Global Change Biology

Global patterns of intraspecific leaf trait responses to elevation

| Abstract: | Elevational gradients are often used to quantify how traits of plant species respond to abiotic and biotic environmental variation. Yet, such analyses are frequently restricted spatially and applied along single slopes or mountain ranges. Since we know little on the response of intraspecific leaf traits to elevation across the globe, we here perform a global meta-analysis of leaf traits in 104 plant species from 71 studies and four continents published between 1983 and 2017. We quantified the intraspecific change of seven morpho-ecophysiological leaf traits along global elevational gradients: specific leaf area (SLA); leaf mass per area (LMA); leaf area (LA); nitrogen concentration per unit of area (N$area$); nitrogen concentration per unit mass (N$mass$); phosphorous concentration per unit mass (P$mass$) and carbon isotope composition (δ^{13}C). We found LMA, N$area$, N$mass$ and δ^{13}C to significantly increase and SLA to decrease with increasing elevation. Conversely, LA and P$mass$ showed no significant pattern with elevation worldwide. Furthermore, we found significantly larger increase in N$area$, N$mass$, P$mass$ and δ^{13}C with elevation in warmer regions. Overall, larger responses to elevation were discernible for SLA, but not for the other traits, of herbaceous compared to woody species. Finally, we also detected strong covariation across morphologial and physiological traits within the same elevational gradient. In sum, we demonstrate that there are common cross-species patterns of intraspecific leaf trait variation across elevational gradients worldwide. Irrespective of whether such variation is genetically determined via local adaption or attributed to phenotypic plasticity, the leaf trait patterns quantified here suggest that plant species have different individuals adapted to live on a range of temperature conditions. Since the distribution of mountain biota is predominantly shifting upslope in response to climate change, our results |

	are important to further our understanding of how plants species adapt to elevation in a warming climate.

1 **Title:** Global patterns of intraspecific leaf trait responses to elevation

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3 **Running Title:** Leaf traits vary with elevation

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Abstract

20

21 Elevational gradients are often used to quantify how traits of plant species respond to abiotic and

22 biotic environmental variation. Yet, such analyses are frequently restricted spatially and applied along

23 single slopes or mountain ranges. Since we know little on the response of intraspecific leaf traits to

24 elevation across the globe, we here perform a global meta-analysis of leaf traits in 104 plant species

25 from 71 studies and four continents published between 1983 and 2017. We quantified the intraspecific

26 change of seven morpho-ecophysiological leaf traits along global elevational gradients: specific leaf

27 area (SLA); leaf mass per area (LMA); leaf area (LA); nitrogen concentration per unit of area (N*area*);

28 nitrogen concentration per unit mass (N*mass*); phosphorous concentration per unit mass (P*mass*) and

29 carbon isotope composition ($\delta^{13}C$). We found LMA, N*area*, N*mass* and $\delta^{13}C$ to significantly increase

30 and SLA to decrease with increasing elevation. Conversely, LA and P*mass* showed no significant

31 pattern with elevation worldwide. Furthermore, we found significantly larger increase in N*area*,

32 N*mass*, P*mass* and $\delta^{13}C$ with elevation in warmer regions. Overall, larger responses to elevation were

33 discernible for SLA, but not for the other traits, of herbaceous compared to woody species. Finally,

34 we also detected strong covariation across morphologial and physiological traits within the same

35 elevational gradient. In sum, we demonstrate that there are common cross-species patterns of

36 intraspecific leaf trait variation across elevational gradients worldwide. Irrespective of whether such

37 variation is genetically determined via local adaption or attributed to phenotypic plasticity, the leaf

38 trait patterns quantified here suggest that plant species have different individuals adapted to live on a

39 range of temperature conditions. Since the distribution of mountain biota is predominantly shifting

40 upslope in response to climate change, our results are important to further our understanding of how

41 plants species adapt to elevation in a warming climate.

42 **Keywords:** altitude, carbon isotope ratio, meta-analysis, leaf nutrient content, intraspecific

43 variability, phenotypic variability, plant functional traits, environmental gradient

Introduction

44

45 Mountain ecosystems are characterized by a rapid change of climatic conditions along elevational

46 gradients (Jump, Matyas, & Penuelas, 2009; Körner, 2007). Spatial heterogeneity in site conditions

47 is further increased by small-scale variation in topography, inclination, exposition and substrate.

48 Steep climate gradients along short horizontal distances and pronounced small scale heterogeneity in

49 site conditions make mountain environments unparalleled natural laboratories to study how plants

50 respond to changes in environmental conditions (Graae et al., 2012; Jump et al., 2009; Sides et al.,

51 2014). The environment selects for the optimal phenotype adapted to a given range of resources and

52 conditions, for instance, temperature, soil moisture, nutrient availability and disturbance in each

53 population (Keddy, 1992; Violle et al., 2007; Wellstein & Kuss, 2011). Thus, various abiotic and

54 biotic environmental conditions occurring across elevations tend to select for different ecological

55 strategies among individuals of the same species. Such strategies are reflected in species-specific

56 patterns of changes in physiological and morphological traits along elevation (Sides et al., 2014),

57 which in turn are expected to greatly affect higher levels of organization (Violle et al., 2007).

58 There is a growing body of evidence showing that intraspecific trait variation (ITV) - due to

59 phenotypic plasticity or local adaptation - has a significant and non-negligible effect on species

60 properties and ecosystem function; for instance, to understand phenotypic plasticity, plant community

61 assembly and ecosystem processes (Burton, Perakis, McKenzie, Lawrence, & Puettmann, 2017;

62 Helsen et al., 2017; Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013). Specifically, changes in

63 leaf morpho-physiological traits have been widely adopted as an indicator of plant's trade-off between

64 growth rate and resource conservation (Reich, Walters, & Ellsworth, 1992; Wright et al., 2004). In

65 addition, leaf traits such as specific leaf area (SLA) and nutrient content are linked to various

66 ecosystem services, such as soil fertility (Ordoñez et al., 2009), litter decomposition (Cornwell et al.,

67 2008) and carbon sequestration (De Deyn, Cornelissen, & Bardgett, 2008).

68 Studies comparing plant species individuals located at different elevations (i.e. along elevational

69 gradients or transects) on single slopes or mountain ranges provide relevant insights on the patterns

70 of the adaptation of the leaf in response to biotic and abiotic variation in the environment (Birmann

71 & Körner, 2009; Seguí, Lázaro, Traveset, Salgado-Luarte, & Gianoli, 2018; Woodward, 1983).

