1 **Manuscript title**

2 Mechanisms driving plant functional trait variation in a tropical forest

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4 **Running title**

5 Drivers of plant functional trait variation

6

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21 **Key-words**

22 Biodiversity, Costa Rica, climate change, plant functional traits, tropical forest

23

24 **Abstract**

25   Plant functional trait variation in tropical forests results from taxonomic differences in

26   phylogeny and associated genetic differences. as well as, phenotypic plastic responses

27   to the environment Accounting for different components driving plant functional trait

28   variation is important for understanding the potential rate of change of ecosystems since

29   trait acclimation via phenotypic plasticity is very fast compared to shifts in community

30   composition and genetic adaptation. We here applied a statistical technique to

31   decompose the relative role of phenotypic plasticity, genetic adaptation and

32   phylogenetic constraints. We examined typically obtained plant functional traits, such

33   as wood density, plant height, specific leaf area, leaf area, leaf thickness, leaf dry mass

34   content, leaf nitrogen content and leaf phosphorus content. We assumed that genetic

35   differences in plant functional traits between species increases with geographic

36   distance, whereas trait variation due to plastic acclimation to the local environment is

37   independent of spatial constraints. Results suggest that most of the observed trait

38   variation could not be explained by a single component, thus indicating a limited

39   potential to predict individual plant traits from commonly measured environmental

40   variables. However, we found a non-uniform response between different plant tissues

41   in accordance with the plant economic spectrum, such that leaf traits varied in response

42   to canopy light regime and nutrient availability, whereas wood traits were related to

43   topoedaphic factors and water availability. Our analysis furthermore indicated

44   differences in the functional response between coexisting tropical tree species, such that

45   endemic species with conservative ecological strategies appear especially prone to

46   competitive exclusion under projected climate change.

47

48   **Introduction**

49   In general, variation of plant functional characteristics should enhance a plant's ability

50   to cope with shifts in the local environment as species with higher trait variability

51   should exhibit greater trait–environment matching than less variable species (Mitchell

52   et al. 2016). Such trait variation includes plasticity in a species' characteristics that

53   enhances its ability to quickly respond to environmental changes (Fox et al. 2019), as

54   well as genotypic adaptation (evolution) in response to environmental variation over

55   longer timespans (Murren et al. 2015). Consequently, species with a high degree of trait

56   plasticity have been found much more likely to succeed in a given environment (Hulme

57   2008) and, vice versa, species showing low plasticity have been found more vulnerable

58   to changing environmental conditions (Sides et al. 2014). Hence, accounting for the

59   different underlying mechanisms driving trait variation, and in particular to

60   differentiate plasticity from other mechanisms of trait variation, is important for

61   understanding and accurate modeling of vegetation dynamics (Franklin et al. 2020).

62   The different mechanisms of trait variation are associated with different drivers. Factors

63   shaping species composition, and thus determining associated plant functional traits,

64   have been reported to shift across latitudinal and altitudinal gradients (Ackerly &

65   Cornwell 2007). For tropical forests, it has been shown that across larger spatial scales

66   abiotic factors, such as temperature and precipitation, are key determinants of

67   ecosystem processes (Cleveland et al. 2011; Taylor et al. 2017). In contrast, at smaller

68   spatial scales other biotic factors, such as competition among coexisting tree species,

69   strongly affect ecosystem structure and functioning via the composition of the local

70   species pool (Fauset et al. 2012; Taylor et al. 2015). Indeed, it has been found that

71   competition can have equally strong impacts on trait expression as the dominant abiotic

72   driver (Albert et al. 2010; Violle et al. 2012; Le Bagousse Pinguet et al. 2015), which

73   further highlights that it is crucial to account for different components driving the plant

74   functional traits variation (Jung et al. 2010). So far, most studies have been assessing

75   mean-species' trait values compiled from published datasets comprising global

76   observations (Swenson & Enquist 2007; Kraft et al. 2008; Freschet et al. 2011), and

77   thus have been unable to differentiate the variation in plant functional traits in response

78   to multiple and interactive controlling factors (Ackerly & Cornwell 2007; Sides et al.

79   2014).

80   Here, we aimed to differentiate the underlying mechanisms controlling plant functional

81   trait variation and to quantify the respective contribution of environmental factors

82   driving trait variation in tropical forests. We analyzed a trait dataset compiled from in-

83   situ measurements of the following plant functional traits: (1) wood density, as an

84   important part of the wood-economics spectrum (Chave et al. 2009) associated with

85   drought tolerance and shade tolerance; (2) maximum plant height, as a strategy to

86   enhance light exposure and linked to drought vulnerability (Rowland et al. 2015); (3)

87   leaf area, (4) leaf thickness, and (5) specific leaf area, which are associated with light

88   capture; (6) leaf dry mass, (7) leaf nitrogen content, and (8) leaf phosphorus content,

89   which are related to the availability of soil water and soil nutrients determined by local

90   site conditions, and which are included in the leaf-economics spectrum (Wright et al.

91   2004).

92   For each of the plant functional traits investigated in this study, we aimed to

93   differentiate respective components of trait variation, in particular, the amount of

94   phenotypic plasticity versus other components, including genetic adaptation and

95   species turnover between sample sites. Whereas phenotypic plasticity is influence by

96   many different factors, here we focus on a particularly relevant aspect with respect to

97   climate change: plasticity driven by environmental variation. We evaluated the

98   components of trait variation based on the assumed driving factors, i.e. local

99   environmental heterogeneity independent of geographic distance among study sites (i.e.

100 the pure environmental factor), spatial distance between sample sites, while accounting

101 for environmental heterogeneity among study sites (i.e. the pure spatial factor), and

102 other factors not accounted for in the analysis (i.e. the unexplained variation factor). In

103 addition, we tested the hypothesis that endemic and widespread species differ in their

104 degree of trait plasticity.

105

106 **Material and Methods**

107 <u>Study region</u>

108 The study was conducted in tropical lowland forests located between 50 and 450 m

109 a.s.l. in the Área de Conservación Osa (ACOSA) at the Pacific slope of southwestern

110 Costa Rica (08.6°N, 83.2°W). The region was declared a biodiversity hotspot with 700

111 tree species among 2369 species of ferns, fern allies, and flowering plants recorded in

112 total (Quesada et al. 1997). The terrain is characterized by parent material originating

113 from the Cretaceous, Tertiary and Quaternary (i.e., basalt, alluvium and sediment) and

114 is divided into six different landforms (i.e., denudational, volcanic, alluvial, structural,

115 littoral, tectonic) and four soil orders (i.e., Entisols, Inceptisols, Mollisols and Ultisols

116 (Lobo 2016)). The dominating, highly weathered, strongly acidic Ultisols on ridges and

117 upper slopes are replaced by younger, moderately weathered Inceptisols in ravines and

118 lower slopes and little developed Mollisols in fluvial deposits (Lobo 2016). Starting in

119 1997, daily climatologic data for temperature and precipitation are available from a

120 nearby meteorological weather station located at La Gamba field station:

121 https://www.lagamba.at/en/tropical-field-station/scientific-data-of-the-golfo-dulce-

122 region/. Mean annual precipitation for the period 1998-2008 was 5892 mm, with no

123 month receiving less than 180 mm on average. The rainy season usually lasts from April

124   to December, and the driest months are January to March. Mean annual temperature for

125   the period 1998-2008 was 28.0 °C and ranged between 23.7°C and 33.7°C

126   (Weissenhofer et al. 2008).

127

128   <u>Environmental variation among sampling sites</u>

129   In order to account for environmental variation among sampling sites and associated

130   effects on trait variation among congeneric tree species, we measured the slope of the

131   forest stand (using a clinometer) and estimated crown exposure to light using an index

132   from 0 to 5. Moreover, we took geographical coordinates using a GPS device (Garmin

133   60 CSX, with a mean relative standard error of 6 m). Based on these coordinates, we

134   extracted bioclimatic variables (at a resolution of ~1 km^2) from Worldclim (Hijmans et

135   al. 2005), including annual mean temperature, mean diurnal temperature range,

136   isothermality (ratio of day-to-night temperature oscillation to summer-to-winter

137   temperature oscillation), annual precipitation, precipitation seasonality, and

138   precipitation during warmest quarter.

139

140   <u>Selection of tropical tree species and plant functional traits</u>

141   A full description of tropical tree species selected for sampling of plant functional traits

142   has been reported in a foregoing study (Chacón-Madrigal, Wanek, Hietz, & Dullinger

143   2018a). Briefly, we selected 34 tree species from 14 genera and grouped them into pairs

144   of congeneric species (Table 1). Each congeneric pair comprised one narrowly endemic

145   species (either restricted to the central and southern Pacific slope of Costa Rica, or, in

146   some cases, reaching western Panama or the Caribbean slope in Costa Rica), and one

147   species distributed more widely. From each of the ten selected tree individuals per

148   species (n=335), we collected five fully expanded, mature leaves with no signs of

149   damage and one wood core from each tree. For each tree, we determined wood density,

150   quantified by wood specific gravity (WSG) on a collected wood core, and measured

151   total plant size, i.e., tree height (Height). For each leaf of each tree, we analyzed four

152   functional traits: leaf area (LA), leaf thickness (LT), leaf dry matter content (LDMC),

153   and specific leaf area (SLA) according to standard protocols (Pérez-Harguindeguy et

154   al. 2013). On a pooled leaf sample per individual, we further measured leaf nitrogen

155   content (N) and leaf phosphorus content (P). Leaf nitrogen content was measured by

156   dry combustion using an auto analyzer (Rapid Exceed, Elementar, Langenselbold,

157   Germany), and leaf phosphorus content was determined by acid digestion and

158   inductively coupled plasma-optical emission spectroscopy (ICP-OES) using a

159   spectrometer Optima 8300 (Perkin Elmer, Waltham, US) at the laboratory of the

160   Agronomic Research Center (Centro de Investigaciones Agronómicas) of the

161   University of Costa Rica.

162

163   <u>Theory and assumptions</u>

164   While functional trait variation and phenotypic plasticity are governed by complex

165   interactions among genetic and environmental factors, here we address solely the

166   component of plasticity driven environmental variation. Our approach does not separate

167   plasticity from ontogenetic effects or possible micro-scale adaptation (Richardson et al.

168   2014; Brousseau et al. 2015), as this was not feasible based on the available dataset.

