
44 studied the most in plants (Kokko, 2007). Plant morphology can be summarised in several ways,
45 each with distinct strengths and limitations. Poorter and Sack (2012) reviewed these methods and
46 concluded that fractions of biomass allocation, especially after correcting for confounding
47 allocation parameters such as size, represent a particularly effective measure. Plant morphology
48 has high functional importance, so the influence of environment on morphology has been well
49 studied. Some representative parameters that have been studied extensively for their influence on
50 plant allometry are the size of individual plants (Reich *et al.*, 2005; Poorter *et al.*, 2012),
51 historical environmental abiotic parameters such as stressors (e.g. uniform stress hypothesis)
52 (Mogan & Gannell, 1994; Dean *et al.*, 2002), shading (Lusk *et al.*, 2008; Duursma *et al.*, 2010;
53 Forster *et al.*, 2011), temperature (Reich *et al.*, 2014), precipitation (McCarthy & Enquist, 2007),
54 biotic interactions such as competition and diversity (Forrester *et al.*, 2017a); the growth form of
55 plants (Wyka *et al.*, 2013) and species-specific ontogeny (Forrester *et al.*, 2017b). Plant age,
56 however, is an influential factor that is often not available for integration into such analyses
57 (Nikklas, 1997; Nikklas *et al.*, 2003; Barthélémy & Caraglio, 2007; Duursma *et al.*, 2010).
58 Analysts often use plant size as a proxy of age (Nikklas, 2004; Bowman *et al.*, 2013).

59 Biomass-allocation fractions (BAFs) describe biomass ratios, usually at a logarithmic
60 scale, of plant organs. BAFs are measurable to an individual level and thus constitute plant
61 traits (Müller *et al.*, 2000; Reich *et al.*, 2003). Trait variance is often comparable to or even more
62 important than trait means (Messier *et al.*, 2010; Bolnick *et al.*, 2011; Violle *et al.*, 2012). High
63 variance in trait values could facilitate, for example, the evolution and adaptation of a species to
64 new environmental settings (Bolnick *et al.*, 2011). Quantifying variation in BAFs could improve
65 modelling uncertainty in the standing biomass of woody habitats because most of our estimates
66 of standing biomass are projections of allometric equations (Chave *et al.*, 2005; Muukkonen,
67 2007).

68 Plant morphology has been described as an equilibrium between constraints to plant
69 growth and exogenous environmental stressors (Barthélémy & Caraglio, 2007). Constraints to

70 plant growth and other intrinsic factors can negate the influence of the environment to varying
71 degrees, i.e. environmental conditions tend to shift BAFs against the stabilising influence of
72 intrinsic factors. We would then expect that BAFs would be more variable in plant species that
73 experience extreme environmental conditions more often. Reyer et al. (2013) argued that
74 extreme conditions occur mainly at the edges of the distribution of a species. Source-sink
75 population dynamics describe instances where species only occur in an area because of a
76 constant influx of propagules from surrounding areas where the species grows better. At the
77 edges of the distribution of a species it is more likely to observe source-sink population
78 dynamics (Remeš, 2000) than in the kernel of the distribution which could induce unique
79 phenotypes. Plant species that have a small distribution should more frequently experience such
80 “extreme edge” conditions so plants with smaller distributions may have the most variable BAFs.
81 The reason is that environmental heterogeneity mainly increases the variance in BAFs in these
82 species (Fig. 1a). We thus hypothesize that plant species with smaller distributions have more
83 variable BAFs (*hypothesis one*). Alternatively, the higher effective population sizes and genetic
84 variability could allow plant species that have extensive distributions to be those showing the
85 highest intraspecific trait variance, including BAFs. The reason could be that environmental
86 variability acts independently of distribution but more populous species show more diverse
87 BAFs due to a higher genetic diversity (Fig. 1b). As a result, plant species with smaller
88 distributions could vary less in their BAFs (*hypothesis two*). A final expectation is that variance
89 in BAFs should indicate the ability of species to adapt to local environmental conditions, so a
90 high variance suggests rapid evolution. Stapley et al. (2017) reported considerably lower
91 recombination rates in gymnosperms than angiosperms. The variance in BAFs should thus be
92 lower in conifers, compared to angiosperms (*hypothesis three*).

93 Most of our existing understanding on the way traits of woody species vary with genetic
94 diversity and the environment originates from provenance tests, where plants differing in their
95 origin are grown under common environmental conditions (Thompson et al. 2008; Wang et al.
96 2010). Some of the limitations of provenance test relate to the choice of the common
97 environment (Leites et al. 2012), the time they require for long-lived species to grow and thus the
98 logistics of destructively harvesting them (e.g. to assess BAFs). Here we worked on an
99 observational approach which synthesizes across existing BAF measurements from records of
100 destructive tree harvests in Europe (Fig. 1). Schepaschenko et al. (2017) have recently released

101 two large data sets detailing the biomass fractions of many trees that had been destructively
102 harvested between 1930 and 2014 in Eurasia. We combined this data set with information on the
103 distributions of many of these plant species in Europe from Mauri et al. (Mauri *et al.*, 2017) to
104 address the above mentioned three hypotheses.

105

106 Materials and Methods

107

108 *Sources of data*

109 We used the two data sets published by Schepaschenko et al. (2017) for our main analysis. The
110 *Biomass-tree* data set provided information on biomass fractions following destructive
111 harvesting for 9613 trees, mainly in Europe. The *Biomass-plot* data set provided information on
112 biomass fractions for 10351 plots distributed throughout Eurasia, each of which provided
113 information for cumulative biomass of two or more trees. The two data sets synthesized across
114 approximately 1200 experiments over the period 1930-2014 and contained information on
115 location and age of the trees as well as biomass information on several different fractions. We
116 used biomass information on foliage vs. woody aboveground biomass for our main analyses. We
117 also used root:shoot ratios as part of our sensitivity analyses. We extracted distributions of tree
118 species in Europe from Mauri et al. (Mauri *et al.*, 2017). Mauri et al. (2017) only described tree
119 distributions in Europe, so we limited our analysis to trees that occur mainly in Europe. We used
120 QGIS v 2.12.3 to estimate the size of the polygonal envelopes provided by Mauri et al. (2017).
121 We used Phylocom v 4.2 to reconstruct the phylogenetic relationships of the tree species in our
122 analysis.

123 We worked with an aggregate of 80 species in our analysis of European trees. A list of
124 the species and the phylogenetic reconstruction used to correct for phylogenetic relatedness can
125 be found in Table S1. The three data sets varied considerably in terms of their resolution and
126 their suitability for the different analyses. The cumulative analysis of the *Biomass-tree* data set
127 used biomass and age information for 4719 trees from 42 species (median observations per
128 species, 10.5; 1st quartile, 7; 3rd quartile, 78.5). The analysis of the *Biomass-plot* data set used
129 information for 3898 plot entries describing 63 species (median observations of plot per species,
130 15; 1st quartile, 8.5; 3rd quartile, 46) making it particularly suitable for assessing how BAFs are
131 influenced by environmental heterogeneity. The analysis of individual stands in the *Biomass-tree*

132 data set used an aggregate of 1854 tree observations from 40 species (median observations per
133 species, 8.5; 1st quartile, 7; 3rd quartile, 33.25). Because for the analysis on individual stands (i.e.
134 plots) in the *Biomass-tree* data set we only used per species information of trees in a single stand
135 (i.e. plot with most tree observations in the *Biomass-tree* data set), this made it particularly
136 suitable for quantifying the influence upon BAFs of genetic diversity. The *Biomass-tree* data set
137 contained proportionally more observations located in Europe than *Biomass-plot* data set did
138 (Fig.2 – inserts).