72 Changes in leaf morpho-physiology observed along elevation is not due to elevation per se, but they

73 depend on a set of abiotic and biotic environmental factors that typically change with elevation

74 (Körner, 2007; Read, Moorhead, Swenson, Bailey, & Sanders, 2014). As elevation increases,

75 temperature and atmospheric pressure tend to decrease, and solar radiation under clear-sky conditions

76 to increase (Körner, 2007). Especially air temperature has been described as a key factor that strongly

77 covaries with elevation worldwide and determines vegetation distribution in mountain environments

78 (Jump et al., 2009; Körner, 2007; Körner & Paulsen, 2004). Among other factors affecting plant

79 growth, increased elevation usually implies changes in precipitation, solar radiation, wind velocity,

80 soil fertility and disturbances by land use (Fisher et al., 2013; Lembrechts et al., 2016; Macek,

81 Macková, & Bello, 2009), but the direction and strength of the relationship between elevation and

82 these factors may vary strongly across the globe (Körner, 2007). Although there is no clear elevation-

83 climate relationship in mountain environments worldwide, lower elevation conditions tend to favour

84 resource-acquisitive strategies that help individuals to face higher competition due to higher

85 temperature and resource availability (Callaway et al., 2002; Read et al., 2014). Conversely, higher

86 elevations tend to be characterized by lower temperature and lower competition, pushing individuals

87 to invest more energy in the conservation of resources (Callaway et al., 2002; Callis-Duehl, Vittoz,

88 Defossez, & Rasmann, 2017; Pfennigwerth, Bailey, & Schweitzer, 2017). In general, individuals of

89 the same species growing at higher elevation are expected to show lower leaf area and higher SLA

90 due to increased density of leaf tissues as morphological adaptation to colder conditions (Körner,

91 2003; Poorter, Niinemets, Poorter, Wright, & Villar, 2009). Given the strong relationship between

92 different leaf traits (Poorter & Bongers, 2006; Reich et al., 1992), concentrations of essential

93 macronutrients such as nitrogen and phosphorus in the leaf can also be expected to decrease with

94 elevation together with increasing leaf carbon isotope composition ($\delta^{13}C$) (Birmann & Körner, 2009;

95 Hultine & Marshall, 2000). In addition, decreasing temperature with elevation can also be

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96   accompanied by decreasing herbivory pressure (Rasmann, Pellissier, Defossez, Jactel, & Kunstler,

97   2014), allowing plants to produce morphologically different leaves at higher elevations [i.e. with

98   lower phenolic content, richer in N content and deprived of spines (Callis-Duehl et al., 2017)].

99   Several studies addressed the response of intraspecific leaf trait variation along elevational transects

100   on single slopes or mountain ranges. However, the direction of such changes is expected to vary

101   considerably among studies observed [see e.g. different SLA responses in Seguí et al. (2018), Macek

102   et al. (2009), Woodward (1983)], as the sources of such heterogeneity are manifold. First, studies

103   often report data for only one or few species that largely differ in their ecology and life form. For

104   example, tree species perceive clearly different micro-climatic conditions compared to shorter herbs

105   (Frey et al., 2016; Körner, 2007). Furthermore, woody species are expected to show larger

106   heterogeneity in trait variation due to broader ontogenetic plasticity (Borges, 2009; Siefert et al.,

107   2015). Another source of heterogeneity is the divergent response of precipitation to elevation

108   worldwide (Körner, 2007) because precipitation considerably determines moisture supply and might

109   affect the trait-elevation relationship (Martin & Asner, 2009). Moreover, it has been shown that

110   intraspecific leaf-trait response to aridity can differ between functional groups and between

111   biogeographic species pools, emphasizing the relevance of the evolutionary differences in species

112   strategies (Wellstein et al., 2017). However, applying meta-analytical approaches based on multi-

113   level mixed effect models allows us to compare results from different contexts by controlling for

114   species-specific responses and for the climatic conditions of each gradient (see e.g. Benítez-López et

115   al., 2017; Midolo et al., 2019).

116   Here, we tested the overarching hypothesis that intraspecific leaf trait adjustment appears in the same

117   direction showing a common trait-elevation relationship across different plant species worldwide.

118   Therefore, we summarize with a meta-analysis the intraspecific leaf-trait variation along 92

119   elevational gradients worldwide in order to (i) reveal the overall effects of elevation on leaf-trait

120   variation and (ii) test whether average environmental conditions of each gradient (mean temperature

121   of the growing season, mean annual radiation, aridity and mean absolute elevation of the lowest site),

122   and (iii) the plant functional types considered (herbaceous vs woody) have an effect on the overall

123   trait-elevation relationship. Finally, given the covariation of traits along elevational gradients (Hultine

124   & Marshall, 2000; Zhu, Siegwolf, Durka, & Körner, 2010), we (iv) explore whether variation of

125   single leaf traits along elevation follow consistent patterns with other traits reported in the same study.

126

127   **Materials and Methods**

128   *Trait selection*

129   We analyzed intraspecific variation of seven leaf functional traits in our analysis: specific leaf area

130   (SLA); leaf mass per area (LMA); leaf area (LA); nitrogen content (N$mass$); nitrogen content per unit

131   of area (N$area$); phosphorous content (P$mass$) and carbon stable isotope composition (δ^{13}C). We

132   focused our analysis on leaf traits given their influence on plant growth, development and ecological

133   performance (Poorter & Bongers, 2006; Wright et al., 2004). Our choice was also based on data

134   availability; since the chosen leaf traits are relatively easy to measure, for instance compared to many

135   belowground root traits (Pérez-Harguindeguy et al., 2013), they are consequently more frequently

136   reported in the literature.

137   The SLA is the inverse of LMA and both indicate the ratio between leaf size and leaf dry weight.

138   Since elevational gradients normally report either the mean SLA or the mean LMA, and very rarely

139   the values for every leaf sampled in a given site, it was not possible to convert SLA in LMA, or vice

140   versa. Thus, to maximize the information in the meta-analysis, we included both SLA and LMA and

141   analyzed the traits in two separate datasets. In rare cases that original publications reported data of

142   leaf dry weight and leaf area for every sample or both the SLA and LMA means, we included mean

143   SLA and LMA in both datasets for that study (10.5 % of the studies).

144   *Study selection*

145   We searched for studies on Web of Science combining keywords related to elevational gradients and

146   reflecting different dimensions of leaf traits, for example: ("altitude*" OR "elevation") AND

147   ("specific leaf area" OR "leaf traits" OR "leaf nutrients") (see Appendix S1 for complete search

6

148   string). This resulted in a sample of 659 studies published up to March 2018, of which we scanned

149   the titles and abstracts and then selected 71 studies that fitted to our criteria. Studies eligible for

150   inclusion reported means of traits of individuals of the same species sampled across at least two

151   different elevations within a single slope or mountain range. We only included studies explicitly

152   quantifying trait response along elevational gradients in their experimental design. We excluded

153   studies that investigated trait variation across a large geographical range such as latitudinal gradient

154   studies without clear focus on the effect of elevation only.

155   Studies selected in the meta-analysis reported 92 elevational gradients published between 1983 and

156   2017 across the globe (Figure 1) and focused on intraspecific leaf traits variation of 104 seed plant

157   species in total (see summary list in Table S2.1; Appendix S2). Each study reported data for one or

158   more of the leaf traits selected for the meta-analysis.

159   *Data collection*

160   We extracted the mean, standard error and sample size of each trait reported in each site sampled

161   along the elevational gradient and the absolute elevation (m a.s.l.) of the sites sampled. We used

162   WebPlotDigitizer (Rohatgi, 2018) to extract the data if available only in graphs or retrieved data

163   directly from tables or the main text. In addition, we extracted the name of each species analyzed and

164   the geographical coordinates of the location where the study was performed. Species names were

165   checked across the datasets to standardize species synonyms.

166   We calculated elevation (m) [sensu McVicar and Körner (2013)] as the vertical distance between

167   sites sampled along the gradient and the lowest site sampled as main predictor in the analysis (see the

168   graphical framework in Figure S3.1; Appendix S3). In addition, we collected six other predictors

169   from each elevational gradient that we expected to moderate the response of traits to elevation: 1)

170   absolute elevation of the lowest point sampled (m a.s.l.); 2) mean growing season temperature (°C);

171   3) aridity index (the ratio between mean annual precipitation and mean annual potential

172   evapotranspiration); 4) mean annual solar radiation (W m^{-2}); average latitude of site sampled along

173   the gradient; and 5) plant functional type (herbaceous or woody).