169   Here, we focus on trait variation among sampled tree individuals, while accounting for

170   species and intra-specific genetic differences, both of which are influenced by the

171   environment but will additionally be affected by other factors, such as spatial distance

172   between individuals. We here applied a statistical technique to separate environment-

173   driven plasticity from other sources of trait variation (i.e. spatial distance effects) based

174 on the observed variation of plant functional traits sampled from tree individuals at

175 different locations in the study region. We tried to avoid ontogenetic effects on trait

176 variation by selecting only mature individuals (classified as such based on their

177 diameter at breast height) and accounted for species phylogeny and differences in range

178 size among coexisting widespread and congeneric endemic tree species by analyzing

179 species mean values.

180

181 Statistical analysis

182 Statistical analyses were performed using the R statistical software environment and

183 respective packages "cati", "ecodist", "fmsb", "lme4", "vegan" (R Core Team 2018).

184 We performed a principal component analysis (PCA) relating the investigated eight

185 plant functional traits to in-situ observed environmental variables (slope of the forest

186 stands and estimated crown exposure to light). In addition, for unmeasured climatic

187 variables we extracted Worldclim bioclimatic variables (i.e., annual mean temperature,

188 mean diurnal temperature range, isothermality (ratio of day-to-night temperature

189 oscillation to summer-to-winter oscillation), annual precipitation, precipitation

190 seasonality and precipitation of warmest quarter). We then combined these

191 environmental variables after normalization by means of z-scores (first ordination axis

192 explaining 86% of the variation) to characterize the mesoclimatic environment of the

193 sampled plant functional traits and plotted respective factor loadings for mean annual

194 temperature and relative humidity ("Climate"), soil clay, sand and silt content ("Soil"),

195 topography ("Slope") and canopy light index ("Light").

196 We used linear mixed effects models to test for significant factors driving plant

197 functional trait variation, while accounting for random effects due differences in sites,

198 plot   location,   species   composition   and   random   factors: [lme(factor~1,

199   random=~1|Locality/Plot/Species/UID)]. To furthermore account for spatial

200   autocorrelation between sample sites and taxonomic constraints among species we

201   applied multiple regression on distance matrices (MRM), which has been used to

202   disentangle the influence of space and environmental factors in ecological data

203   (Lichstein, 2006), and to relate phylogenetic or functional beta diversity to spatial and

204   environmental distance (Swenson 2014). In this study, we used MRM to relate a

205   response distance matrix (∂_Y) with respective distance matrices accounting for

206   environmental, spatial, and interactive effects. To this end, we calculated correlation

207   coefficients between distance matrices of plant functional traits (∂_T), environmental

208   factors (∂_E), and geographic distance (∂_S), and partitioned the total observed variation

209   into components of pure environment (E), pure spatial distance (S), and spatial

210   distance-environment interaction (SxE) respectively. This approach allowed to

211   quantified the relative contribution of factors driving plant functional trait variation due

212   to (i) the correlation between trait distance matrix and environmental distance matrix

213   (while accounting for spatial autocorrelation), (ii) the correlation between trait distance

214   matrix and spatial distance matrix (while accounting for environmental heterogeneity),

215   and (iii) the correlation between the geographic distance matrix and environmental

216   distance matrix).

217   We used variance partitioning to quantify respective amounts of variation for each of

218   the plant functional traits, and environmental controlling factors, applied one-sided

219   Wilcoxon signed-rank test to assess differences in trait medians between the congeneric

220   pairs of endemic and widespread tropical tree species, and tested for phylogenetic

221   constraints on trait variance for each of the eight plant functional traits, i.e. wood

222   density (WSG), plant height (Height), specific leaf area (SLA), leaf area (LA), leaf

223   thickness (LT), leaf dry-matter content (LMDC), leaf nitrogen content (N), leaf

224 phosphorous content (P), by constructing a taxonomic dendrogram for the 34 tropical

225 tree species investigated in this study.

226

227 **Results**

228 <u>Drivers of plant functional trait variation in tropical forests</u>

229 We quantified relative amounts of variance observed within eight plant functional traits

230 obtained from tropical trees located in southwestern Costa Rica (Fig. 1). Observed

231 variation in plant functional traits ranged from 38.0 to 1645 cm^2 for LA, from 0.16 to

232 0.61 mm for LT, from 66.4 to 236 cm^2 g^{-1} for SLA, from 195 to 472 mg g^{-1} for LDMC,

233 from 0.26 to 0.86 for WSG, from 1.17 to 3.07% for nitrogen content, and from 0.05 to

234 0.23 mg g^{-1} for phosphorus content (Table 1). A PCA investigating relationships

235 between plant functional traits and environmental factors indicated that leaf traits varied

236 in association with light regime and soil nutrient content, whereas wood traits were

237 related to slope position and soil water content (Fig. 2). Analyzing the underlying

238 drivers of these relationships, we found that trait variation was relatively more strongly

239 related to spatial distance, thus often masking trait variation in response to

240 environmental factors due to autocorrelation of space with the environment (Table 2).

241

242 <u>Trait variation due to spatial distance and environmental factors</u>

243 We found that the relative amount of explained variation differed between the

244 environmental and spatial components of trait variation identified in this study (Fig.

245 3a). Our findings indicate that the relationship between wood density and spatial

246 variation in soil texture (p=0.02), slope inclination (p=0.03), light availability (p=0.02)

247 and climatic drivers (p=0.02) was primarily due to *spatial variation* in woody tissue

248 between forest stands, whereas leaf tissue, as well as, leaf chemistry varied in response

10

249   to *environmental factors*, such as light availability (p=0.03 and p=0.01, respectively)

250   and microclimate (p=0.03 and p=0.01, respectively) (Table 2). Testing for the direct

251   environmental drivers (Fig. 3b) revealed that variation in wood density was mostly

252   driven by precipitation (p=0.01), temperature (p=0.03), and light availability (p=0.04),

253   whereas leaf nitrogen content was mostly driven by precipitation (p=0.04), and less so

254   by soil nutrient availability (p=0.05) and light availability (p=0.07) (Table 3).

255

256   <u>Trait variation due to plant life-history strategy and taxonomic species diversity</u>

257   We further found differences in plant functional reaction norms to bioclimatic

258   controlling factors (i.e., slopes of trait response vs. environmental variation) between

259   endemic and widespread tropical tree species, when plotting each plant functional trait

260   against the principal component of the extracted bioclimatic variables (Fig. 4).

261   Although we did not find strict significant differences (p<0.05) in trait variation

262   between endemic and widespread tropical tree species, we found that endemic species

263   tended to exhibit higher wood density (p=0.08), smaller tree size (p=0.08) and higher

264   leaf nitrogen content (p=0.07) compared to widespread tropical tree species (Fig. 5),

265   which might reflect differences in plant life-history strategy between endemic and

266   widespread tropical tree species. Eventually, we found a significant relationship

267   between phylogenetic distance and functional trait variance due to taxonomic

268   relatedness of the sampled tree individuals (belonging to congeneric pairs of

269   widespread and endemic tree species), such that a clear phylogenetic pattern was found

270   for tree height, SLA, LA, LDMC, and leaf N content, whereas such pattern was missing

271   for WSG and leaf P content (Fig. 6).

272

273   **Discussion**

274   We applied a statistical technique accounting for multiple and interrelated components

275   of plant functional trait variation by partitioning total observed variation into

276   components uniquely and jointly explained by environmental heterogeneity, and spatial

277   distance between sampling sites. We found (i) significant interactions between spatial

278   distance and environmental controlling factors, (ii) different environmental controls

279   across plant tissues and associated functional traits, and (iii) non-uniform functional

280   responses among coexisting tropical tree species. We conclude that our current

281   understanding of tropical ecosystem functioning in response to projected climate

282   change would benefit from accounting for the underlying mechanisms driving plant

283   functional trait variation in tropical forests.

284

285   <u>Controls over plant functional trait variation in tropical forests</u>

286   We found that plant functional trait variation is the product of multiple mechanisms and

287   different drivers, including climate but also topoedaphic factors and biotic interactions.

288   In line with our findings, it has been reported that tradeoffs at the species level were

289   only weakly associated with climate and soil conditions when analyzing global trait-

290   environment relationships at the global scale (Bruelheide et al. 2018), because trait

291   combinations were predominantly filtered by local-scale factors such as disturbance,

292   fine-scale soil conditions, niche partitioning, and biotic interactions (Grime 2006).

293   However, because both biotic and abiotic factors do not mutually exclusively affect

294   trait variation, and usually shift in their relative dominance over trait expression across

295   spatial gradients in response to multiple environmental factors, ideally all of these

296   factors should be accounted for when analyzing plant functional trait variation. Here,

297   we found that all of the plant functional traits investigated in this study varied with both

298   spatial distance and environmental factors and therefore applied a statistical method to

299   decompose respective components driving trait variation in response to multiple

300   environmental factors, i.e., soil texture, canopy-light index, slope position, temperature

301   and rainfall (Fig. 3).

302

303   <u>Plant functional trait variation in response to environmental factors and spatial distance</u>

304   Despite a relatively large amount of unexplained variation due to factors not accounted

305   for in the analysis (see R^2 values in Table 2), we were able to identify plant functional

306   trait variation in response to environmental heterogeneity among, and spatial distance

307   between sampling sites. Recalling our assumption about respective components of trait

308   variation, the intra-specific component due to phenotypic plasticity between individuals

309   of one species would be driven by the heterogeneity of the local environment,

310   independent from spatial factors, whereas the inter-specific component due to genetic

311   adaptation and species turnover would be expected to increase with geographic distance

312   between forest stands. Most strikingly, we found this pattern reflected among different

313   plant tissues, such that wood traits varied in response to the spatial component and thus

314   appear less plastic, while leaf traits were more related to the environmental component

315   and thus appear more plastic (Fig. 3), both of which would be in line with the proposed

316   tradeoffs along the plant-economics spectrum (Reich 2014).

317

318   <u>Plant functional trait variation and the plant-economics spectrum</u>

319   Our results, highlighting differences in the strength of relationships between respective

320   components and plant tissues, mirror the underlying mechanisms driving the proposed

321   trade-offs in relative investment between canopy and woody tissues in response to

322   multiple limiting factors (Townsend et al. 2008). We found that leaf nitrogen content

323   and leaf phosphorous content was related to canopy-light regime, while wood density

324 and plant height was associated with slope position and soil texture (Fig. 2). Our results

325 indicate that short-term eco-physiological responses at the canopy-level or leaf-level

326 are associated with canopy light regime, whereas rather longer-term investments into

327 woody tissue are related to topoedaphic and climatic factors (Fig. 3). Overall, this

328 confirms our assumption that plant functional trait variation is controlled by multiple

329 mechanisms and interrelated driving factors, and our findings of trade-offs in relative

330 investment between canopy and woody tissues furthermore indicates that along

331 environmental gradients of resource availability species should be filtered according to

332 differences in their life-history strategy.