139

140 *Rationale for the analyses*

141 We modelled three sources of variance in BAFs, age, environment and genetic diversity. We
142 inferred genetic diversity from genetic variability (i.e. the degree to which the genetic
143 characteristics of populations vary) using a phenomenological approach that determined the
144 variance of morphological characteristics in populations after controlling for sources of variance
145 that were not of genetic origin such as age, environment and latitude. To control for age-related
146 differences in BAFs we used the slopes of linear models with BAFs as response variables and
147 age as predictor. To assess the fraction of BAFs that is explained by **genetic diversity** we
148 assessed how variance in BAFs scaled with tree species distribution in tree individuals which
149 belonged to the same species and stand after correcting them for tree age (individual stands in the
150 *Biomass-tree* data set; Fig. 1b). To assess the fraction of BAFs that is explained by
151 **environmental variability** we assumed that environmental variability is mainly due to
152 latitudinal range (de Frenne et al. 2013; we provide more details at the section poling effect
153 sizes) and quantified how much the variance in BAFs changed with each degree of latitudinal
154 range (i.e. latitudinal breadth – to avoid an overrepresentation of stands we used the *Biomass-*
155 *plot* dataset).

156

157 *Statistical analyses*

158 Our analyses only considered tree species (which were the unit of our analysis) for which a
159 minimum of five observations of age, foliage biomass and aboveground woody biomass were
160 available, because we needed a minimum of three observations to fit a linear model and then two
161 additional residuals to yield meaningful estimates of variance for the fit of the regression line
162 (results from a sensitivity test on the inclusion threshold are presented in Appendix 1 and Fig.

163 S1). To extract the fraction of variance in BAFs that was not due to age differences we fitted
164 linear models with BAFs as a response variable and age as predictor and then quantified the
165 standard deviation of the residuals. We explain the procedure in higher detail below (also
166 Appendix 2; Table S2):

167 1. We calculated the natural log response ratio (logRR) of foliage over aboveground woody
168 biomass ($\log RR = \ln\left(\frac{m_{foliage}}{m_{woody}}\right)$, where m stands for biomass) for each individual tree in the case of

169 the *Biomass-tree* data base or plot in the case of the *Biomass-plot* data base (Appendix 2). In the
170 form of a sensitivity analysis we also analysed logRR of root over shoot BAFs. LogRR
171 represents a widely used nonstandard effect size in synthesis studies. A large logRR indicates a
172 higher investment in foliage than woody biomass.

173 2. We fitted a linear model with logRR as a response variable and age as the sole predictor. The
174 single most important idiosyncratic cause of variability in BAFs is age (Nikklas *et al.*, 2003;
175 Nikklas, 2004; Barthélémy & Caraglio, 2007; Duursma *et al.*, 2010). To correct our data for this
176 source of variance, we extracted the residuals of the linear model and assessed their standard
177 deviations. We assumed a first-order linear correlation between logRR and age using the
178 standard deviation of the residuals as a measure of the variance, in agreement with preliminary
179 analyses (Appendix 2).

180 3. We correlated our metric of variance of the relationship between BAFs and age with the
181 distribution of the plants.

182 In the first of our three analyses (Table S2) we used all observations of individual trees in
183 the *Biomass-tree* data set, which consisted of multiple trees per stand and multiple stands per
184 species. We then used information for all plots in the *Biomass-plot* data set, consisting of a single
185 plot per stand, which allowed us to correct for spatial autocorrelation. Finally, we reanalysed the
186 *Biomass-tree* data set but only using the information for each species in a single stand, with the
187 sole criterion that the stand had provided most observations for that species. This analysis
188 addressed the concern that the cause of higher variance in BAFs was due to a larger distance
189 across observations and thus a higher variability in environmental conditions. We conducted this
190 analysis both with and without phylogenetic correction. We used an analysis of phylogenetically
191 independent contrasts to correct for phylogeny.

192 We further compared our estimates of variance between angiosperms and gymnosperms.
193 We thus used *t*-tests, assuming unequal variance.

194

195 *Sensitivity analyses*

196

197 We tested the specificity of our observations to logRR between foliage and aboveground woody
198 biomass by replicating the analysis for logRR between total root biomass vs. total aboveground
199 biomass. The two data sets contained unequal numbers of observations of total root biomass, and
200 the number of species which we could analyse was low. We directly assessed how the variance
201 in biomass fractions scaled with distribution (i.e. independent of age) by directly assessing the
202 standard deviation of biomass-allocation ranges and correlating it with distribution (Appendix 2).

203 We further replicated the analysis with the Legacy Tree Data data set (Radtke *et al.*,
204 2016). To estimate the distribution of North American trees we used information from the United
205 States Department of Agriculture (USDA 2017). This data set did not contain any information on
206 tree age. We used data from the *Legacy_Tree* table and used the variability of logRR foliage over
207 aboveground woody biomass for single locations. Sufficient information was available for only
208 three species, which were assessed for four locations. All three species belonged to the Pinaceae
209 family, had nested distributions and occurred in southeastern North America. We assessed
210 distribution by extracting information from the USDA for the number of states in which the
211 species occurred and regressed this metric against the variance of logRR. The amount of
212 information we extracted from the Legacy Tree Data base and the resolution, given that the size
213 of US states varies considerably, were much lower than in our main analysis so we only used as
214 a means of supporting the main results with a different dataset. Because we did not have accurate
215 distribution range data, we used here non-parametric statistics.

216 To assess the degree to which our observations were sensitive to the inclusion of invasive
217 tree species we classified tree species in native vs invasive as in Veresoglou *et al.* (2018; Table
218 S3). We repeated the analysis separately for the subsets of native and invasive species.

219

220 *The influence of latitude*

221 Latitude is an influential predictor of variance in plant traits (Heibo *et al.*, 2005; Aerts *et al.*,
222 2012), and as such it was important for us to show that it was not driving our results. We

223 assessed the degree to which our patterns were explained by latitude using two analyses. (a) We
224 first extracted the average latitudes of the distributions of the woody species in Europe reported
225 by Mauri et al. (2017). We compared these values with the variances in BAFs corrected for plant
226 age (i.e. the standard deviation of the residuals of the linear model described above). (b) We then
227 divided Europe into northern and southern Europe. We thus used the average of the two
228 latitudinal extremes of Europe: 82°N for the northern region and 35°N for the southern region,
229 averaging 58.5°N. We used the subset of points west of 69°W. We separately calculated the
230 variance of BAFs corrected for age for the woody species for which the *Biomass-tree* data set
231 contained a minimum of five observations both north and south of the latitudinal average
232 threshold, which we then combined in a new logRR (i.e. northern variance over southern
233 variance). We calculated the variance for these two sites and used them to recalculate logRR.

234

235 *Pooling effect sizes to quantify genetic and environmental variance in BAFs*

236 We partitioned here variance in BAFs into a fraction due to genetic variability and a fraction due
237 to environmental variability. We used a phenomenological approach for this (Fig. 1; Appendix
238 4). We made the following three assumptions:

- 239 1. The key factor contributing to environmental variability was latitudinal range of the
240 distribution of an organism. In support to this simplistic statement, see de Frenne et al. (2013)
241 demonstrating that some key environmental parameters such as temperature, precipitation, soil
242 pH and human influence covary with latitude. We assumed that there is a first order linear
243 relationship between latitudinal range and environmental variability in BAFs.
- 244 2. Genetic variability in BAFs increased with distribution at a slope equivalent to that in Fig. 2b.
- 245 3. The relative importance of the two fractions was assessed for an imaginary species with an
246 “average” latitudinal range which in this case was 19.4° latitude and a mean distribution range of
247 10,000 km².

248 We use the additive principle of variances in statistics to add the two fractions on the assumption
249 that the observed variance was independent of our sample sizes. Our variance partitioning was
250 carried out for an idealized species having an average latitudinal range of $58.9^\circ - 39.5^\circ = 19.4^\circ$
251 latitudinal range and a distribution of 10,000 km² which represented averages in our dataset and
252 were also consistent with (Tkach *et al.*, 2008). We estimated the overall form of the model and

253 we calculated relative effect sizes for mean parameters of distribution and latitude in Europe. We
254 provide more information on the analysis in Appendix 4.