174 Climatic data (temperature, aridity and solar radiation) were estimated using the mean coordinates of

175 all sites of the gradient, or by using the generic coordinates for the study area in case geographical

176 coordinates of sites sampled within each gradient were not provided. We extracted the mean growing

177 season temperature as the three warmest months of the year from the WorldClim database ('BIO10')

178 [version 2.0; www.worldclim.org, Fick and Hijmans (2017)]. Similarly, we also calculated the

179 average solar radiation and the aridity index from the CliMond database (Kriticos et al., 2012) and

180 from the CGIAR-CSI GeoPortal (Trabucco & Zomer, 2010), respectively. The aridity index was

181 calculated as the ratio of annual precipitation (estimated by WorldClim database) to potential

182 evapotranspiration, meaning that higher aridity index values indicate lower aridity. Climatic data

183 were extracted with the 'raster' function of the R package *raster* (Hijmans, 2017) with 30 seconds

184 $(0.93 \times 0.93 = 0.86 \text{ km}^2)$ resolution at the equator.

185 *Data analysis*

186 We calculated log-response ratios (lnRR) for each trait along environmental gradients and species

187 and used those as the effect size in our meta-analysis (Hedges, Gurevitch, & Curtis, 1999). Response

188 ratios were calculated as follows:

$$\text{lnRR}_i = \ln\left(\overline{T}_{A_i}\right) - \ln\left(\overline{T}_B\right)$$

189 where T_A is the mean value of a trait measured at the higher elevational level i compared to the mean

190 of the same trait measured on the same species at a lowest elevation present along the gradient (T_B)

191 (see the graphical framework in Figure S3.1; Appendix S3). Since the selected studies normally

192 reported data for multiple elevational levels i along the gradient, we calculated lnRR for each

193 elevation compared with the lowest. This made the effect sizes non-independent within each study

194 (i.e. multiple mean values compared to one mean value) (see Nakagawa, Noble, Senior, & Lagisz,

195 2017). Thus, we accounted for such correlation by computing the variance-covariance matrix

196 proposed by Lajeunesse (2011) when modeling the data. For non-negative trait values (i.e. all traits

197 considered except for $\delta^{13}C$), a positive value of lnRR indicates that the mean of a certain trait for a

198 given species increases relatively to the mean sampled at the lowest elevational level. Thus, for $\delta^{13}C$

199 a negative value of lnRR means that leaf $\delta^{13}C$ is increasing with elevation, and vice versa.

200 We calculated the sampling variance for each pairwise comparison following Hedges et al. (1999) by

201 using the standard deviations of the means and the number of replicates extracted from the papers

202 and used it to weight each effect size in the meta-analysis. We imputed missing standard deviations

203 values using the coefficient of variation from all complete cases using the 'impute_SD' function of

204 the R package *metagear* (Lajeunesse, 2016).

205 We analyzed the data with multilevel linear mixed-effect models using the 'rma.mv' function of the

206 R package *metafor* (Viechtbauer, 2010). These models weight the precision of each effect size by the

207 inverse of its sampling variance and allows to control for non-independence in the data due to multiple

208 effect sizes per study and species (Nakagawa & Santos, 2012). Models were fitted with a crossed

209 random effect structure including both the identity of each elevational gradients and the species as

210 non-nested random components (Benítez-López et al., 2017; Midolo et al., 2019). Following

211 Konstantopoulos (2011), we nested each observation within the grouping-level in the random

212 structure of the models to account for the possibility that the underlying true effects within each

213 elevational gradient are not homogeneous.

214 To quantify overall relative changes of traits for increasing elevation, we first fitted single meta-

215 regression models using elevation only as moderator. Secondly, starting from the full model including

216 each predictor, we performed a multi-model inference analysis quantifying the importance of

217 predictors to moderate traits variation. For each response variable (i.e. each leaf trait), we ranked a

218 set of models according to the small-sample-size corrected Akaike information criterion (AICc) using

219 the 'glmulti' function of the R package *glmulti* (Calcagno, 2013). The relative importance of each

220 predictor was evaluated with the AICc weight (AICcW), calculated the sum of the weights for the

221 models in which the predictor appeared (Burnham & Anderson, 2010). For each response variable

222 we used a confidence set of models by selecting the smallest subset of models that have a cumulative

223 sum of AICc$W \geq 0.95$ (Johnson & Omland, 2004). We calculated the unconditional estimates of the

224   predictors over the confidence set of models averaged. The relative importance of each predictor in

225   the confidence set was calculated as the sum of the Akaike weights over all the models in which the

226   predictor appeared. Continuous variables were log-transformed (when showing a positive skewness)

227   and then scaled prior to modelling. We checked for collinearity among continuous predictors prior to

228   modelling and found no correlation among predictors (Spearman's $\rho < 0.7$) in any of the datasets

229   analyzed. We checked for potential overparameterization for each of the lowest AICc models selected

230   by plotting the profile of the (restricted) log-likelihood over all the variance and the correlation

231   components of the models (Viechtbauer, 2010).

232   To test how traits covaried along elevational gradients, we estimated the relationship between traits

233   by fitting a model with the lnRR of the first trait as response and the second trait as predictor

234   (Vanneste et al., 2018). These models were estimated on a subset of data retaining only the studies

235   reporting both traits. We did not apply multivariate meta-analytic models to estimate the relationship

236   among our response variables, as the correlation among leaf traits reported by the individual studies

237   were not available and they are necessary to compute the variance-covariance matrix in meta-analysis

238   with multiple correlated outcomes (Berkey, Hoaglin, Antczak-Bouckoms, Mosteller, & Colditz,

239   1998; Lajeunesse, 2011).

240   We checked for publication bias by using the 'funnel' function of the R package *metafor*

241   (Viechtbauer, 2010) and used the modification of the Egger's test proposed by Nakagawa and Santos

242   (2012) to assess funnel plots' asymmetry of the null-models' residuals. We found no evidence for

243   funnel plot asymmetry for all traits analyzed except for P*mass*. The funnel plot of P*mass* was found

244   to be asymmetric due to the large heterogeneity of the true effect, which was not reduced significantly

245   by the inclusion of any predictor in the model. However, the asymmetry of the residuals did not

246   support evidence of publication bias for P*mass* when analyzed in a contour-enhanced funnel plot

247   (Nakagawa & Santos, 2012) (see Appendix S4).