333

334 <u>Plant functional traits and species composition across environmental gradients</u>

335 Our analysis revealed differences in the functional response among coexisting tropical

336 tree species, which indicated that under projected climate change range-restricted

337 endemic species might be more susceptible to competitive exclusion than their

338 widespread congeners (Fig. 4). Such, a differential response of tropical tree species to

339 climate change has been reported in a study indicating a shift to more dry-affiliated taxa

340 across Amazonia, where tree communities have become increasingly dominated by

341 large-statured pioneers, while short-statured taxa decreased over the observation period

342 (Esquivel-Muelbert et al. 2019). Indeed, we here found that endemic species were on

343 average characterized by higher wood density and lower leaf nitrogen content compared

344 to their widespread congeners (Fig. 5). Our findings are in line with a foregoing analysis

345 conducted in the same study region, which found that range restricted species with

346 conservative ecological strategies were characterized by high wood density and low

347 leaf nitrogen content, in comparison to coexisting but more widespread species

348 (Chacón-Madrigal, Wanek, Hietz, & Dullinger 2018b). Hence, such differences in plant

14

349   functional traits between coexisting widespread and congeneric endemic tree species

350   might trigger the observed differences in the functional response to environmental

351   variation due to differences in their life-history strategy.

352   According to life-history theory, the physical and chemical properties of forest soils

353   determining forest structure and dynamics across the Amazon Basin (Quesada et al.

354   2012) shape plant-community composition by differentially favoring species depending

355   on their life-history strategy (Oliveira et al. 2018). In particular, while relatively stable

356   environments on flat terrain with high clay content and low nutrient availability favor

357   slow-growing tree species, more frequently disturbed environments on steep terrain

358   with low clay content and high nutrient availability favor fast-growing tree species

359   competing for limiting resources (Werner & Homeier 2015). Accordingly, it has been

360   found that tropical plant species composition was strongly related to local topoedaphic

361   factors affecting resource availability (Hofhansl et al., 2020), which furthermore

362   determined the climate sensitivity of neotropical forests in the region (Hofhansl et al.

363   2014). Hence, the opposed functional response between coexisting neotropical tree

364   species sampled in this study might reflect their ability to compete for limiting

365   resources, thus suggesting that endemic species are prone to competitive exclusion

366   under projected climate change.

367

368   <u>Implications for trait-based vegetation models</u>

369   So far, it has remained elusive to what extent the available information on trait variance

370   and trade-offs in life-history strategy among coexisting species could be used to derive

371   mathematical models capable of reliably predicting future ecosystem functioning. On

372   the one hand, studies exploring plant functional traits have suggested that a

373   classification based on trait co-variations should be a powerful candidate for building a

374 new generation of vegetation models capable of predicting the response of vegetation

375 to future climate changes (Zhao 2019). On the other hand, studies have found that trait

376 variation was not predictable because factors other than climate, such as site conditions,

377 growth form, and phylogeny were important determinants of the observed trait variation

378 (Yang et al. 2018). Accordingly, a trait-based forest model exploring the relative roles

379 of climate and plant traits in controlling forest productivity and structure found that,

380 while differences in productivity were driven by climate, demographic rates, such as

381 mortality and recruitment, were linked to plant traits (Fauset et al. 2019). These findings

382 are in line with our observation that multiple and interrelated factors determined plant

383 functional trait variation in tropical forests, however, our results also indicated that most

384 of the variation in plant functional traits could not be explained by the comprehensive

385 set of environmental factors analyzed in this study. Potentially, some of this variation

386 could be accounted for by other quantifiable, deterministic factors, however, our

387 findings (of relatively large amounts of unexplained trait variation) suggest that

388 interactive effects and non-deterministic factors are of similar importance, which would

389 imply that spatial autocorrelation and stochasticity should be accounted for in next-

390 generation approaches. Recently some studies have proposed novel concepts based on

391 multi-dimensional hypervolume (Blonder et al. 2014), trait probability density

392 (Carmona et al. 2016), and the biochemical niche (Peñuelas et al. 2019), thus allowing

393 to more realistically assess the functional responses of hyper-diverse ecosystems to

394 climate change (Bartlett et al. 2018). Implementation of the findings presented in this

395 study allows to account for different components of trait variation, which should

396 improve predictions of plant functional response spectra to environmental variation and

397 therefore result in more reliably projections of ecosystem functioning under future

398 scenarios (Franklin et al., 2020).

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Authors' Contributions and Conflict of Interest

FH and OF conceived the ideas and designed methodology; EC collected the data; FH and EC analyzed the data; FH led the writing of the manuscript with contributions from AB, EC, UD, and OF. All authors contributed critically to the drafts and gave final approval for publication. The authors have no conflicts of interest to declare.

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Data availability statement

Data are available from the Plant Trait Database (https://www.try-db. org/TryWeb/Home.php) with DOI 10.17871/TRY.12 (https://www.try-db.org/TryWeb/Data.php#12).

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429   **References**

430   Ackerly, D.D., & Cornwell, W.K. (2007). A trait-based approach to community

431   assembly: partitioning of species trait values into within- and among-community

432   components. *Ecology Letters* 10: 135–145.

433   Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P. and

434   Lavorel, S. (2010), Intraspecific functional variability: extent, structure and

435   sources of variation. *Journal of Ecology* 98: 604–613.

436   Bartlett, M.K., Detto, M., & Pacala, S.W. (2018). Predicting shifts in the functional

437   composition of tropical forests under increased drought and CO 2from trade-offs

438   among plant hydraulic traits. *Ecology Letters* 12: 1–11.

439   Blonder, B., Lamanna, C., Violle, C., & Enquist, B.J. (2014). The n-dimensional

440   hypervolume. *Global Ecology and Biogeography* 23: 595–609.

441   Brousseau, L., Foll, M., Scotti-Saintagne, C., Scotti, I. (2015). Neutral and Adaptive

442   Drivers of Microgeographic Genetic Divergence within Continuous Populations:

443   The Case of the Neotropical Tree Eperua falcata (Aubl.). PLOS ONE, 10(3),

444   e0121394. https://doi.org/10.1371/journal.pone.0121394

445   Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens,

446   S.M., ... Jandt, U. (2018). Global trait–environment relationships of plant

447   communities. *Nature Ecology & Evolution* 2: 1906–1917.

448   Carmona, C.P., de Bello, F., Mason, N.W.H., & Lepš, J. (2016). Traits Without

449   Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology &*

450   *Evolution* 31: 382–394.

451   Chacón-Madrigal, E., Wanek, W., Hietz, P., & Dullinger, S. (2018a). Is local trait

452   variation related to total range size of tropical trees? *PLoS ONE* 13: e0193268–

453   19.

454   Chacón-Madrigal, E., Wanek, W., Hietz, P., & Dullinger, S. (2018b). Traits indicating

455   a conservative resource strategy are weakly related to narrow range size in a

456   group of neotropical trees. *Journal of PPEES Sources* 32: 30–37.

457   Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., & Zanne, A.E. (2009).

458   Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

459   Cleveland, C.C., Townsend, A.R., Taylor, P., Alvarez-Clare, S., Bustamante, M.M.C.,

460   Chuyong, G., ... Wieder, W.R. (2011). Relationships among net primary

461   productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis.

462   *Ecology Letters* 14: 939–947.

463   Darwin, C. & Wallace, A. R. (1858). "On the Tendency of Species to form Varieties;

464   and on the Perpetuation of Varieties and Species by Natural Means of Selection".

465   Journal of the Proceedings of the Linnean Society of London. Zoology 3. 3 (9):

466   46–50. doi:10.1111/j.1096-3642.1858.tb02500.x.

467   Esquivel-Muelbert, A.E., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienen, R.J.W.,

468   Feldpausch, T.R., ... Phillips, O.L. (2019). Compositional response of Amazon

469   forests to climate change. *Global Change Biology* 25: 39–56

470   Fauset, S., Baker, T.R., Lewis, S.L., Feldpausch, T.R., Affum-Baffoe, K., Foli, E.G.,

471   Hamer, K.C., & Swaine, M.D. (2012). Drought-induced shifts in the floristic and

472   functional composition of tropical forests in Ghana. *Ecology Letters* 15: 1120–

473   1129.

474   Fauset, S., Gloor, M., Fyllas, N., Earth, O.P.F.I., (2019). Individual-based modelling

475   of Amazon forests suggests that climate controls productivity while traits control

476   demography. *frontiersin.org*. doi: 10.3389/feart.2019.00083

477   Fox, R.J., Donelson, J.M., Schunter, C., Ravasi, T., & Gaitán-Espitia, J.D. (2019).

478   Beyond buying time: the role of plasticity in phenotypic adaptation to rapid

479   environmental change. *Philosophical Transactions of the Royal Society of London*

480   *Series B-Biological Sciences* 374: 20180174–9.

481   Franklin, O., Harrison, S.P., Dewar, R. *et al.* Organizing principles for vegetation

482   dynamics. *Nat. Plants* **6,** 444–453 (2020). https://doi.org/10.1038/s41477-020-

483   0655-x

484   Freschet, G.T., Aerts, R., & Cornelissen, J.H.C. (2011). A plant economics spectrum

485   of litter decomposability. *Functional Ecology* 26: 56–65.

486   Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant

487   communities: Mechanisms and consequences. *Journal of Vegetation Science* 17:

488   255–260.

489   Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. (2005). Very high resolution

490   interpolated climate surfaces for global land areas. *International journal of*

491   *Climatology* 25: 1965–1978.

492   Hofhansl, F., Kobler, J., Ofner, J., Drage, S., Poelz, E.-M., & Wanek, W. (2014).

493   Sensitivity of tropical forest aboveground productivity to climate anomalies in

494   SW Costa Rica. *Global Biogeochemical Cycles* 28: 1437–1454.

495   Hofhansl, F., Chacón-Madrigal, E., Fuchslueger, L. *et al.* Climatic and edaphic

496   controls over tropical forest diversity and vegetation carbon storage. *Sci Rep* 10,

497   5066 (2020). https://doi.org/10.1038/s41598-020-61868-5.