255

256

257

258

259 Results

260

261 The main results are on records throughout Eurasia but these were supported by a
262 reanalysis exclusively to the records from Europe. Our main analysis gave consistent results for
263 all three data sets (Fig. 2), namely that variance in BAFs increases with the distribution size of a
264 species. LogRR of foliage vs aboveground woody biomass was significantly positively
265 correlated with distribution in all three tests (Fig. 2). The correlation was strongest (i.e. highest
266 Kendall's tau) for individual trees in the same stand ($\tau=0.51$, Fig. 2c). We found yet stronger
267 correlations when we narrowed down the analysis on tree records occurring in Europe which we
268 here define as those with a longitude smaller than 69°W (Fig. S2). Correlations would have been
269 considerably weaker if we had not corrected for age of the trees (Fig. S3). No phylogenetic
270 conservatism was found in either the variance of biomass fractions (Blomberg's K in the
271 cumulative analysis of the *Biomass-tree* data set was 0.37 with $P = 0.95$) or the distribution of
272 the species (Blomberg's K in the same data set was 0.53 with $P = 0.12$; Appendix 3). The
273 correlations were weaker after correction for phylogeny with phylogenetically independent
274 contrasts, except for the *Biomass-tree* data set (Fig. 3). The variances of the BAFs did not differ
275 significantly between angiosperms and gymnosperms in any of the three data sets (Fig. 4 –
276 evidence against hypothesis three).

277 The analysis using root:shoot ratios produced comparable results but with lower
278 statistical power (Fig. 5a,b). The results of our analysis of the biomass data from America agreed
279 with those for European trees (Fig. 5c; $\tau=0.91$, $P=0.07$). Most of the trees in the datasets were
280 classified as native and there were minimal differences in the additional analyses targeting
281 natives (Fig. S4). There was insufficient statistical power to reach robust conclusions for
282 invasives (Fig. S4).

283

284 *The influence of latitude*

285 There was no relationship between mean latitude and the variance of BAFs between foliage over
286 woody aboveground biomass in the *Biomass-tree* data set (Fig. 6a). The five tree species that
287 were observed both North and South of the latitudinal threshold of 58.5°N did not display any
288 patterns with regards to their BAFs (Fig. 6a – insert). *Picea obovata* showed higher BAFs in the
289 southern extent of its distribution, *Pinus sylvestris* and *Betula alba* in the northern extent of their
290 distribution whereas *Larix sukaczewii* and *Pinus sibirica* showed relatively balanced BAFs in
291 both extents. The lack of a relationship was even more apparent when we narrowed down our
292 analysis to individual stands in the *Biomass-tree* data set (data not shown). By contrast we could
293 observe a strong relationship between mean latitude and the variance of BAFs in the *Biomass-*
294 *plot* data set (Fig. 6b).

295

296 *Relative effect sizes of genetic and environmental variability*

297 We had 40 observations and a mean slope of $3.324 \cdot 10^{-5}$ per thousand km² of distribution in the
298 case of the individual stands in the *Biomass-tree* data set assessing genetic variability and 18
299 observations and a mean slope of $3.05 \cdot 10^{-2}$ per degree latitudinal range in the case of the
300 *Biomass-plot* data set measuring environmental variability. The resulting expression of variance
301 (Appendix 4) was $s_p = 10^{-4} \sqrt{(0.11D^2 + 93,025\phi^2)}$ with D representing distribution range and ϕ
302 degrees latitudinal range. For average European settings of $D \approx 10,000$ thousands km² (also
303 consistent with (Tkach *et al.*, 2008)) and ϕ differences of 58.9° – 39.5° latitudinal range the two
304 factors inside the parenthesis take the values $11 \cdot 10^6$ and $35 \cdot 10^6$ suggesting that latitudinal range
305 (i.e. here used as a proxy of environmental variability) exerts on average a 48% stronger (i.e. the
306 resulting variances for genetic and environmental variability, if that the other factor was zero,
307 would be 0.33 and 0.59, respectively, giving relative proportions of 36% and 64%) influence on
308 variance in logRR of BAFs than distribution (i.e. here genetic variability) does. Genetic diversity
309 and latitudinal range, both induce strong changes on the variance in BAFs and the respective
310 standard deviations were multifold higher for species with extensive distributions (Fig. 2c) and
311 high latitudes (Fig. 6b).

312

313

314 Discussion

315

316 Living organisms are constantly challenged to optimally allocate their finite resources to
317 maximise fitness. This challenge leads to multiple investment trade-offs, many of which have
318 been extensively studied (Poorter *et al.*, 2006; Cadotte, 2007; Huot *et al.*, 2014). BAFs represent
319 direct expressions of some of these trade-offs and the phenotypes of the organisms. We
320 experimented with two such BAFs, foliage over woody aboveground biomass and the root:shoot
321 ratio, to show that both these fractions were more variable in tree species with extensive
322 distributions, even after limiting our analysis to neighbouring trees (Fig. 2c), in agreement with
323 hypothesis two. Our results were also valid after correcting for phylogenetic relatedness
324 (Appendix 3). A higher ability to adapt to a changing environment is one of the implications of
325 higher trait variance (Bolnick *et al.*, 2011). The causality of this relationship is unclear and could
326 imply either that tree species that experience a higher phenotypic variability tend to have larger
327 distributions (e.g. van Vallen, 1973) or that some species are phenotypically more diverse in
328 response to a larger distribution and most likely a larger effective population size. Environmental
329 heterogeneity has been identified as a mechanism that facilitates genetic variation in plants
330 (Delph & Kelly, 2013), and a larger distribution implies a higher environmental heterogeneity.
331 Many tree species have extensive distributions, but individual trees can also disperse over very
332 large distances (Bacles *et al.*, 2006; Petit & Hampe, 2006; Kremer *et al.*, 2012) and cross-fertilise
333 with individuals experiencing differing environmental conditions. We thus favour the
334 interpretation that a larger distribution most likely induces a higher variance in BAFs.

335 BAFs in plants represent expressions of an equilibrium between stabilising
336 intrinsic/genetic factors such as ontogeny and the destabilising influence of the environment
337 (Barthélémy & Caraglio, 2007), i.e. any biomass-allocation fraction is an aggregate of these two
338 mechanisms. We thus present an argument detailing why our results were likely due to a higher
339 genetic variability of trees with more extensive distributions and not because of the
340 environmental conditions that the trees experienced (in support of hypothesis two and against
341 hypothesis one). The influence of the environment is expected to be only moderately important
342 at sites close to the centres of species distributions (compared to the edges). Most of the trees in
343 our data sets had been harvested near the centres of their distributions, because moderate
344 environmental conditions facilitate silvicultural practices. Most importantly, our results were
345 valid when using individual sites per species in which case the differences were most likely due

346 to rapid evolution (i.e. the absence of systematic differences between angiosperms and
347 gymnosperms provided evidence against hypothesis three). Co-occurring tree species experience
348 comparable environmental conditions, so the resulting phenotypic variance should best represent
349 the genetic diversity (Fig. 2c).

350 Does latitude influence BAFs? We found no relationship in the *Biomass-tree* data set but
351 there was a strong positive relationship in the *Biomass-plot* data set (Fig. 6). A reason why the
352 results across the two data sets were incongruent probably relates to the way these were
353 standardized. The *Biomass-tree* data set contained multiple tree records per sampling site and
354 there were few replicate sites per tree species. Co-occurring woody species are likely to
355 experience comparable environmental conditions and the resulting BAFs should mainly reflect
356 genetic diversity. Because of the few replicate sites per tree species any influences of latitude
357 were masked in the data set by those of genetic diversity. This was even more pronounced when
358 we narrowed the analysis to a single site per tree species. By contrast in the *Biomass-plot* data set
359 via being limited to a single record per sampling site, we could effectively investigate differences
360 arising from environmental variability. Based on this analysis, trees that typically occur closer to
361 the poles exhibit higher variances of BAFs. Even though it has been disputed in the past
362 (Vázquez & Stevens, 2004), it is widely appreciated that environmental variability increases with
363 latitudinal range (MacArthur, 1972). This result is in accordance with our first hypothesis that
364 environmental variability should increase BAFs variance (Fig. 1a). The effect size we estimated
365 for environmental variability exceeded that for genetic diversity.