248   All the analyses were performed in R version 3.4.4 (R Core Team, 2018).
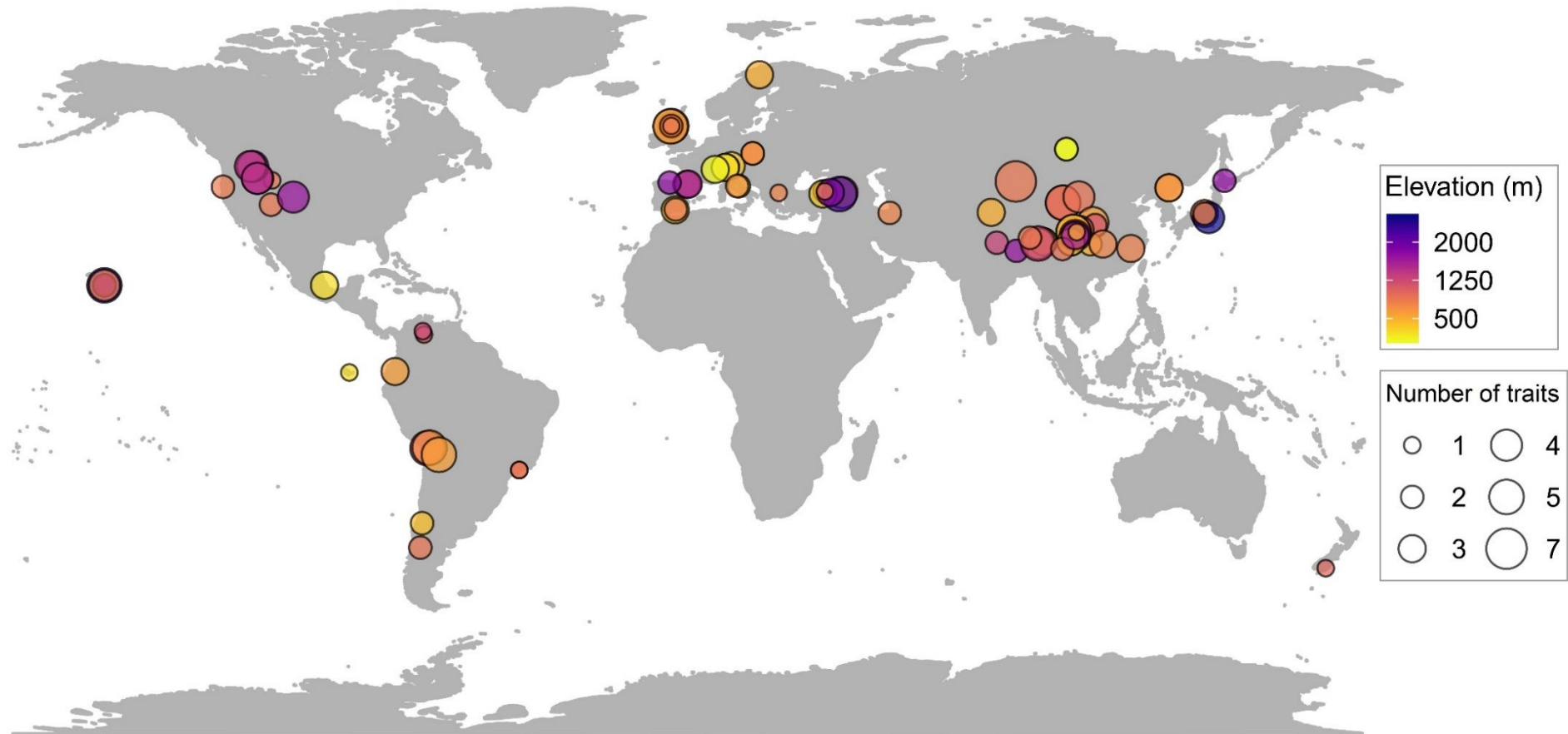
Figure 1: Geographical distribution of the 92 elevational gradients included in the meta-analysis. For each gradient, point size depict the number of leaf traits available and the colours depict the total elevation (i.e the vertical distance between the highest site sampled along the gradient and the lowest site sampled).

Results

Despite large variation, we found clear evidence that intraspecific leaf traits of plants follow convergent patterns of change in response to increasing elevation worldwide. Both sets of models analysing the effect of elevation alone (Figure 2) and the multi-model analysis (Figure 3), indicated that SLA and δ^{13}C response ratios (lnRRs) linearly decreased with increasing elevation, while LMA, N*area* and N*mass* lnRRs increased with elevation. Elevation showed the highest relative importance (AICc*W*) across candidate models (Figure 3) for SLA, LMA, N*area*, N*mass* and δ^{13}C. Conversely, we found no significant evidence of a consistent trend in LA and P*mass*. Leaf area (LA) had a regression slope estimate close to zero, while P*mass* overall increased with elevation, but with a large confidence interval of the slope estimate (Figure 2).

Among relevant predictors moderating overall trait-elevation relationship, the multi-model analysis indicated that only N*mass* was significantly influenced by mean growing season temperature (MGST) (Figure 3). However, the lowest AICc models of N*area*, N*mass*, P*mass* and δ^{13}C retained MGST as significant predictor, indicating that overall larger positive trait variation occured along elevational gradients with relatively warmer growing seasons (Figure 4). The meta-regression analysis also indicated that both herbaceous and woody species tended to have leaf traits changing with the same direction along elevation. However, we found response ratios of SLA to decrease more strongly in herbaceous species than woody species (Figure 3), although the same pattern was not observed in the dataset of LMA. We found no significant evidence for the absolute elevation at the lowest site, mean annual solar radiation, latitude and aridity index to significantly affect the trait variation of any of the leaf functional traits analysed.

The comparisons of response ratios of different traits reported in the same study and species revealed that leaf traits tend to co-vary along elevational gradients (Figure 5). We found δ^{13}C to increase with decreasing SLA and LA, and with increasing LMA and N*area*; while N*mass* and P*mass* variations were not correlated with δ^{13}C variation. In addition, we found that changes in P*mass* do not change

278   consistently with any other traits except N*mass* indicating that two traits positively covary along

279   elevation.