498   Hulme, P.E. (2008). Phenotypic plasticity and plant invasions: is it all Jack?

499   *Functional Ecology* 22: 3–7.

500   Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. 2010. Intraspecific

501   variability and trait-based community assembly. *Journal of Ecology* 98: 1134–

502   1140.

503   Kraft, N.J.B., Valencia, R., & Ackerly, D.D. (2008). Functional Traits and Niche-

504   Based Tree Community Assembly in an Amazonian Forest. *Science* 322: 580–

505   582.

506   Le Bagousse Pinguet, Y., Börger, L., Quero, J.L., García-Gómez, M., Soriano, S.,

507   Maestre, F.T., & Gross, N. (2015). Traits of neighbouring plants and space

508   limitation determine intraspecific trait variability in semi-arid shrublands. *Journal*

509   *of Ecology* 103: 1647–1657.

510   Lichstein, J.W. 2006. Multiple regression on distance matrices: a multivariate spatial

511   analysis tool. *Plant Ecology* 188: 117–131.

512   Lobo, R.G. 2016. *Costa Rican Ecosystems*. University of Chicago Press.

513   Mitchell, R.M., Wright, J.P., & Ames, G.M. (2016). Intraspecific variability improves

514   environmental matching, but does not increase ecological breadth along a wet-to-

515   dry ecotone. *Oikos* 126: 988–995.

516   Murren, C.J., Auld, J.R., Callahan, H., Ghalambor, C.K., Handelsman, C.A., Heskel,

517   M.A., ... Schlichting, C.D. (2015). Constraints on the evolution of phenotypic

518   plasticity: limits and costs of phenotype and plasticity. *Heredity* 115: 293–301.

519   Oliveira, R.S., Costa, F.R.C., van Baalen, E., de Jonge, A., Bittencourt, P.R.,

520   Almanza, Y., ... Poorter, L. (2018). Embolism resistance drives the distribution of

521   Amazonian rainforest tree species along hydro-topographic gradients. *New*

522   *Phytologist* 221: 1457–1465.

523   Peñuelas, J., Fernández-Martínez, M., Ciais, P., Jou, D., Piao, S., Obersteiner, M., ...

524   Sardans, J. (2019). The bioelements, the elementome, and the biogeochemical

525   niche. *Ecology* 26: e02652–15.

526   Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry,

527   P., ... Cornelissen, J.H.C. (2013). New handbook for standardised measurement of

528   plant functional traits worldwide. *Australian Journal of Botany* 61: 167–68.

529   Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patino, S., ...

530   Lloyd, J. (2012). Basin-wide variations in Amazon forest structure and function

531   are mediated by both soils and climate. *Biogeosciences* 9: 2203–2246.

532   Quesada FJ, Jiménez Madrigal Q, Zamora Villalobos N, Aguilar Fernández R,

533   González Ramírez J. (1997). Árboles de la Península de Osa. Santo Domingo,

534   Heredia: Instituto Nacional de Biodiversidad.

535   R Core Team (2018). R: A language and environment for statistical computing. R

536   Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-

537   project.org/.

538   Reich, P.B. (2014). The world-wide "fast-slow" plant economics spectrum: a traits

539   manifesto (H. Cornelissen, Ed.). *Journal of Ecology* 102: 275–301.

540   Richardson, J. L., Urban, M. C., Bolnick, D. I., Skelly, D. K. (2014).

541   Microgeographic adaptation and the spatial scale of evolution. Trends in Ecology

542   and Evolution, 29(3), 165-176. https://doi.org/10.1016/j.tree.2014.01.002

543   Rowland, L., da Costa, A.C.L., Galbraith, D.R., Oliveira, R.S., Binks, O.J., Oliveira,

544   A.A.R., ... Meir, P. (2015). Death from drought in tropical forests is triggered by

545   hydraulics not carbon starvation. *Nature*. doi: 10.1038/nature15539

546   Sides, C.B., Enquist, B.J., Ebersole, J.J., Smith, M.N., Henderson, A.N., & Sloat, L.L.

547   (2014). Revisiting Darwin"s hypothesis: Does greater intraspecific variability

548   increase species" ecological breadth? 101: 56–62.

549   Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T.,

550   Cameron, D.D., ... Wiegand, T. (2012). Identification of 100 fundamental

551   ecological questions. *Journal of Ecology* 101: 58–67.

552   Swenson, N.G. (2014). *Functional and phylogenetic ecology in R*. Springer New

553   York, New York, NY.

554   Swenson, N.G., & Enquist, B.J. (2007). Ecological and evolutionary determinants of a

555   key plant functional trait: Wood density and its community-wide variation across

556   latitude and elevation. *American Journal of Botany* 94: 451–459.
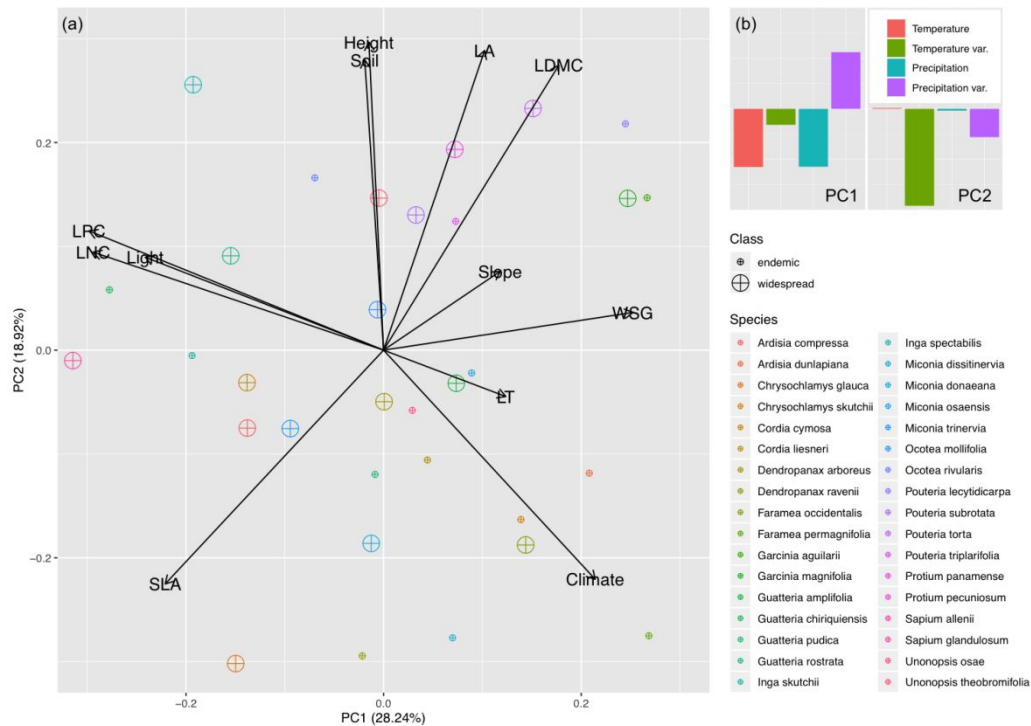
557   Taylor, P.G., Cleveland, C.C., Wieder, W.R., Sullivan, B.W., Doughty, C.E.,

558   Dobrowski, S.Z., & Townsend, A.R. (2017). Temperature and rainfall interact to

559   control carbon cycling in tropical forests (L. Liu, Ed.). *Ecology Letters* 20: 779–

560   788.

561   Taylor, P., Asner, G., Dahlin, K., Anderson, C., Knapp, D., Martin, R., ... Townsend,

562   A. (2015). Landscape-Scale Controls on Aboveground Forest Carbon Stocks on

563   the Osa Peninsula, Costa Rica. *PLoS ONE* 10: e0126748.

564   Townsend, A., Asner, G., & Cleveland, C. (2008). The biogeochemical heterogeneity

565   of tropical forests. *Trends in Ecology & Evolution* 23: 424–431.

566   Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V.,

567   & Messier, J. (2012). The return of the variance: intraspecific variability in

568   community ecology. *Trends in Ecology & Evolution* 27: 244–252.

569   Weissenhofer, A., Huber, W., Mayer, V., Pamperl, S., Weber, A., & Aubrecht, G.

570   (2008). *Natural and cultural history of the Golfo Dulce region, Costa Rica*.

571   Stapfia 88, zugleich Kataloge der Oberösterreichischen Landesmuseen NS 80.

572   Werner, F.A., & Homeier, J. (2015). Is tropical montane forest heterogeneity

573   promoted by a resource-driven feedback cycle? Evidence from nutrient relations,

574   herbivory and litter decomposition along a topographical gradient (M. J. Briones,

575   Ed.). *Functional Ecology* 29: 430–440.

576   Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., ...

577   Villar, R. (2004). The worldwide leaf economics spectrum. *Nature* 428: 821–827.

578   Yang, Y., Wang, H., Harrison, S.P., Prentice, I.C., Wright, I.J., Peng, C., & LIN, G.

579   (2018). Quantifying leaf-trait covariation and its controls across climates and

580   biomes. *New Phytologist* 221: 155–168.

581   Zhao, P. (2019). Trait-Based Climate Change Predictions of Vegetation Sensitivity

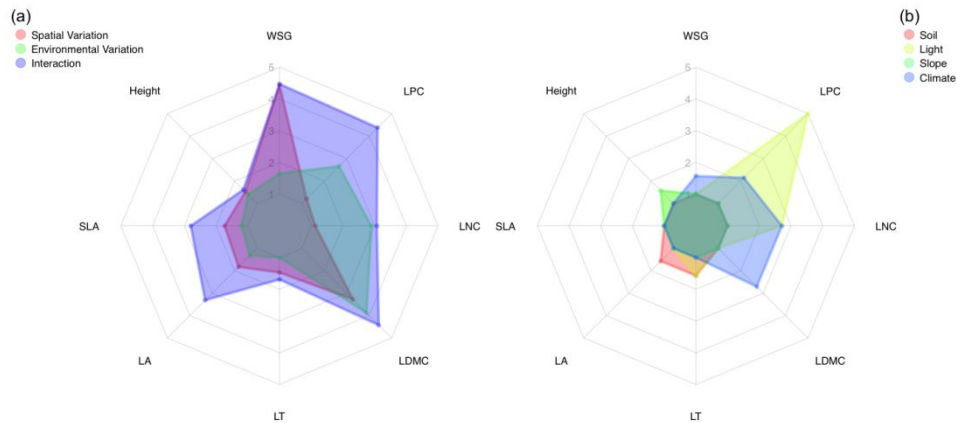582   and Distribution in China. *fpls-10-00908.tex* 10: 1–10.