366 The survival challenges of tree species to the accelerating pace of global change is a key
367 topic in the biology of global change (Lenoir *et al.*, 2008; Bertrand *et al.*, 2016; Veresoglou &
368 Halley, 2018). Identifying tree species at a high risk of extinction is important. Several traits such
369 as longevity (Morin & Thuiller, 2009) and seed size (Veresoglou & Halley, 2018) might be
370 informative in terms of tree susceptibility to extinction. The loss of habitat is a key factor that
371 drives the eventual risk of extinction, but the relationship between habitat size and genetic
372 variability is poorly understood. The loss of genetic diversity following habitat loss can further
373 limit the ability of a species to cope with environmental conditions (Sexton *et al.*, 2009) and
374 eventually accelerate extinction. The implications of extensive distributions have been debated.
375 A review of 31 studies by Lowe *et al.* (Lowe *et al.*, 2005) found that habitat loss usually did not
376 significantly affect the genetic variability of tree species. Another meta-analysis by Vranckx *et*

377 al. (2012), however, found that habitat loss induced losses in the genetic diversity of species. An
378 extensive synthesis by Morueta-Holme et al. (2013) reported that plant species with extensive
379 geographic ranges were more genetically variable, and Kremer et al. (Kremer *et al.*, 2012)
380 argued that long-distance gene flow amongst trees likely conferred an evolutionary advantage. In
381 contrast, the implications of habitat loss in trees may be fully reversible if the former habitat of
382 these species can be restored before extinction (Newmark *et al.*, 2017).

383 Our results suggest that it is tree genetic diversity that induces variance in BAFs (Fig. 1b;
384 we found higher variance in BAFs in species with large distributions). Our analysis makes the
385 assumption that genetic variability is a good proxy of genetic diversity, which despite being a
386 common and well supported assumption in the literature (e.g. Avolio *et al.*, 2012; Jöqvist and
387 Kremp, 2016), remains less robust than direct estimates of genetic diversity. Most importantly,
388 our general models did not discriminate between native and non-native plant species and used
389 real distributions to assess effect sizes. We often observe that the distributions of non-native (i.e.
390 invasive) species are not at equilibrium with their environment and that they possess a lower than
391 expected genetic diversity (Beaumont *et al.*, 2009; Bradley *et al.*, 2010). We would have
392 expected, as a result, relatively weak relationships between genetic diversity and realized
393 distributions for the subset of non-native trees which was not the case (Fig. S4). This finding
394 implies that changes in genetic diversity can occur quickly and develop after a few generations
395 of growth in isolation. Genetic diversity should thus play a key role in regulating the response of
396 species to future climate change, because of the extensive fitness implications of BAFs on the
397 ability of a species to adapt. The loss of habitat, even if transient, could lead to a loss of genetic
398 diversity, which would hinder species survival.

399 Human activity has sped up gene flow in almost all types of ecosystems and this should
400 continue in the near future (Wilson et al. 2009). On the short term, assisted gene flow
401 homogenizes populations (i.e. and their genetic diversity), allowing species to more effectively
402 cope with unfavourable environmental conditions (e.g. through acquiring more favourable
403 BAFs). Assisted gene flow should thus steepen the positive relationship between variance in
404 BAFs and distribution (Fig. 1b), benefiting disproportionately species with a large distribution at
405 the risk of species that maintain a limited genetic diversity. It has been documented, for example,
406 that invasions, which represent an alternative form of introductions of species with a high
407 competitive ability, induce extinctions of native species (Colautti et al. 2017; Catford et al.

408 2018). Even though we did not directly model assisted gene flow (as for example in Adams et al.
409 1998), the strong relationship between distribution and genetic diversity should be instructive for
410 forest management. Silvicultural practices such as the artificial regeneration of stands from
411 commercial genetic material (e.g. Bradshaw 2004; Finkeldey Ziehe 2004) might, therefore, be
412 precarious for the native species diversity.

413 In summary, BAFs were more variable in trees with extensive distributions, i.e. our
414 results supported only the second of our hypotheses. Most notably, we made the point that it was
415 a higher genetic variability that resulted in more variable BAFs for tree species with extensive
416 distributions. We thus present evidence that the loss of habitat for tree species through a quick
417 loss of genetic diversity could lower the ability of a species to modify its architecture (BAFs) in
418 response to changes in the environment (Fig. 1). It is thus likely that any loss of habitat may not
419 be as reversible as many believe.

420

421 Acknowledgements

422 We want to thank two anonymous reviewers and the editor for constructive criticism on our
423 paper. JP was funded by the European Research Council Synergy grant ERC-SyG-2013-610028
424 IMBALANCE-P.

425

426 Contributions

427 Conceived the study and carried out the analysis: SDV. The two authors wrote together the
428 article and approved the final version.

429

430

431 Data availability

432 All the data we analyse here are already in the public domain. We present intermediate data in
433 our analysis in the form of Appendix 8.

434

435

436 Competing interests

437 The authors declare no conflicts of interest.

438

439 Supplementary Information

440 **Fig. S1:** Sensitivity analysis on the inclusion criterion of five full records

441 **Fig. S2:** Relationships between the variance in BAFs in records from Europe

442 **Fig. S3:** Weighted regressions between the variance in BAFs and the distribution of the species
443 without correcting for age

444 **Fig. S4:** Sensitivity analysis on how relationships differed between native and invasive tree species

445 **Table S1:** List of the plant species that we used in our analyses.

446 **Table S2:** Overview of all analyses.

447 **Table S3:** : Classification of tree species into native vs invasive

448 **Appendix 1:** Inclusion Criteria

449 **Appendix 2:** Effect sizes and model specifications

450 **Appendix 3:** Strength of BAF relationships

451 **Appendix 4:** Partitioning of BAFs into environmental and genetic variability

452 **Appendix 5:** Biases due to differences in coverage of the databases

453 **Appendix 6:** Phylogenetic tree

454 **Appendix 7:** Supplementary references

455 **Appendix 8:** Raw data

456

457

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642

643 Legends to Figures

644

645 Fig. 1 Conceptual diagram illustrating the three hypotheses we address in the manuscript. Four
646 hypothetical species, the broadleaves blue triangle and yellow circle (represented with an
647 elliptical leaf) and the conifers red rhomb and green square (represented by an acicular
648 leaf) are each sampled at four locations (map on top; note that distribution envelopes
649 differ). The ranking of their distributions is as follows: red rhomb, blue triangle, yellow
650 circle and green square. In Hypothesis One (a) we expect that the fraction of variance in
651 biomass allocation fractions that is explained by genetic variability (purple discontinuous
652 lines) is independent of distribution and that environmental factors increase the variance
653 (green arrow) more in those species that have a small distribution (larger arrow) resulting
654 in a negative relationship between observed variance and distribution (green
655 discontinuous lines). In Hypothesis Two (b) we expect that a larger distribution results in
656 a higher genetic diversity which is depicted with a purple line. The environment increases
657 variance irrespective of distribution (green arrows) resulting in a positive relationship
658 between observed variance and distribution (green discontinuous lines). In Hypothesis
659 Three (c) the biomass allocation fractions vary independently of distribution and can be
660 explained by the evolutionary history of the plant (here angiosperms vs gymnosperms).
661 We could assess genetic variance in BAFs by comparing conspecific trees in the same
662 stand after correcting for age-differences and the sum of genetic and environmental
663 variability by comparing across stands, also after correcting for age.

664

665

666 Fig. 2 Relationships between the variance in biomass-allocation fractions (foliage over woody
667 aboveground biomass) and distribution of the tree species. (a) *Biomass-tree* data set, all
668 possible observations (multiple trees per location) of the specific data set (lower than in
669 *Biomass-plot*); (b) *Biomass-plot* data set, one observation per location (at a plot level); (c)
670 *Biomass-tree* data set, observations per species only describe trees in the stand (plot) that
671 contained the most tree observations. The dashed lines represent the best fits. Numbers
672 next to the data points indicate the number of observations per species used to calculate
673 the variance. Overlaid map shows in red the location of the sites where the data

674 originated from – we only analysed woody species with an extensive distribution (over 2
675 million km²) in Europe. Phylogenetic correction was not applied. Relationships were
676 stronger when we repeated the analyses with the subset of sites located in Europe (Fig.
677 S2).