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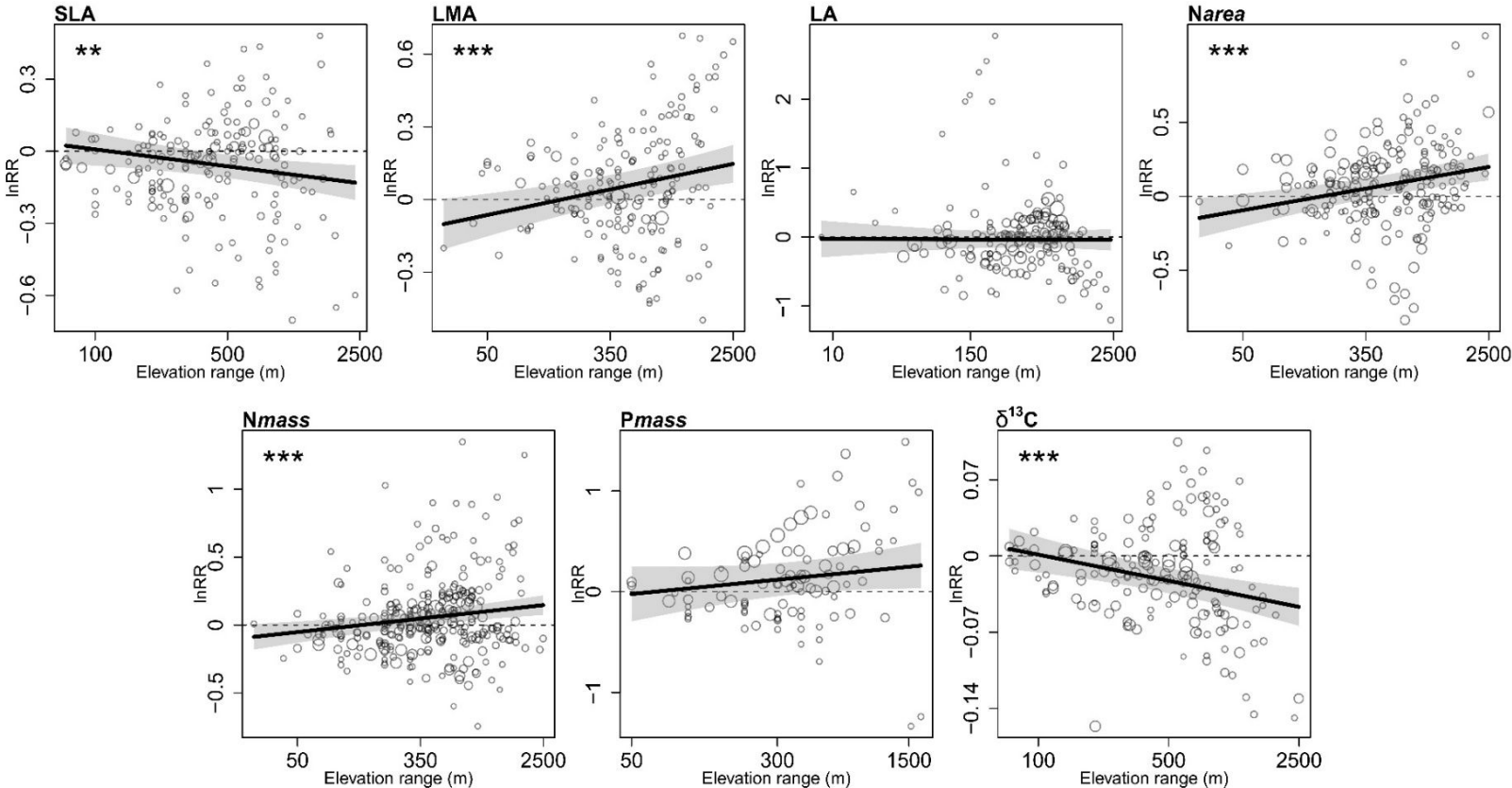
Figure 2: Intraspecific leaf traits variation (lnRRs) in response to elevation (i.e. the vertical distance between two sites sampled along a gradient; log-transformed) across gradients included in the meta-analysis. Solid lines represent the slope estimate of the model (and 95% confidence intervals) with elevation as predictor only. Significance levels (**$P < 0.01$; ***$P < 0.001$) are provided for the slope estimates. A positive value of lnRR indicates that the mean of a certain trait for a given species increases relatively to the mean sampled at the lowest elevational level, except for carbon isotope composition ($\delta^{13}C$) (see 'Materials & Methods'). The dashed lines indicate no change compared to the site sampled at the lowest elevation. Point size depicts the observation weight (weighted by 1/SE).

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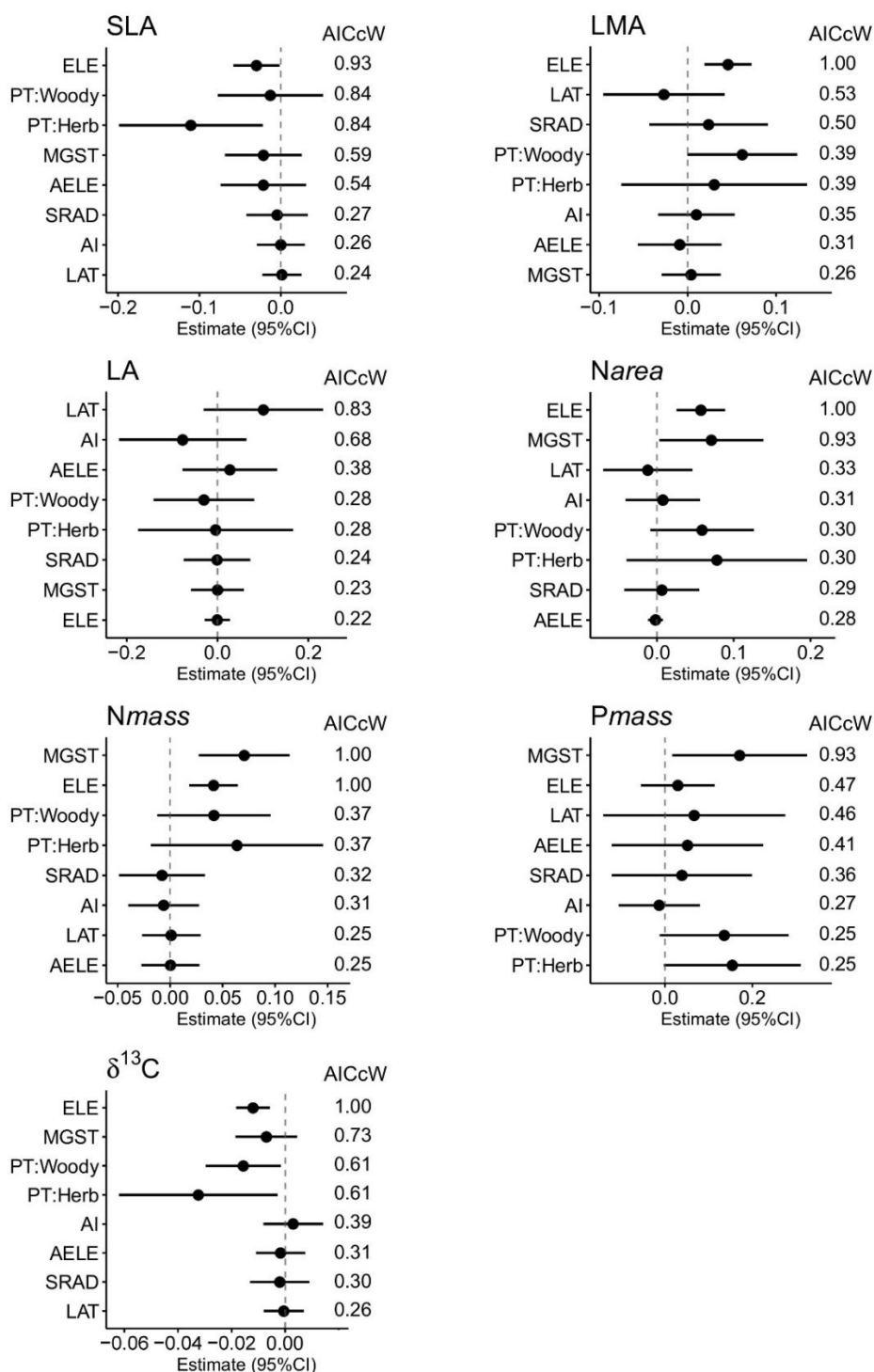
287
288 **Figure 3**: Unconditional estimates and 95% confidence intervals (CI) for fixed effects included in the
289 confidence set of models explaining response ratios (lnRR) of intraspecific leaf trait variation
290 observed across elevational gradients. Continuous predictors are scaled to standardize the magnitudes
291 of the estimates. The relative importance (AICcW) is the sum of AICc weights of models in which a
292 given predictor is retained. ELE = elevation range; AELE = absolute elevation of the lowest site
293 sampled in a gradient; MGST = mean growing season temperature; PT = plant functional types mean
294 pooled effect size (woody or herbaceous); LAT = latitude; AI = aridity index; SRAD = mean annual
295 solar radiation.
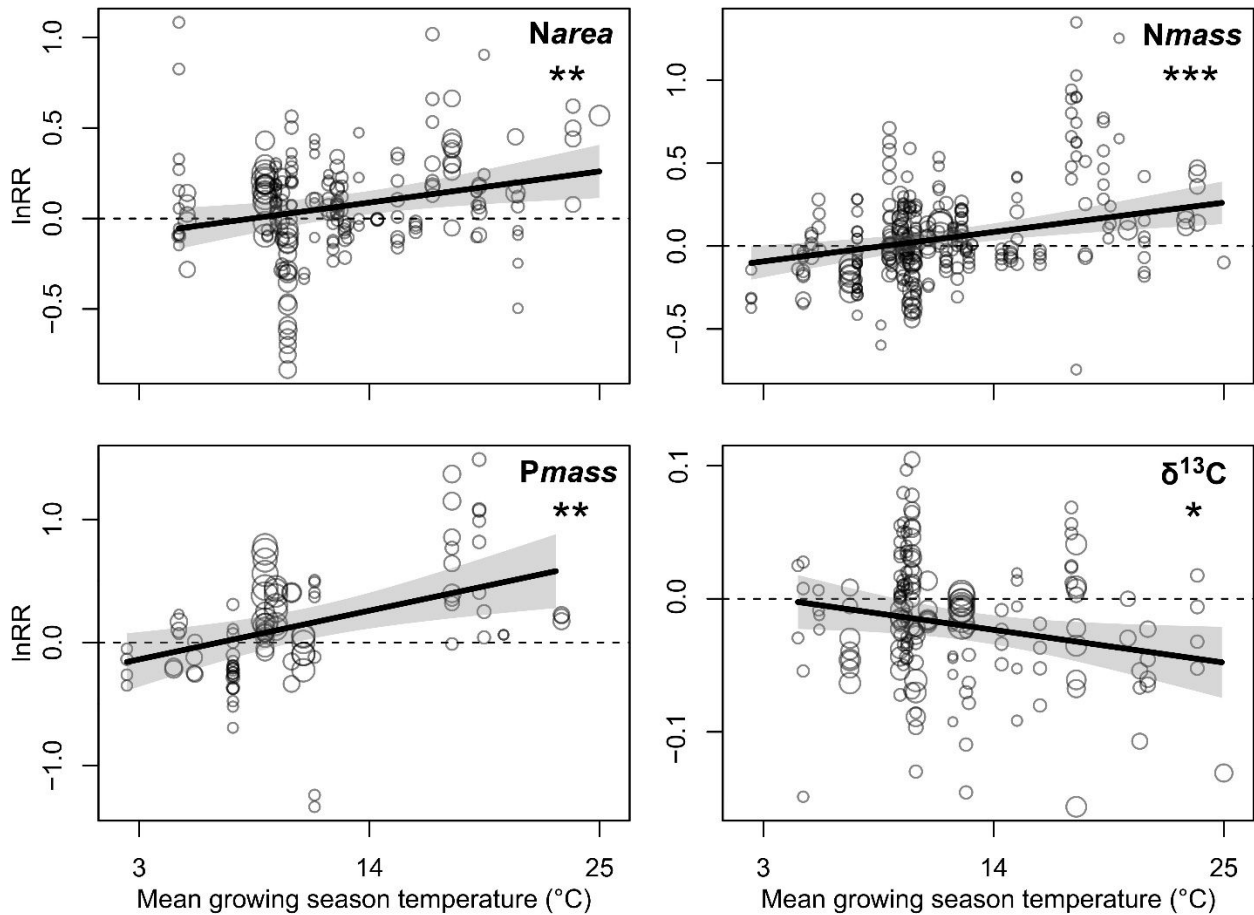
Figure 4: Intraspecific leaf trait variation along elevational gradients (lnRRs) of N*area*, N*mass*, P*mass* and δ¹³C in response to the average mean growing season temperature (MGST) (°C, three warmest months) of each elevational gradient. Solid lines represent the slope estimate (and 95% confidence intervals) obtained from the lowest AICc model in which MGST was retained as moderator. Significance level (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) is provided for the slope estimate. A positive value of lnRR indicates that the mean of a certain trait for a given species increases relatively to the mean sampled at the lowest elevational level, except for carbon isotope composition (δ¹³C) (see 'Materials & Methods'). The dashed lines indicate no change compared to the site sampled at the lowest elevation. Point size depicts the observation weight (weighted by 1/SE).