583

584 **Figures and Tables**

585
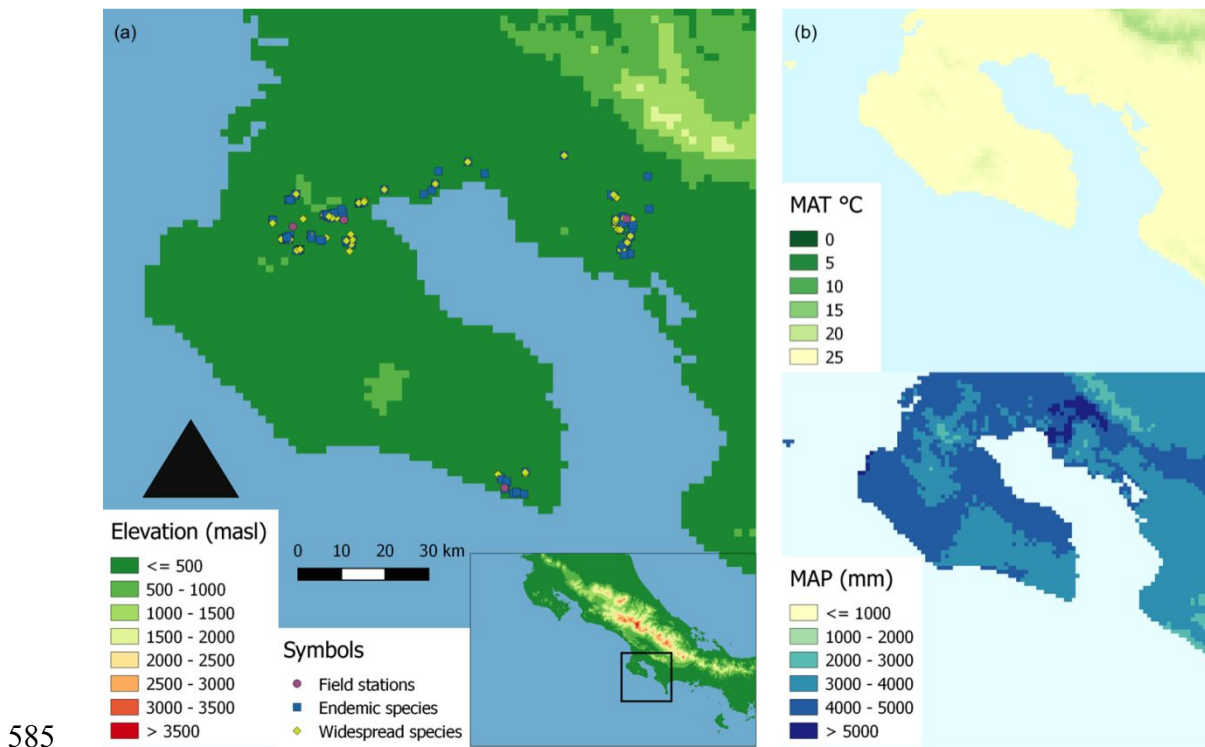
586 **Figure 1.** Study area and sampling sites of neotropical tree species in southwestern

587 Costa Rica (Peninsula de Osa and Golfo Dulce). Colored points indicate locations of

588 (1) field stations (purple), (2) endemic tropical tree species (blue) and (3) widespread

589 congeners (yellow) surveyed for plant functional traits. Landscape heterogeneity in (a)

590 topography, i.e., elevation (in m a.s.l.) and (b) climate, i.e., mean annual temperature

591 (in °C) and mean annual precipitation (in mm) is displayed according to Hijmans et al.

592 (2005). This figure was reproduced from (Chacón-Madrigal, Wanek, Hietz, &

593 Dullinger 2018a) according to Creative Commons Attribution 4.0 International Public
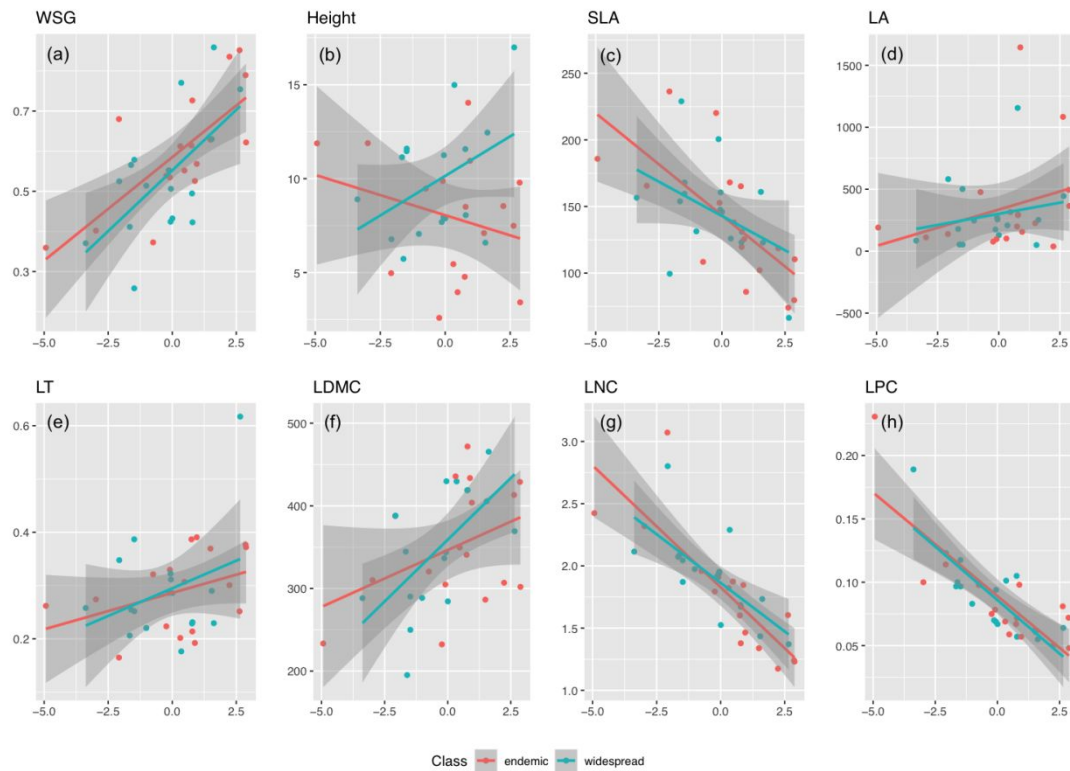
594 License.

Figure 2. Principal component analysis (PCA) of eight plant functional traits – wood density (WSG), plant height (Height), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter content (LDMC), leaf nitrogen content (LNC), and leaf phosphorous content (LPC) – obtained from 335 tree individuals comprising 34 tree species (point color) classified into endemic and widespread species according to differences in range size (point size). Factor loadings reflect (a) in-situ measurements, i.e., microclimate (Climate), soil clay, sand, silt content (Soil), topography (Slope) and canopy light index (Light), as well as, (b) bioclimatic variables extracted from Worldclim, i.e., temperature (red bar), temperature variation (green bar), precipitation (blue bar), and precipitation variation (purple bar).
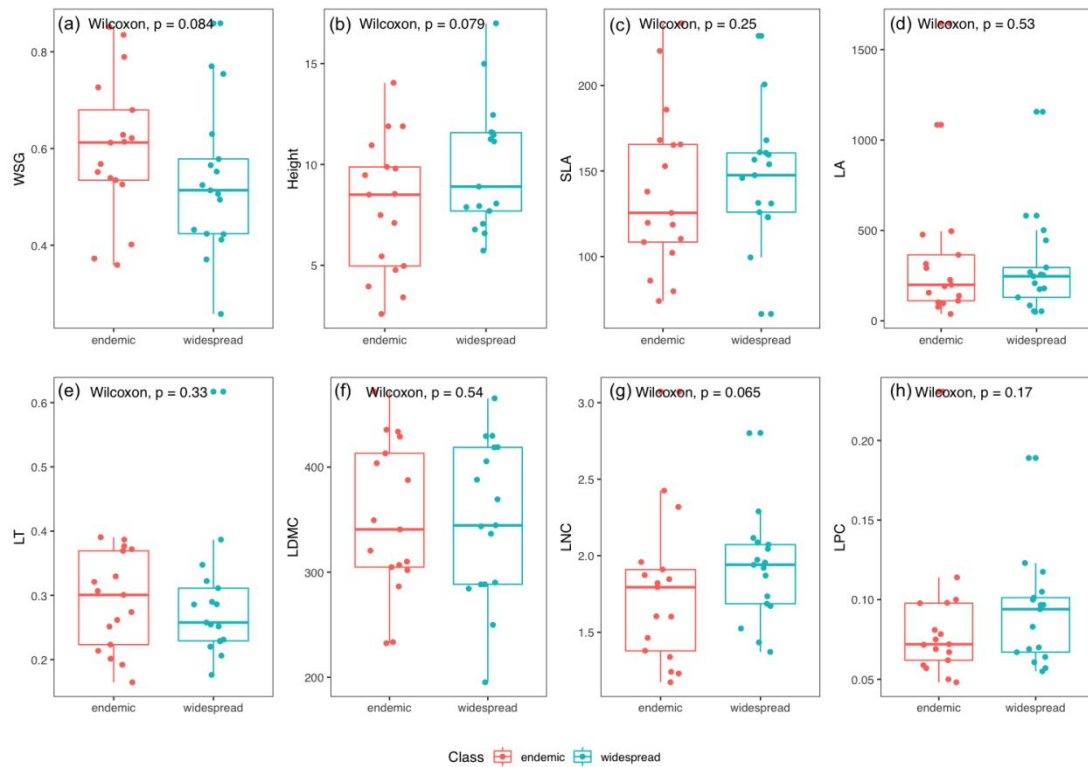
Figure 3. Radar plots displaying the relative amount of explained variance in multiple regression on distance matrices between respective components accounting for (a) spatial variation (red area), environmental variation (green area), and interaction between space and environment (blue area), as well as, for (b) environmental factors, such as: soil texture "Soil" (red area), canopy-light index "Light" (yellow area), slope position "Slope" (green area), and microclimate "Climate" (blue area), for each of the eight plant functional traits – wood density (WSG), plant height (Height), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter content (LMDC), leaf nitrogen content (N), and leaf phosphorous content (P) investigated in this study.