678
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681

682 Fig. 3 Relationships between variance in biomass-allocation fractions (foliage over woody
683 aboveground biomass) and distribution of the tree species for phylogenetically corrected
684 data using phylogenetically independent contrasts (PIC). (a) *Biomass-tree* data set, all
685 possible observations; (b) *Biomass-plot* data set, one observation per location; (c)
686 *Biomass-tree* data set, observations per species are from the stand that contained most
687 observations. The dashed red lines represent the best fits. The overlaid phylogenetic tree
688 depicts in the form of squares information (blue: first quartile; white middle two
689 quartiles; red 4th quartile) on variance in biomass allocation fractions (left) and
690 distribution (right) of the woody species included in the analysis and their phylogenetic
691 relationships (tree). Note the absence of phylogenetic signal which was confirmed with
692 Blomberg K tests.

693

694 Fig. 4 Differences in variance in biomass-allocation fractions (foliage over woody aboveground
695 biomass) between angiosperms (elliptical leaf in yellow) and gymnosperms (acicular leaf
696 in green). (a) *Biomass-tree* data set, all possible observations; (b) *Biomass-plot* data set,
697 one observation per location; (c) *Biomass-tree* data set, observations per species are from
698 the stand that contained most observations. None of the t-tests were significant.

699
700

701 Fig. 5: (a; b) Relationships between the variance in biomass-allocation fractions (root over shoot
702 fractions) and distribution of the tree species. (a) *Biomass-tree* data set, all possible
703 observations; (b) *Biomass-tree* data set, observations per species are from the stand that
704 contained most observations; (c) variance in biomass-allocation ratios for *Pinus echinata*

705 (observed in 23 states), *Pinus taeda* (observed in 20 states, from two studies) and *Pinus*
706 *palustris* (observed in 10 states) across four studies in the Legacy Tree Data database
707 (USA). The three species have nested distributions in America. The dashed lines
708 represent the best fits. Numbers next to the data points indicate the number of
709 observations per species used to calculate the variance. Overlaid map shows in red the
710 location of the sites where the data originated from.

711

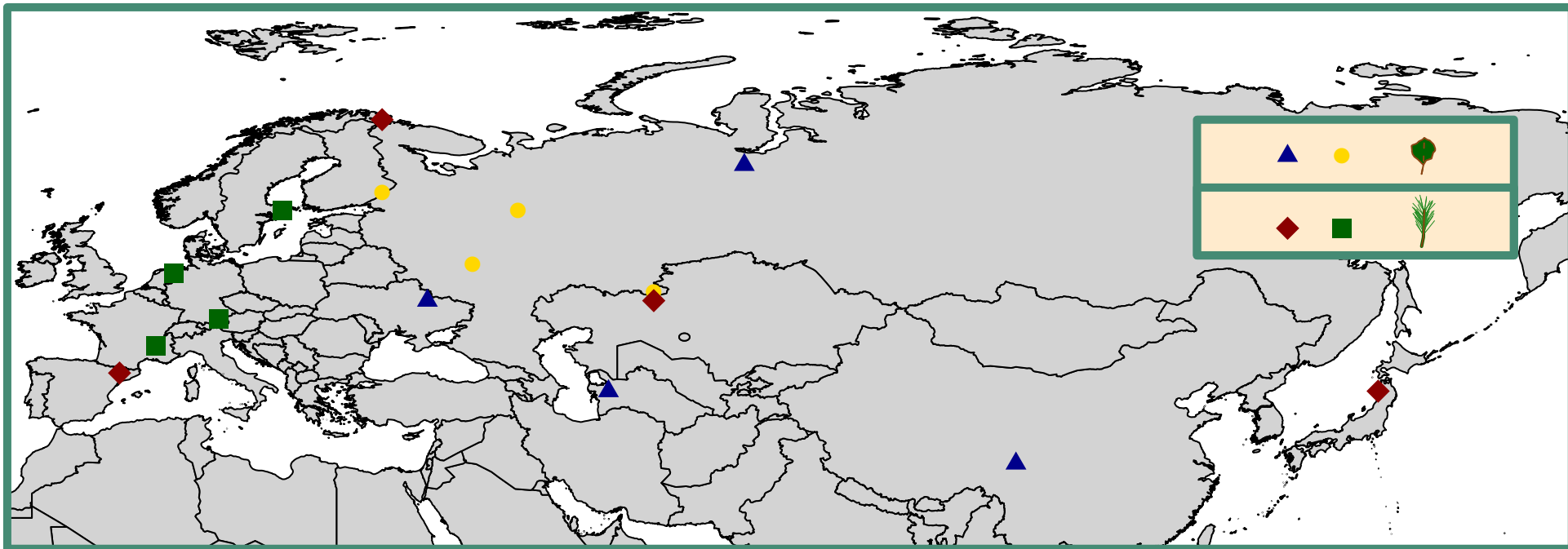
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713 Fig. 6 Influence of latitude on variance in biomass-allocation fractions (foliage over woody
714 biomass). The x-axis describes the average latitude of the distribution range of the woody
715 species whereas the y-axis the variance in biomass-allocation fractions. Panel (a)
716 describes the *Biomass-tree* data set whereas panel (b) the *Biomass-plot* data set. The
717 insert in panel (a) shows how variance differs in the north and south distribution of five
718 tree species in the Biomass-tree data set (opaque triangles). North here describes latitudes
719 in Europe higher than 58.5°N (mean of the latitudinal extremes of European territory) and
720 South lower than this value. These five species were the only ones that met the inclusion
721 criterion, namely being represented with a minimum of five entries both in North and
722 South Europe. The continuous opaque line is an isocline where variance in the North
723 equals that in the South.

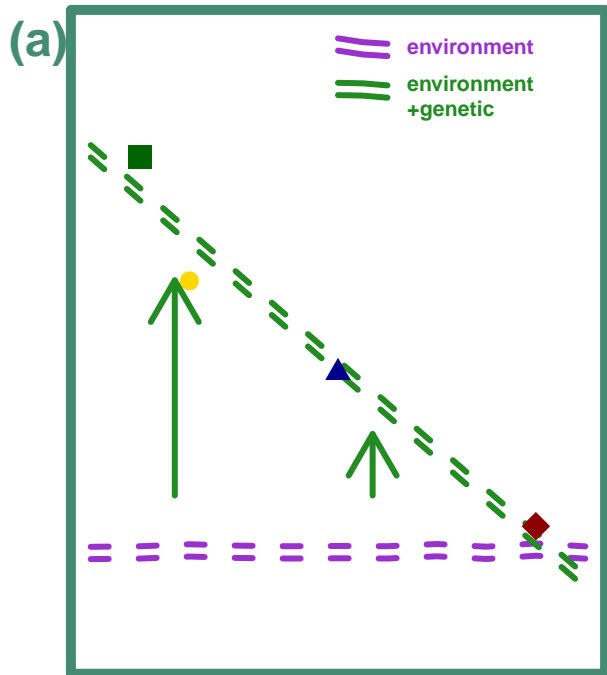
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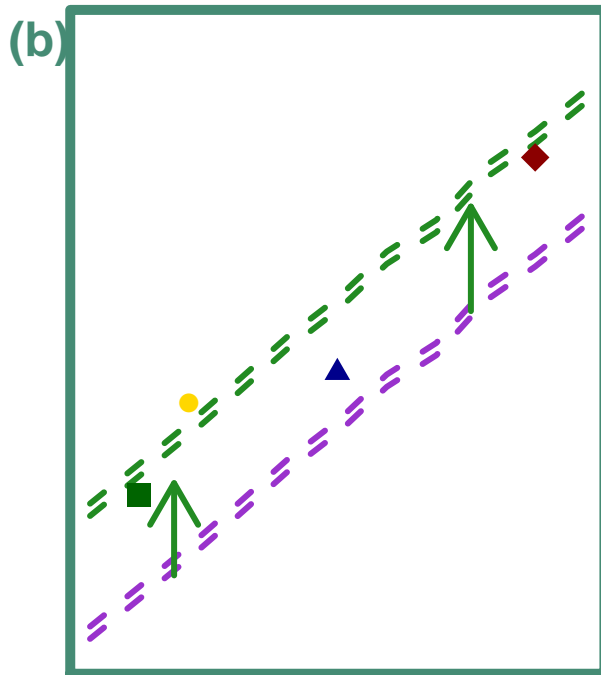