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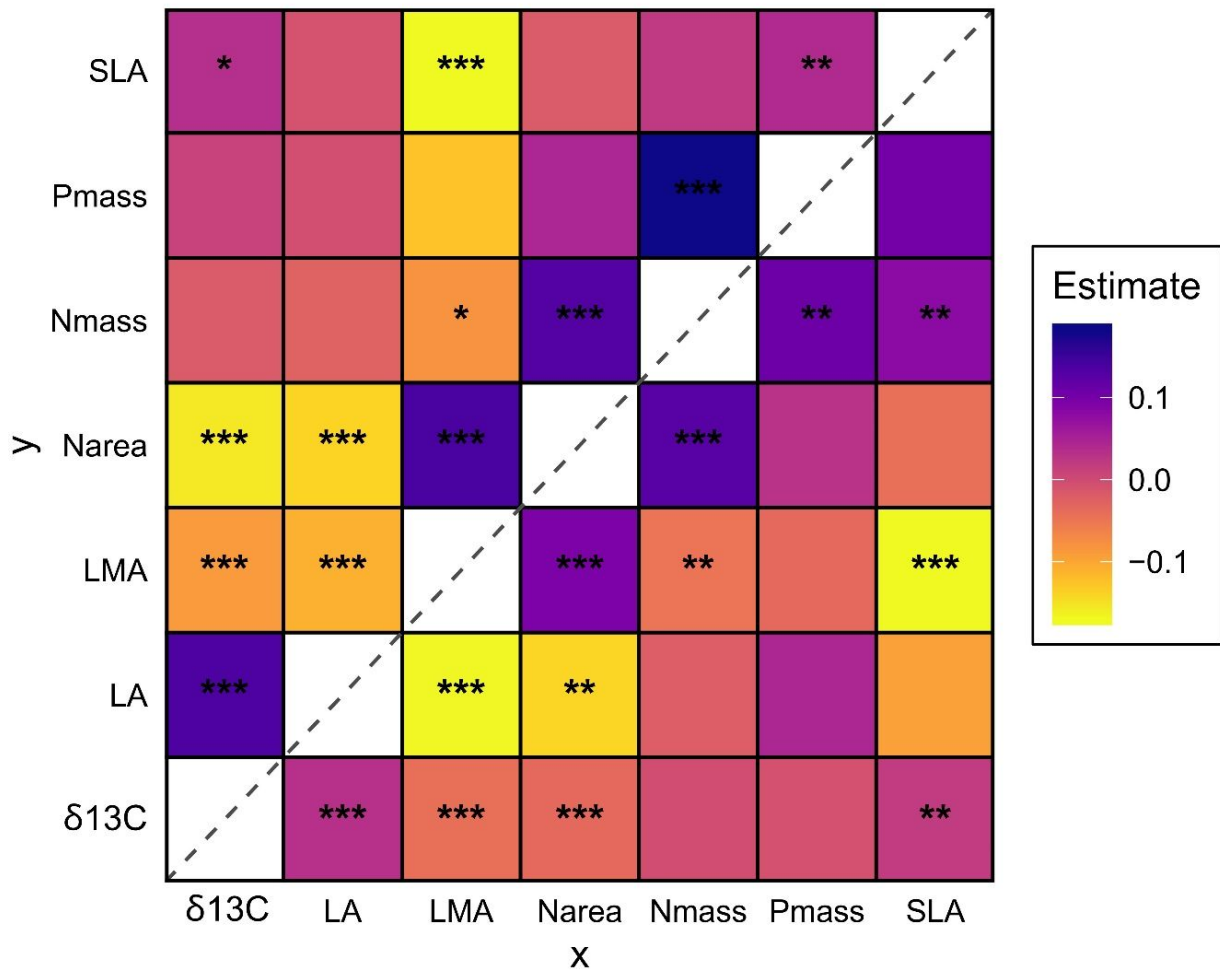
Figure 5: Heatmap of the slope estimates of models obtained from the regression between response ratios (lnRR) of the leaf traits included in the meta-analysis. Models are obtained from a subset of studies reporting data for both traits used in the regression. Values are slope estimates obtained by fitting a model with the lnRR of the first trait as response (y-axis) and the second trait as predictor (x-axis). Significance levels of slope estimates are given (*P < .05; **P < .01; ***P < .001) for each combination. A negative estimate of leaf carbon isotope composition response ratio (δ^{13}C) indicate that δ^{13}C is increasing positively correlated with a given trait (see 'Materials & Methods').