Figure 4. Scatterplots depicting the functional response of endemic (red points and regression line) and widespread (green points and regression line) tropical tree species to factors loadings of the first principal component of environmental factors (i.e., increasing temperature and precipitation variation as presented in Fig. 2b), for each of the eight plant functional traits – (a) wood density (WSG), (b) plant height (Height), (c) specific leaf area (SLA), (d) leaf area (LA), (e) leaf thickness (LT), (f) leaf dry-matter content (LMDC), (g) leaf nitrogen content (LNC), and (h) leaf phosphorous content (LPC) investigated in this study.

29

Figure 5. Boxplots indicating differences between endemic (red dots and boxes) and widespread (green dots and boxes) tropical tree species for each of the eight plant functional traits – (a) wood density (WSG), (b) plant height (Height), (c) specific leaf area (SLA), (d) leaf area (LA), (e) leaf thickness (LT), (f) leaf dry-matter content (LMDC), (g) leaf nitrogen content (LNC), and (h) leaf phosphorous content (LPC) investigated in this study. Test statistics indicate significant differences between endemic and widespread species, based on Wilcoxon rank-sum test and p values.

633

Figure 6. Taxonomic dendrogram depicting phylogenetic constraints on trait variance

for each of the eight plant functional traits, i.e. wood density (WSG), plant height

(Height), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter

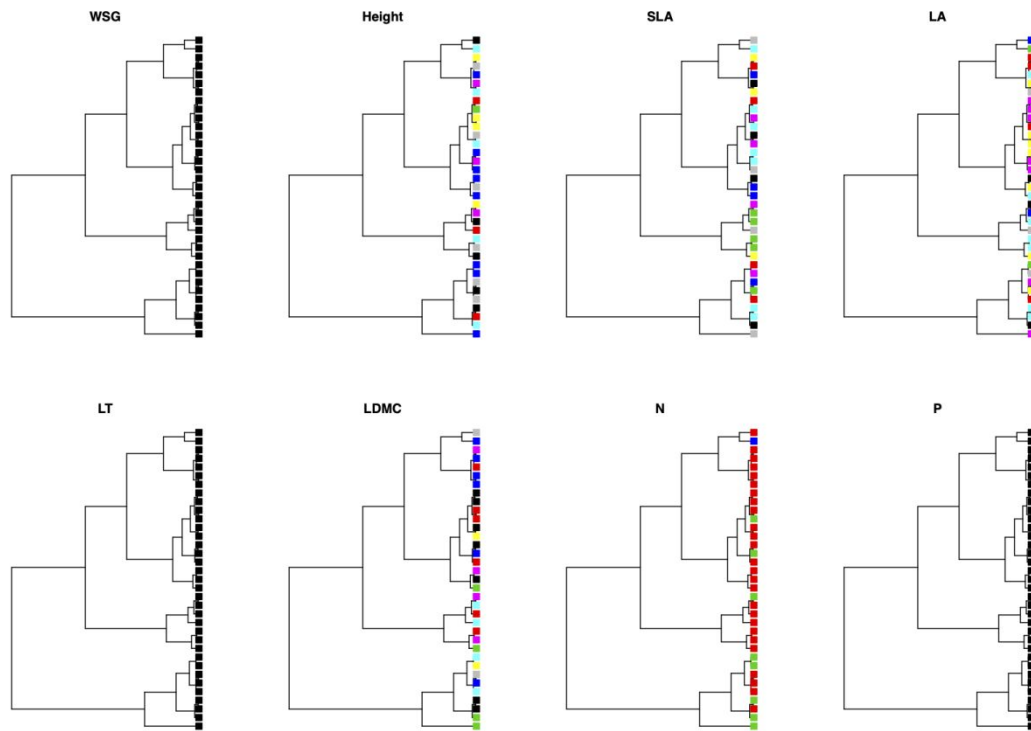content (LMDC), leaf nitrogen content (N), leaf phosphorous content (P) investigated

in this study. Branch node color indicates a phylogenetically conserved signal among

the nodes for 34 tropical tree species). For information about the tree species please see

Table 1.

641 **Table 1**. Variation in eight plant functional traits – wood density (WSG), plant height (Height), specific leaf area (SLA), leaf area (LA), leaf

642 thickness (LT), leaf dry-matter content (LMDC), leaf nitrogen content (LNC), and leaf phosphorous content (LPC) – among 34 tree species

643 sampled in tropical lowland forests located in southwestern Costa Rica. Values represent the mean ± the standard error of sampled tree individuals

644 with the actual number of samples indicated in the column titled *n*. Species are classified as being either widespread or endemic.

Family name	Species name	Range class	n	WSG	±	SE	Height	±	SE	SLA	±	SE	LA	±	SE	LT	±	SE	LDMC	±
Annonaceae	*Guatteria amplifolia Triana & Planch.*	widespread	10	0.42	±	0.01	8.06	±	0.91	130.97	±	4.12	294.90	±	27.10	0.23	±	0.01	419.01	±
Annonaceae	*Guatteria chiriquiensis R. E. Fr.*	endemic	9	0.40	±	0.01	11.89	±	0.93	165.52	±	13.32	111.03	±	4.30	0.27	±	0.01	310.12	±
Annonaceae	*Guatteria pudica N.Zamora & Maas*	endemic	16	0.53	±	0.01	9.88	±	1.02	152.77	±	7.44	96.51	±	7.88	0.33	±	0.01	304.82	±
Annonaceae	*Guatteria rostrata Erkens & Maas*	widespread	10	0.41	±	0.01	11.14	±	1.54	153.89	±	3.52	179.31	±	15.20	0.21	±	0.01	344.58	±
Annonaceae	*Unonopsis osae Maas & Westra*	endemic	10	0.61	±	0.01	5.45	±	0.44	168.09	±	7.10	102.18	±	8.29	0.20	±	0.00	435.68	±
Annonaceae	*Unonopsis theobromifolia N. Zamora & Poveda*	widespread	10	0.51	±	0.01	11.25	±	1.46	160.57	±	5.54	256.30	±	12.40	0.31	±	0.01	429.76	±
Araliaceae	*Dendropanax arboreus (L.) Decne. & Planch.*	widespread	10	0.43	±	0.01	7.89	±	0.54	145.92	±	5.18	129.59	±	10.73	0.29	±	0.01	284.37	±
Araliaceae	*Dendropanax ravenii M. J. Cannon & Cannon*	endemic	10	0.54	±	0.01	2.59	±	0.27	220.19	±	6.13	77.08	±	5.59	0.22	±	0.01	232.35	±
Boraginaceae	*Cordia cymosa (Donn. Sm.) Standl.*	widespread	8	0.26	±	0.02	11.46	±	1.16	159.53	±	13.47	501.48	±	22.91	0.39	±	0.02	290.21	±
Boraginaceae	*Cordia liesneri J. S. Mill.*	endemic	9	0.55	±	0.02	3.96	±	0.29	137.97	±	9.65	315.31	±	32.57	0.31	±	0.01	349.54	±
Burseraceae	*Protium panamense (Rose) I. M. Johnst.*	widespread	8	0.49	±	0.03	11.58	±	1.11	123.17	±	6.04	1156.28	±	156.65	0.23	±	0.03	418.82	±
Burseraceae	*Protium pecuniosum D. C. Daly*	endemic	10	0.53	±	0.02	14.04	±	1.38	125.52	±	5.11	1645.36	±	101.30	0.19	±	0.00	433.66	±
Clusiaceae	*Chrysochlamys glauca (Oerst. ex Planch. & Triana) Hemsl.*	widespread	10	0.57	±	0.02	5.73	±	0.75	228.97	±	9.19	53.84	±	4.38	0.25	±	0.01	195.21	±

Family	Species																				
Clusiaceae	*Chrysochlamys skutchii Hammel*	endemic	9	0.63	±	0.02	7.10	±	0.47	102.18	±	8.58	226.22	±	35.19	0.37	±	0.02	286.44	±
Clusiaceae	*Garcinia aguilari Hammel*	endemic	10	0.79	±	0.01	9.79	±	1.35	79.69	±	3.63	495.55	±	69.72	0.38	±	0.01	428.95	±
Clusiaceae	*Garcinia magnifolia (Pittier) Hammel*	widespread	10	0.75	±	0.01	16.99	±	1.95	66.41	±	3.87	444.92	±	26.95	0.62	±	0.02	369.33	±
Euphorbiaceae	*Sapium allenii Huft*	endemic	11	0.36	±	0.02	11.88	±	1.56	185.81	±	22.24	190.86	±	28.12	0.26	±	0.02	233.38	±
Euphorbiaceae	*Sapium glandulosum (L.) Morong*	widespread	10	0.37	±	0.01	8.90	±	0.78	156.57	±	15.28	84.79	±	5.16	0.26	±	0.01	288.29	±
Fabaceae	*Inga skutchii Standl.*	endemic	10	0.68	±	0.02	4.97	±	0.69	236.33	±	12.63	138.55	±	11.30	0.16	±	0.01	387.73	±
Fabaceae	*Inga spectabilis (Vahl) Willd*	widespread	9	0.52	±	0.02	6.78	±	0.32	99.51	±	4.73	581.74	±	47.89	0.35	±	0.02	388.09	±
Lauraceae	*Ocotea mollifolia Mez & Pittier*	widespread	10	0.42	±	0.02	7.94	±	0.48	147.55	±	10.56	269.38	±	21.48	0.32	±	0.01	343.69	±
Lauraceae	*Ocotea rivularis Standl. & L. O. Williams*	endemic	9	0.37	±	0.01	9.47	±	0.75	108.44	±	4.43	476.92	±	49.80	0.32	±	0.01	320.47	±
Melastomataceae	*Miconia dissitinervia Kriebel, Almeda & A. Estrada*	endemic	11	0.61	±	0.01	4.77	±	0.28	165.19	±	4.97	199.10	±	19.41	0.39	±	0.01	340.76	±
Melastomataceae	*Miconia donaeana Naudin*	widespread	10	0.55	±	0.01	7.69	±	0.80	200.58	±	9.16	174.91	±	14.65	0.29	±	0.01	336.58	±
Melastomataceae	*Miconia osaensis Aguilar, Kriebel & Almeda*	endemic	10	0.57	±	0.01	10.95	±	1.30	85.94	±	2.55	155.83	±	22.43	0.39	±	0.01	403.81	±
Melastomataceae	*Miconia trinervia (Sw.) D. Don ex Loudon*	widespread	10	0.51	±	0.01	7.06	±	0.57	131.34	±	7.64	246.38	±	18.34	0.22	±	0.01	288.52	±
Primulaceae	*Ardisia compressa Kunth*	widespread	9	0.58	±	0.02	11.60	±	2.07	167.98	±	7.41	53.17	±	3.66	0.25	±	0.01	249.92	±
Primulaceae	*Ardisia dunlapiana P. H. Allen*	endemic	10	0.84	±	0.01	8.54	±	1.01	118.64	±	3.56	38.04	±	2.78	0.30	±	0.01	306.92	±
Rubiaceae	*Faramea occidentalis (L.) A. Rich.*	widespread	11	0.63	±	0.01	6.59	±	0.75	160.95	±	3.98	49.63	±	3.77	0.29	±	0.01	405.56	±
Rubiaceae	*Faramea permagnifolia Dwyer ex C. M. Taylor*	endemic	12	0.62	±	0.02	3.42	±	0.19	110.39	±	5.22	364.84	±	21.26	0.37	±	0.01	301.95	±
Sapotaceae	*Pouteria lecythidicarpa P. E. Sa´nchez & Poveda*	endemic	10	0.85	±	0.01	7.49	±	0.56	74.05	±	4.14	1084.26	±	163.68	0.25	±	0.01	413.20	±
Sapotaceae	*Pouteria subrotata Cronquist*	widespread	8	0.77	±	0.02	14.99	±	1.67	125.95	±	5.25	208.22	±	11.45	0.18	±	0.00	429.58	±
Sapotaceae	*Pouteria torta (Mart.) Radlk.*	widespread	10	0.86	±	0.02	12.45	±	2.16	122.88	±	6.61	252.83	±	38.69	0.23	±	0.02	465.45	±
Sapotaceae	*Pouteria triplarifolia C. K. Allen ex T. D. Pennington*	endemic	6	0.73	±	0.02	8.50	±	1.69	119.68	±	2.10	291.31	±	31.92	0.21	±	0.00	471.84	±