Variance in biomass allocation fractions



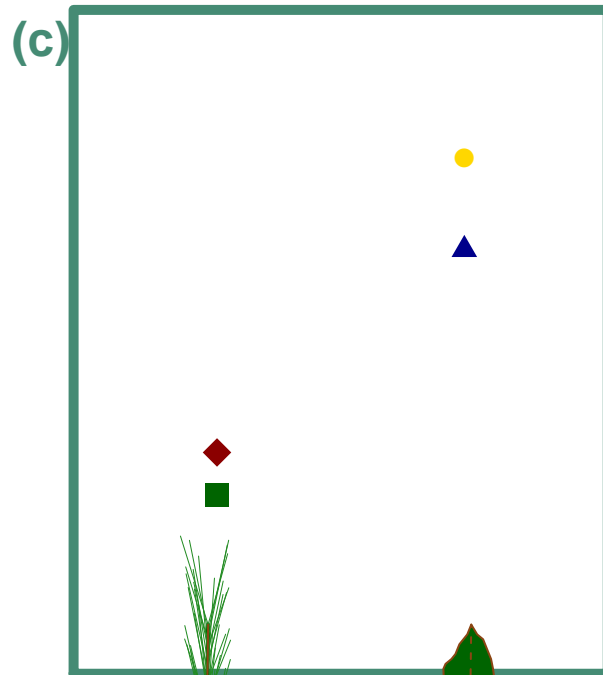
Distribution

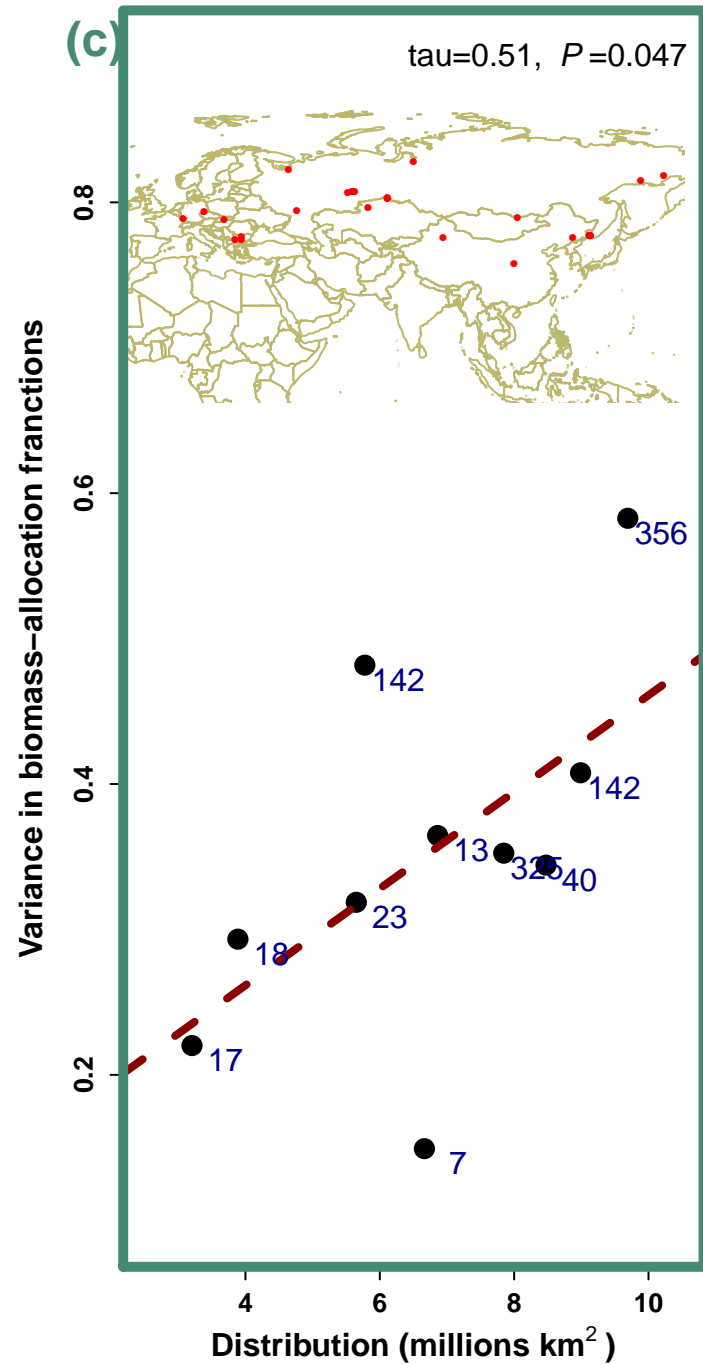
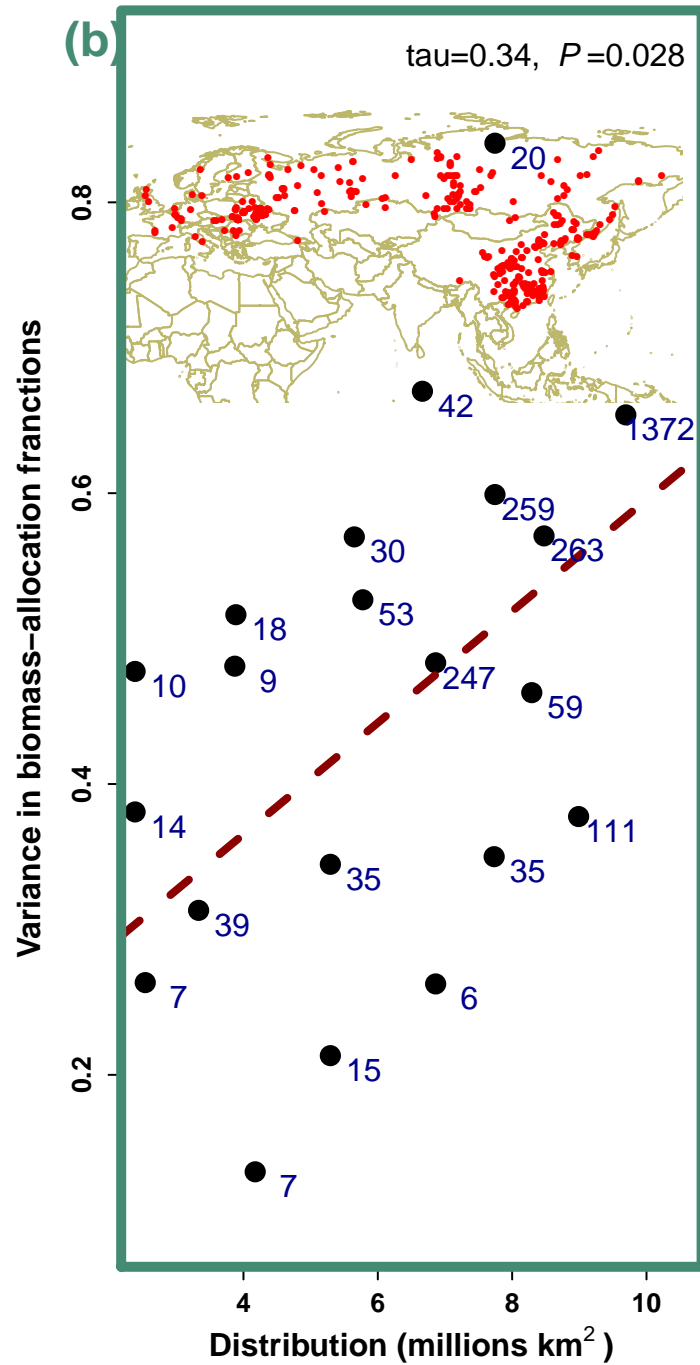
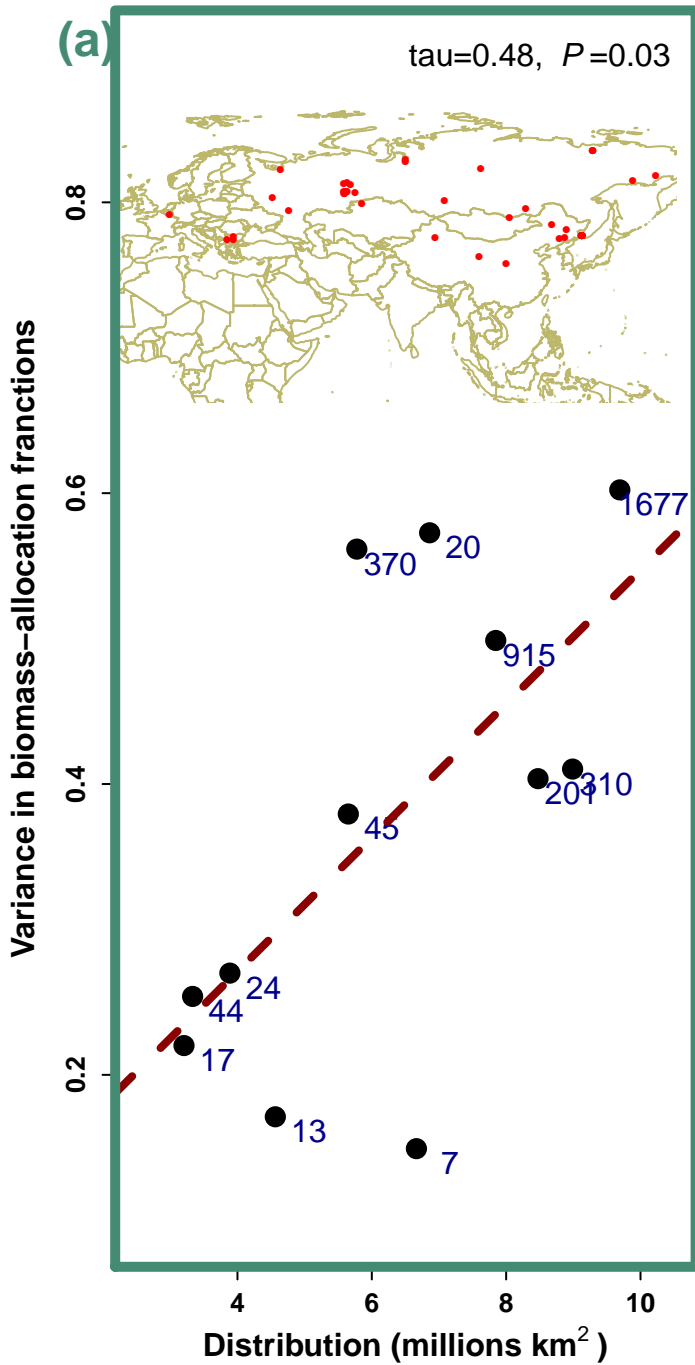
Variance in biomass allocation fractions