315

Discussion

Leaf traits response to elevation

316 Our results corroborate that intraspecific leaf traits follow general patterns of change in response to

317 elevation and that such patterns occur across different plant species and mountain ranges worldwide.

This is consistent with previous meta-analyses which found plant traits convergence across multiple

elevational (Read et al., 2014) and latitudinal (De Frenne et al., 2013) gradient studies. Despite large

variation, we found that elevation significantly affected all leaf traits analyzed (SLA/LMA, N$area$,

N$mass$ and δ^{13}C) except LA and P$mass$. Overall, we showed that with increasing elevation, plants of

the same species thus produce leaves adapted to abiotic stress (low temperature). At the same time,

leaves exhibit lowered competitive abilities (e.g. lower SLA) and decreasing susceptibility to

herbivore pressure (i.e. higher N$area$ and N$mass$) with increasing elevation (Callis-Duehl et al.,

2017). It remains uncertain whether trait variation across elevations is genetically fixed via local

adaption or can be attributed to phenotypic plasticity (Bresson, Vitasse, Kremer, & Delzon, 2011;

Morecroft & Woodward, 1996; Pfennigwerth et al., 2017). With a review of common garden

experiments, Read et al. (2014) found that genetic differentiation often explains a significant amount

of intraspecific variation of LMA, N$mass$ and N$area$ among populations at different elevations and

latitudes.

The detected changes in SLA and LMA along elevational gradients indicate that the leaves tend to be

thicker and the tissues denser in response to decreasing temperature and increasing irradiance (Poorter

et al., 2009). Although plants species growing at high elevations worldwide tend to produce small

leaves (Wright et al., 2017), our results indicated that interspecific LA variation is not affected by

increasing elevation. Our findings suggest that individuals may need to maintain large LA to capture

light while compensating the lower photosynthetic efficiency driven by the increased leaf tissue

density as expressed in SLA and LMA (Poorter et al., 2009).

The N$area$, N$mass$ and P$mass$ are traits representing the amount of proteins and nucleic acids stored

in the leaf that can be invested for photosynthesis and growth. We found evidence that leaf nutrient

342   content generally tends to increase with elevation. In addition, we showed that there is a strong

343   positive covariation between P*mass* and N*mass* across elevational gradient studies reporting data on

344   both traits (Figure 5). A positive response of N*area* was expected based on the results of a previous

345   meta-analysis on elevational gradients (Read et al., 2014), on the positive correlation between N*area*

346   and LMA (Wright et al., 2004), and because leaf size was expected to decrease with elevation,

347   resulting in N dilution per unit of leaf area (Weih & Karlsson, 2001). Similarly, we were expecting

348   N*mass* to decrease because of the LMA increase and given their negative correlation in the leaf

349   economic spectrum (Wright et al., 2004). In addition, a previous meta-analysis of Read et al. (2014)

350   showed no specific pattern of N*mass* with elevation across the globe, possibly because of the strong

351   interdependence of N*mass* with soil fertility, which does not covary with elevation (Körner, 2007).

352   For the same reasons, we were not expecting P*mass* to increase across elevations either. Thus, the

353   positive trends we found for N*mass* and P*mass* were in contrast with the hypothesis that leaf traits

354   shows resource-conservative strategies with increasing elevation (Pfennigwerth et al., 2017; Read et

355   al., 2014). However, the changes in leaf nutrient content we observed are consistent with Körner

356   (1989) and with the increase in leaf N and P concentration toward the poles as average temperature

357   decreases (Reich & Oleksyn, 2004). The increasing leaf nutrient content at lower temperatures might

358   reflect the acclimation of optimal N use-efficiency and decreased N dilution due to the reduced

359   aboveground biomass growth rate (Weih & Karlsson, 1999; Weih & Karlsson, 2001). Furthermore,

360   N*area*, N*mass* and P*mass* positive variation along elevation might be interpreted as a physiological

361   compensation to the decreasing photosynthetic efficiency caused by decreasing SLA, as higher tissue

362   density enhances the leaf internal resistance to water and CO_2 (see Figure 4) (Morecroft, Woodward,

363   & Marris, 1992).

364   Increasing $\delta^{13}C$ indicated a decreasing ratio of CO_2 partial pressure inside the leaf to that in the

365   atmosphere. Such trend is consistent with the conclusion that plants at higher elevation show higher

366   leaf $\delta^{13}C$ worldwide (Körner, Farquhar, & Roksandic, 1988; Wang et al., 2013). Environmental

367   factors influencing the positive trend of $\delta^{13}C$ along elevational gradients are not fully clear in the

19

368   literature (Körner, Farquhar, & Wong, 1991; Morecroft et al., 1992), but evidence suggest that such

369   trend is linked to both decreasing temperature and atmospheric pressure (Cernusak et al., 2013).

370   Lower oxygen partial pressure increases the carboxylation efficiency of the Rubisco enzyme

371   (Farquhar & Wong, 1984) and the decreasing temperature slows down the transport of water in the

372   plant, resulting in reduced leaf CO_2 diffusion rates (Cernusak et al., 2013). Additionally, the leaf $\delta^{13}C$

373   response may not depend on environmental factors directly but on the morpho-physiological

374   adjustment of the leaf to elevation (Gerdol, Iacumin, & Tonin, 2018; Hultine & Marshall, 2000;

375   Vitousek, Field, & Matson, 1990; Zhu et al., 2010). Indeed, or results indicate that $\delta^{13}C$ increase when

376   leaf area is reduced (Figure 5), possibly because the plant adapts the level of water use efficiency to

377   transpiration rate and light interception, which both depend on the leaf area (Wright et al., 2017).

378   Finally, similarly to what we suggested for N*mass* and P*mass*, the covariation we found for $\delta^{13}C$ with

379   SLA and LMA (Figure 5) in both datasets might reflect leaf physiological compensation to decreasing

380   carboxylation efficiency induced by increasing leaf tissue density (Vitousek et al., 1990).