645

646 **Table 2.** Results of multiple regression on distance matrices (MRM) showing significant relationships between distance matrices of the observed

647 environmental factors (i.e., climate, soil, slope, light) and each of the plant functional traits – wood density (WSG), plant height (Ht), specific leaf

648 area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter content (LMDC), leaf nitrogen content (LNC), and leaf phosphorous content (LPC).

649 Test statistics represent R^2 and p value ($p < 0.05$ highlighted in bold) showing significant relationships between environmental controlling factors

650 and plant functional traits, while separating respective effects of non-plastic (correlation between trait distance matrix and spatial distance matrix

651 while accounting for environmental variation), plastic (correlation between trait distance matrix and environmental distance matrix while

652 accounting for spatial variation) and spatial components (correlation between geographic distance matrix and environmental distance matrix while

653 correcting for trait variation).

COMPONENT	Spatial variation	p-value	Environmental variation	p-value	Total variation	p-value
CLIMATE	R^2	p value		R^2	p value	R^2	p value
WSG	0.04	**0.02**	0.01	0.74	0.04	**0.04**
Height	0.01	0.54	0.00	0.77	0.01	0.60
SLA	0.01	0.12	0.00	0.13	0.02	0.23
LA	0.01	0.12	0.00	0.15	0.03	0.24
LT	0.01	0.24	0.00	0.65	0.01	0.54
LDMC	0.03	0.24	0.03	0.07	0.04	**0.03**
LNC	0.00	0.63	0.03	**0.05**	0.03	0.14

LPC	0.00	0.09	0.02	**0.03**	0.04	0.13
SOIL						
WSG	0.03	**0.02**	0.00	0.32	0.04	0.06
Height	0.00	0.54	0.00	0.74	0.00	0.72
SLA	0.02	0.10	0.00	0.84	0.02	0.26
LA	0.03	0.09	0.01	0.41	0.03	0.18
LT	0.01	0.25	0.01	0.32	0.01	0.34
LDMC	0.01	0.23	0.00	0.74	0.01	0.42
LNC	0.00	0.62	0.00	0.68	0.00	0.81
LPC	0.02	0.11	0.00	0.57	0.02	0.22
SLOPE						
WSG	0.03	**0.03**	0.00	0.64	0.04	**0.04**
Height	0.00	0.53	0.01	0.29	0.01	0.52
SLA	0.02	0.11	0.00	0.73	0.02	0.22
LA	0.02	0.11	0.00	0.79	0.03	0.24
LT	0.01	0.24	0.00	0.52	0.01	0.41
LDMC	0.01	0.24	0.00	0.42	0.01	0.35
LNC	0.00	0.64	0.00	0.46	0.01	0.68
LPC	0.02	0.13	0.00	0.59	0.03	0.20
LIGHT						
WSG	0.03	**0.02**	0.00	0.90	0.04	0.06

Height	0.01	0.54	0.01	0.29	0.01	0.38
SLA	0.02	0.12	0.00	0.80	0.02	0.22
LA	0.03	0.10	0.00	0.96	0.03	0.25
LT	0.01	0.25	0.01	0.25	0.02	0.30
LDMC	0.01	0.25	0.00	0.68	0.01	0.46
LNC	0.00	0.64	0.03	**0.03**	0.04	0.12
LPC	0.01	0.12	0.07	**0.01**	0.09	**0.04**

654

655 **Table 3.** Results of multiple linear regression showing the effects of environmental factors – slope position (Slope), canopy-light index (Light),

656 soil texture (Soil), temperature (Temperature), and rainfall (Precipitation) – on the variation in eight plant functional traits – wood density (WSG),

657 plant height (Height), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter content (LMDC), leaf nitrogen content (N), and

658 leaf phosphorus content (P). Test statistics represent t value (coefficients divided by standard errors) and p value, showing significant relationships

659 ($p < 0.05$ highlighted in bold) between plant functional traits and each of the environmental controlling factors.

| Predictor	Intercept		Slope		Light		Soil		Temperature		Precipitation	
Response	t value	p value	t value	p value	t value	p value	t value	p value	t value	p value	t value	p value
WSG	-1.80	0.08	0.26	0.80	-2.15	**0.04**	-0.28	0.78	2.25	**0.03**	-2.84	**0.01**
Height	0.42	0.68	-0.17	0.87	1.86	*0.07*	1.18	0.25	-0.31	0.76	-0.02	0.99
SLA	0.94	0.35	0.13	0.90	0.69	0.50	-0.07	0.94	-0.84	0.41	0.73	0.47
LA	0.07	0.94	0.73	0.47	-1.04	0.31	0.92	0.36	-0.08	0.94	0.37	0.71
LT	1.17	0.25	-0.01	1.00	0.37	0.71	-0.91	0.37	-1.03	0.31	0.84	0.41
LDMC	-2.26	**0.03**	0.07	0.94	-1.14	0.26	1.26	0.22	2.68	**0.01**	-3.06	**0.00**
LNC	0.94	0.35	-0.64	0.53	1.86	*0.07*	2.02	*0.05*	-1.08	0.29	2.18	**0.04**
LPC	0.57	0.58	-0.93	0.36	1.99	*0.06*	0.73	0.47	-0.81	0.43	1.96	*0.06*

660
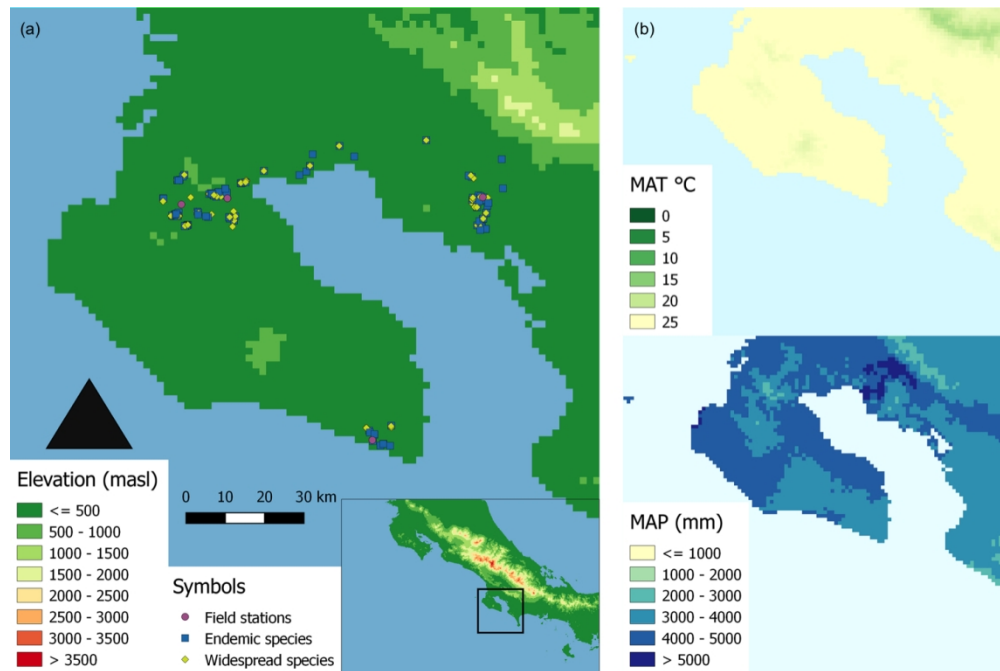
Figure 1. Study area and sampling sites of neotropical tree species in southwestern Costa Rica (Peninsula de Osa and Golfo Dulce). Colored points indicate locations of (1) field stations (purple), (2) endemic tropical tree species (blue) and (3) widespread congeners (yellow) surveyed for plant functional traits. Landscape heterogeneity in (a) topography, i.e., elevation (in m a.s.l.) and (b) climate, i.e., mean annual temperature (in °C) and mean annual precipitation (in mm) is displayed according to Hijmans et al. (2005). This figure was reproduced from (Chacón-Madrigal, Wanek, Hietz, & Dullinger 2018a) according to Creative Commons Attribution 4.0 International Public License.