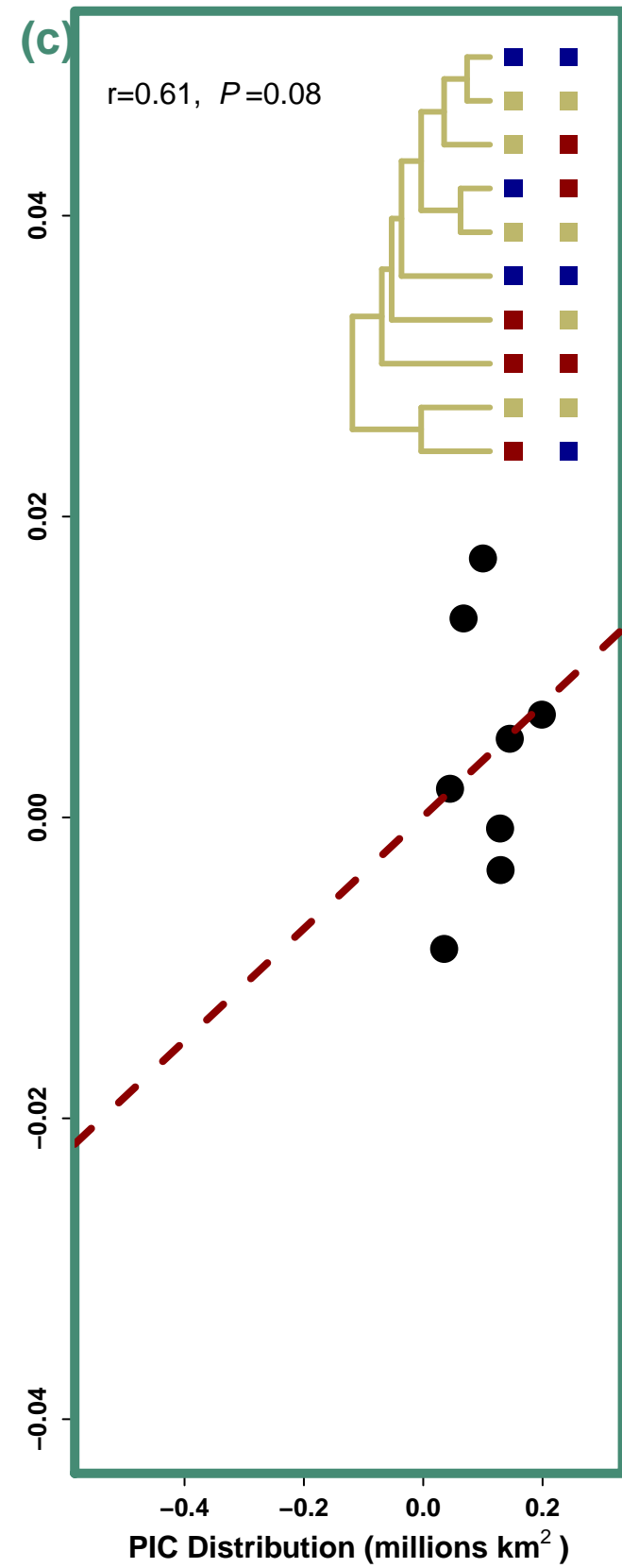
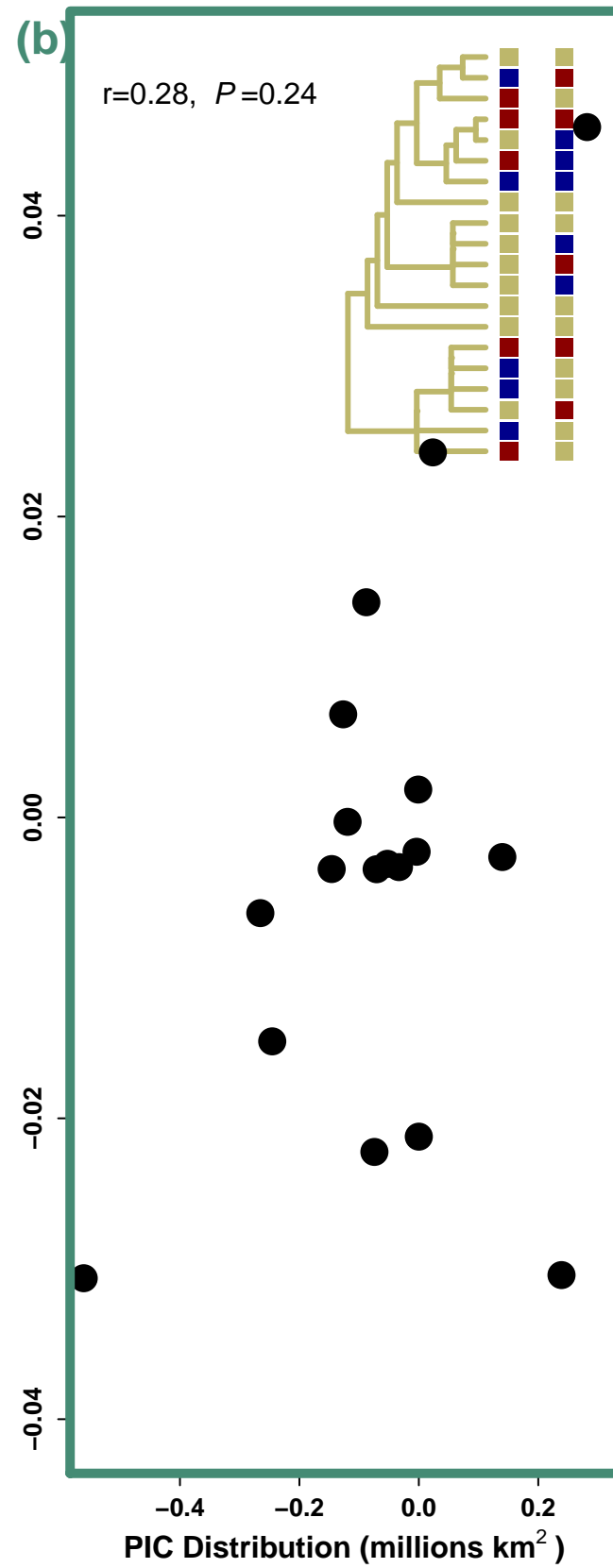
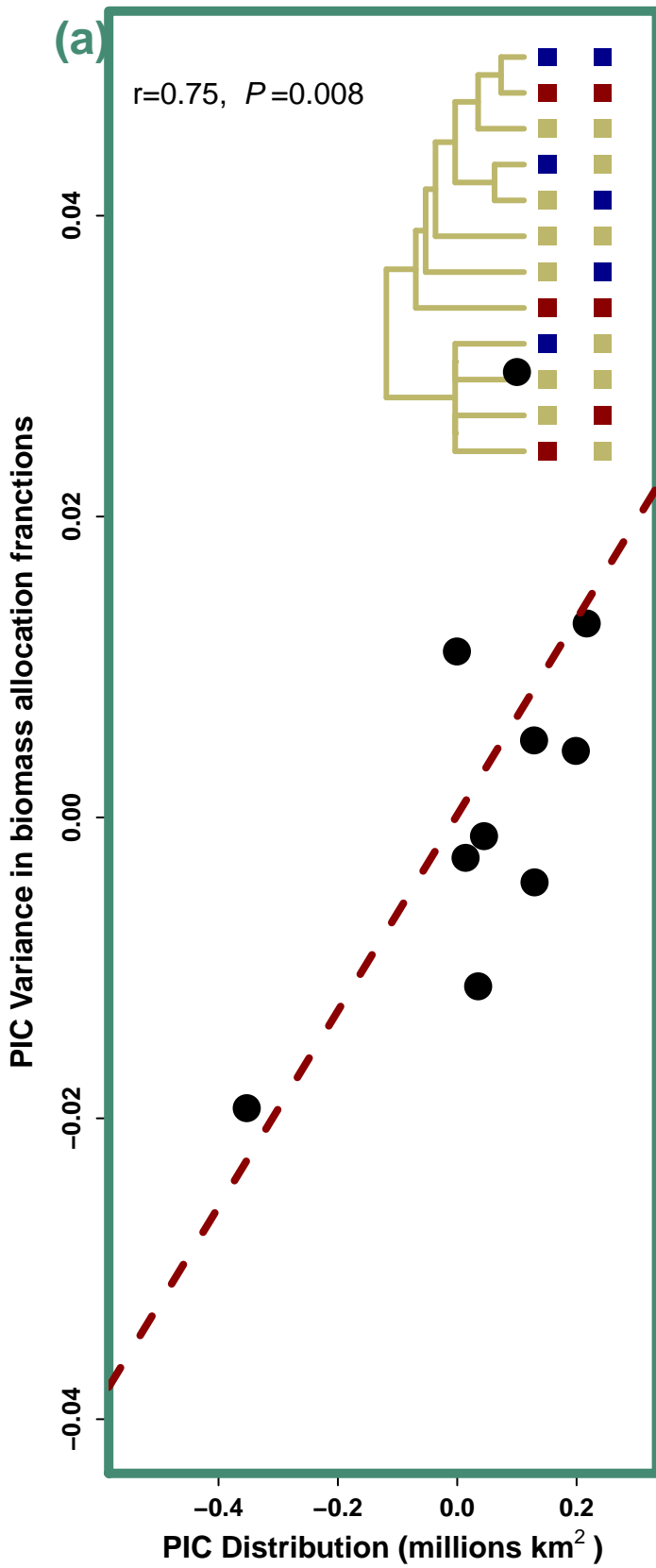