381   ***Biogeographic factors influencing the response of leaf traits to elevation***

382   Our analysis revealed that the directions of trait-elevation relationships do generally not differ across

383   different climates mountain ranges worldwide. However, our multi-model inference analysis revealed

384   that the magnitude of the intraspecific leaf trait variation along elevational gradients is affected by

385   the mean temperature of the growing season. The overall responses of N*area*, N*mass*, P*mass* and $\delta^{13}C$

386   to increasing elevation tended to be stronger along elevational gradients located in warmer

387   macroclimates (Figure 4). This finding shows that plants growing on warmer mountain ranges tend

388   to store larger amounts of N per unit of mass in response to increasing elevation compared to plant

389   species located in mountain ranges where the growing season is characterized by lower temperatures.

390   This is probably linked to the overall higher N concentration in the leaf of plants in cold climates

391   (Körner, 1989), which smoothens the effect of increasing N-content with decreasing temperatures

392   along elevational gradients compared to generally warmer climatic conditions. From an ecological

393   point of view, this also suggests that species growing on warmer mountains tends to become

394   potentially more competitive and resource-acquisitive with elevation compared to species located in

395   colder mountain areas. In addition, the current climate warming trends enhance species richness and

396   abundance along elevational gradients and might thus favor plant species that are adapted to live in

397   N-rich conditions, because these species are expected to show higher nutrient content and resource

398   investment in response to increasing competition (Rumpf et al., 2018).

399   Finally, we found that the response to increased elevation does not depend on the elevation of the

400   lowest site sampled, indicating that leaf traits of plants growing both at higher and lower elevation

401   respond with the same magnitude of change to increasing elevational range. This suggests that

402   although plants growing at higher absolute elevation levels show e.g. higher LMA and nutrient

403   concentration (Körner, 1989; Körner, 2003), their relative change to increasing elevational range is

404   expected to be proportionally equal to the one of species with lower LMA and nutrient concentration

405   at lower elevation, possibly because absolute elevation alone does not significantly impact plant

406   growth on a large geographical extent (Körner, 2007).

407   ***Plant functional types responses***

408   We found significant differences in magnitude of variation in SLA across woody and herbaceous

409   species. Our results indicated a larger negative response in herbaceous species in intraspecific SLA

410   with increasing elevation compared to woody species. These findings support the general hypothesis

411   that fast-growing herbaceous plants characterized by lower costs to plasticity are better able to adapt

412   to environmental filtering compared to woody species (Maire et al., 2013). Although there is evidence

413   of leaf trait variation along climatic gradients differs among plant functional types (e.g. C_3 / C_4 dicots

414   and monocots; Ivanova, Yudina, Ronzhina, Ivanov, & Hölzel, 2018), differences across functional

415   groups found in SLA were not reflected in the LMA dataset nor in any of the other traits analyzed

416   here, possibly because herbaceous and woody functional types overlap substantially in their leaf trait

417   characteristics (Wright et al., 2004). In addition, the overall low differences between plant functional

418   groups response to elevation reflected the results of Siefert et al. (2015) who compared the relative

419   extent of intraspecific trait variation in plant communities and found no significant difference in the

420   magnitude of variation between woody and herbaceous species.

421   ***From elevation range to temperature changes***

422   The relationships between elevational range and leaf traits we explored here showed strong similarity

423   with the trait syndrome characterizing plants adapting to colder environments along spatial

424   temperature gradients (Reich & Oleksyn, 2004; Tian, Yu, He, & Hou, 2016). Indeed, temperature is

425   the main factor affecting plant growth that covaries consistently with elevation range in different

426   mountains worldwide (Jump et al., 2009; Körner, 2007). Similarly to latitudinal gradients (De Frenne

427   et al., 2013), elevational gradients offer a promising tool to infer plant responses to temperature

428   change. Combining information obtained from elevational gradients and latitudinal gradients, is an

429   exciting challenge to elaborate a space-for-time substitution providing insights into plant traits

430   response to global warming (Fukami & Wardle, 2005; Read et al., 2014). However, predicting the

431   potential effects of temperature change based on multiple elevational and latitudinal gradients suffers

432   from various weaknesses. Besides the heterogeneity caused by different experimental designs, study

433   aims and biogeographical contexts, which can be accounted by using meta-analytical approaches (see

434   e.g. Midolo et al., 2019), studies analyzed often do not report data on temperature change along each

435   gradient (Graae et al., 2012) as well as other relevant factors such as humidity, soil fertility and land-

436   use. As a result, both elevational and latitudinal gradients are still currently underused to study climate

437   change on a large geographical extent (De Frenne et al., 2013).

438   However, considering possible further unexplored impacts of climatic variation, it is even more

439   surprising that our findings suggest the same direction of SLA/LMA response to elevation while they

440   had opposing directions of SLA response to drought depending on functional groups and

441   biogeographic history (Wellstein et al., 2017). According to our findings, species across

442   biogeographical groups evolved strategically the same way of key leaf-trait response to temperature

443   (across elevations) while already only within Europe they are differentiated in their strategy to deal

444   with aridity (Wellstein et al., 2017). This means that direction of plant functional responses to

445 temperature changes could be predicted more easily while plant functional response to changes in

446 water availability has to be tested against the evolutionary background of the species. Moreover, in

447 line with De Frenne et al. (2013), Read et al. (2014) and Wellstein et al. (2017) our findings further

448 reinforce the importance of intraspecific variation as important driver of functional plant response to

449 climate changes.

450 *Concluding remarks*

451 We here combined results of multiple elevational gradients studies focusing on leaf traits variation

452 with a meta-analysis to reveal patterns of intraspecific morpho-physiological traits adjustment to

453 high-elevation conditions worldwide. Summarizing evidence from a variety of elevational gradients

454 helps us to understand the potential implications of climate change on individual species in the

455 coming years when focusing on temperature changes taking into account other changes across

456 elevations (Körner, 2007). Irrespective of the mechanisms behind traits variation along elevational

457 transects, we clearly showed that populations located along elevational gradients exhibit individuals

458 adapted to different abiotic conditions. Since the distribution of mountain biota is shifting upslope in

459 response to climate change (Lenoir, Gégout, Marquet, Ruffray, & Brisse, 2008; Rumpf et al., 2018;

460 Steinbauer et al., 2018), our results are particularly important to understand how plants adapt to such

461 elevation shift in a warming planet. Within the considered temperature range, our findings indicate

462 that future upward migrating species most likely will lower their SLA and increase their nitrogen

463 content and $\delta^{13}C$. However, plant-life beyond the here analyzed realized niche, i.e. the emergence of

464 new parts of the realized niche based on the fundamental one has rarely been tested so far (Violle and

465 Jiang, 2009). In this context, experimental research would enable new knowledge on the hidden part

466 of plant variability.

467 Finally, the magnitude of intraspecific trait variation we observed is expected to scale up to higher

468 levels of biological organization (Violle et al., 2007). Thus, when analyzing functional trait response

469 to elevation at the community level, intraspecific variability is expected to significantly contribute to

470 the variation observed among plant assemblages at different elevation levels.

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Conflict of interest

The authors have no conflicts of interest to declare.

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Supporting Information

APPENDIX S1: Search string for primary studies collection

APPENDIX S2: List of primary studies and species analysed in the meta-analysis

APPENDIX S3: Details on the calculation of the effect size

APPENDIX S4: Null models, funnel plots and analysis of publication bias