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Figure 2. Principal component analysis (PCA) of eight plant functional traits – wood density (WSG), plant height (Height), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter content (LDMC), leaf nitrogen content (LNC), and leaf phosphorous content (LPC) – obtained from 335 tree individuals comprising 34 tree species (point color) classified into endemic and widespread species according to differences in range size (point size). Factor loadings reflect (a) in-situ measurements, i.e., microclimate (Climate), soil clay, sand, silt content (Soil), topography (Slope) and canopy light index (Light), as well as, (b) bioclimatic variables extracted from Worldclim, i.e., temperature (red bar), temperature variation (green bar), precipitation (blue bar), and precipitation variation (purple bar).
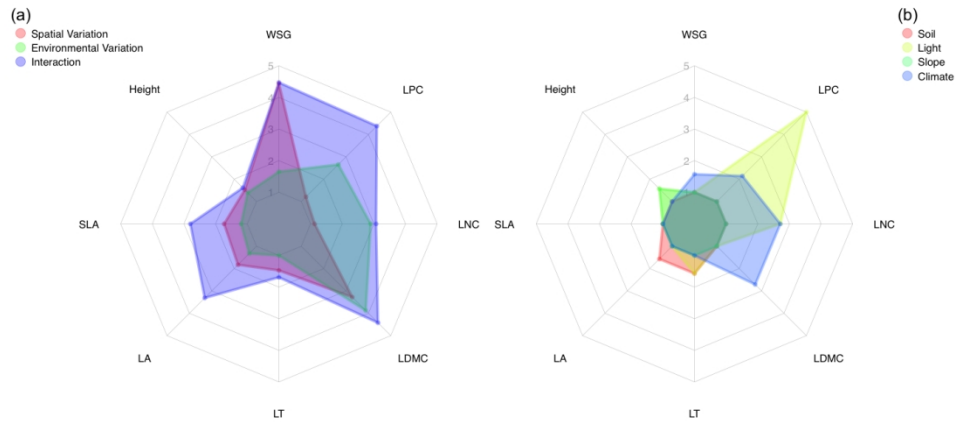
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Figure 3. Radar plots displaying the relative amount of explained variance in multiple regression on distance matrices between respective components accounting for (a) spatial variation (red area), environmental variation (green area), and interaction between space and environment (blue area), as well as, for (b) environmental factors, such as: soil texture "Soil" (red area), canopy-light index "Light" (yellow area), slope position "Slope" (green area), and microclimate "Climate" (blue area), for each of the eight plant functional traits – wood density (WSG), plant height (Height), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter content (LMDC), leaf nitrogen content (N), and leaf phosphorous content (P) investigated in this study.
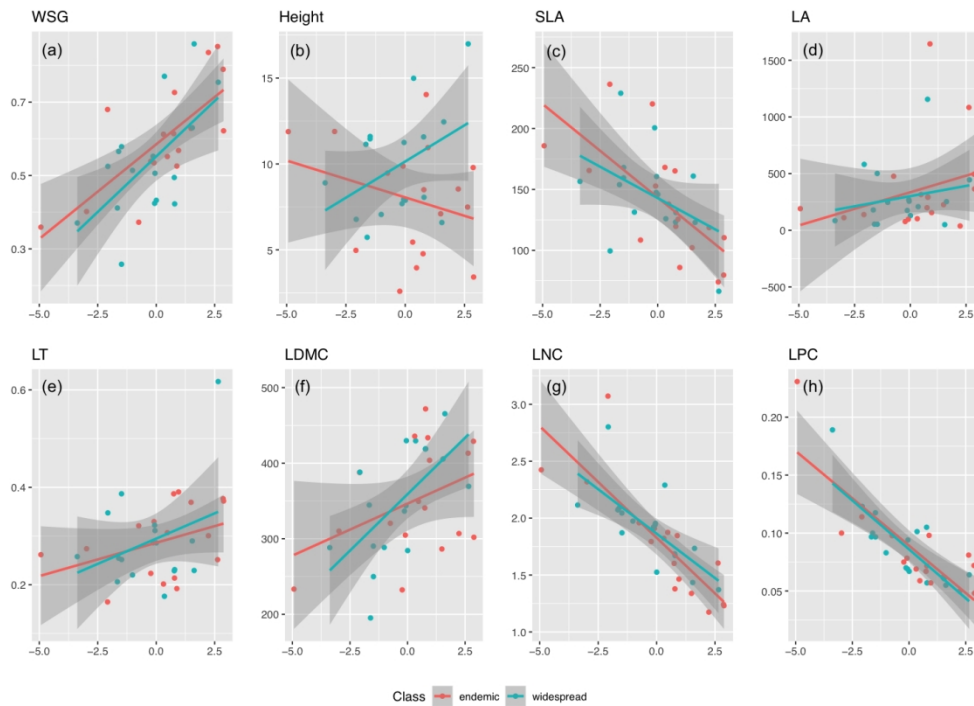
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Figure 4. Scatterplots depicting the functional response of endemic (red points and regression line) and widespread (green points and regression line) tropical tree species to factors loadings of the first principal component of environmental factors (i.e., increasing temperature and precipitation variation as presented in Fig. 2b), for each of the eight plant functional traits – (a) wood density (WSG), (b) plant height (Height), (c) specific leaf area (SLA), (d) leaf area (LA), (e) leaf thickness (LT), (f) leaf dry-matter content (LMDC), (g) leaf nitrogen content (LNC), and (h) leaf phosphorous content (LPC) investigated in this study.
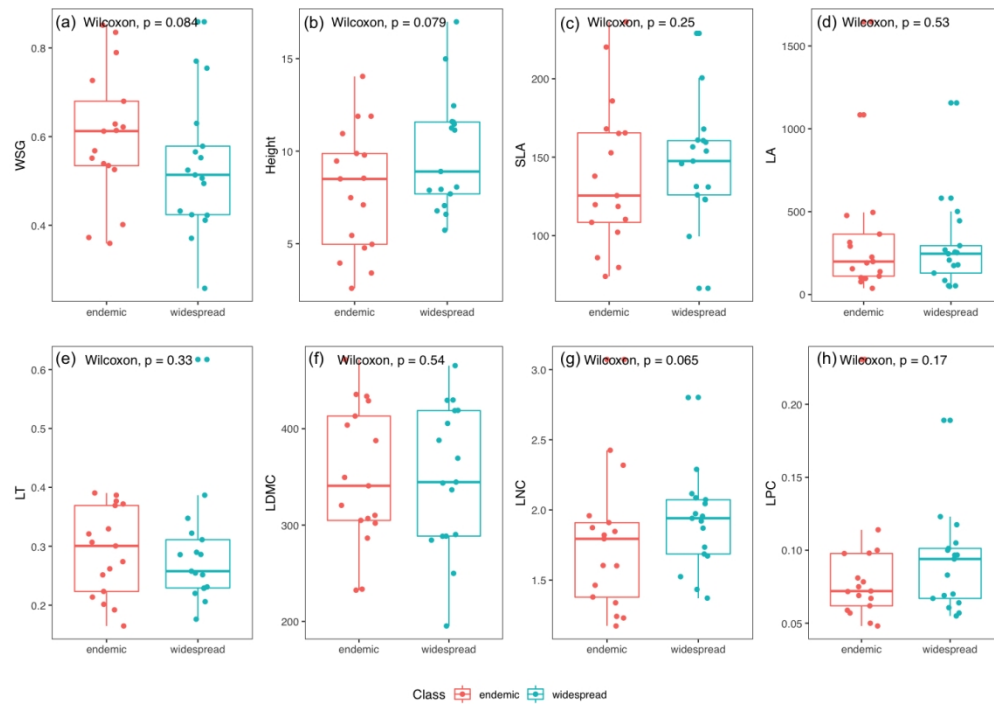
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Figure 5. Boxplots indicating differences between endemic (red dots and boxes) and widespread (green dots and boxes) tropical tree species for each of the eight plant functional traits – (a) wood density (WSG), (b) plant height (Height), (c) specific leaf area (SLA), (d) leaf area (LA), (e) leaf thickness (LT), (f) leaf dry-matter content (LMDC), (g) leaf nitrogen content (LNC), and (h) leaf phosphorous content (LPC) investigated in this study. Test statistics indicate significant differences between endemic and widespread species, based on Wilcoxon rank-sum test and p values.
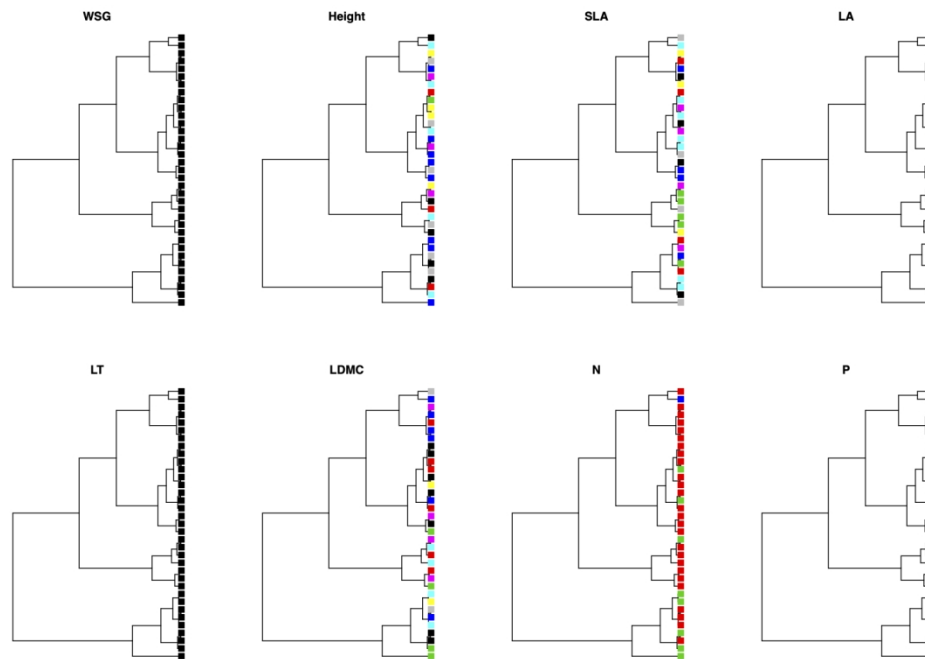
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Figure 6. Taxonomic dendrogram depicting phylogenetic constraints on trait variance for each of the eight plant functional traits, i.e. wood density (WSG), plant height (Height), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry-matter content (LMDC), leaf nitrogen content (N), leaf phosphorous content (P) investigated in this study. Branch node color indicates a phylogenetically conserved signal among the nodes for 34 tropical tree species). For information about the tree species please see Table 1.

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