Distribution

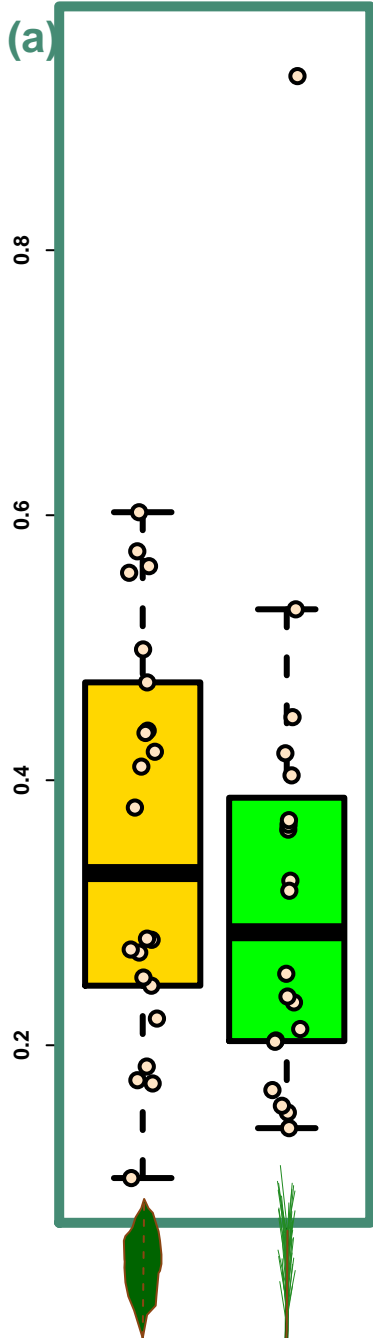
Variance in biomass allocation fractions



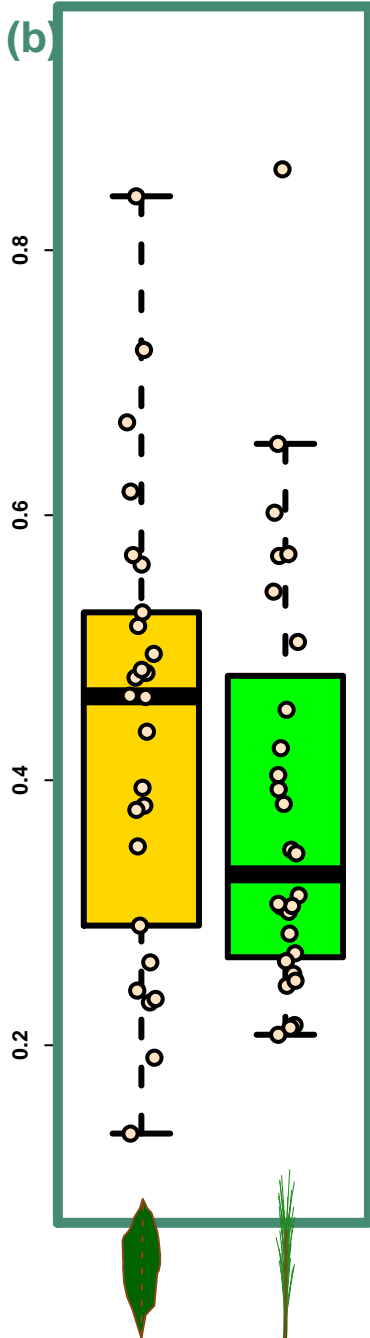




Variance in biomass-allocation fractions



Variance in biomass-allocation fractions



Variance in biomass-allocation fractions

