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8 Running Head: Comparing ITV and inter-specific variation

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11 **Does trait variation within broadly distributed species mirror patterns across species?**

12 **A case study in Puerto Rico**

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21

22 **Abstract**

23 Although populations are phenotypically diverse, the majority of trait-based studies have

24 focused on examining differences among species. The justification for this broadly applied

25 approach is based on the assumption that differences among species are always greater than

26 within species. This is likely true for local communities, but species are often broadly

27 distributed across a wide range of environments and patterns of intraspecific variation might

28 surpass differences among species. Therefore, an appropriate interpretation of the functional

29 diversity requires an assessment of patterns of trait variation across different ecological

30 scales. In this study, we examine and characterize patterns of leaf trait variation for species

31 that are broadly distributed along an elevational gradient. We focus on seven leaf traits that

32 represent a main axis of functional differentiation in plants reflecting the balance between

33   photosynthetic efficiency, display, and stomatal conductance. We evaluated patterns of trait

34   variance across ecological scales (elevation, species, populations, and individuals) and

35   examined trait covariance at both within species and across species levels, along the elevation

36   gradient. Our results show three key patterns: (1) intraspecific leaf trait variation for broadly

37   distributed species is comparable to the inter-specific trait variation, (2) the trait variance

38   structure is highly variable across species and (3) trait coordination between pairs of leaf

39   traits is evident across-species along the gradient, but not always within species. Combined,

40   our results show that trait coordination and covariance are highly idiosyncratic across broadly

41   distributed and co-occurring species, indicating that species may achieve similar functional

42   roles even when exhibiting different phenotypes. This result challenges the traditional

43   paradigm of functional ecology that assumes single trait values as optimal solutions for

44   environments. In conclusion, patterns of trait variation both across and within species should

45   be considered in future studies that assess trade-offs among traits over environmental

46   gradients.

47   **Key words**: Intraspecific trait variation, leaf area, leaf carbon content, leaf thickness, plant

48   functional traits, variance components, specific leaf area, trait covariance.

49   **Introduction**

50   A conspicuous characteristic of life is the enormous amount of variation in form and

51   function. Organisms exhibit complex arrangements of morphological and physiological traits

52   that do not appear to be the result of pure chance. Instead, this phenotypic variation is likely

53   the result of ecological factors such as biotic and abiotic interactions, as well as genetic and

54   evolutionary constraints that operate within and across species. Although many ecological

55   studies focus on local and relatively homogeneous environments where inter-specific trait

56   variation typically exceeds intra-species variation, these homogeneous conditions usually do

57   not represent the entire distribution of a species and might not reflect its actual trait

58   distribution (Hulshof and Swenson 2010, Messier et al. 2010). Recent literature on

59   intraspecific trait variation (ITV) suggests that species have the potential to exhibit extensive

60   intraspecific trait variation (Albert et al. 2011, Siefert et al. 2015, Umaña et al. 2018).

61   Therefore, understanding how phenotypes vary, not only across species, but also within

62   broadly distributed species, is fundamental for fostering insights into the potential

63   mechanisms driving community structure and for determining future species responses under

64   ongoing climate change.

65   Ecological forces exert a sustained influence on natural communities by selecting

66   species with particular traits that fit the local abiotic demands (Keddy 1992). For example,

67 previous studies have shown that leaf traits exhibit strong variation across plant communities

68 distributed along environmental gradients (Reich et al. 1999, Wright et al. 2004, Messier et

69 al. 2010, Swenson et al. 2011). This observed variation in community-level traits across

70 resource gradients results from variation across species as well as within species (Albert et al.

71 2010, Messier et al. 2010, Kichenin et al. 2013). In particular, for broadly distributed species,

72 trait variance across populations or ecotypes (conspecific organisms located at different

73 portions of environmental gradients) could be comparable in magnitude to the trait variance

74 across species if differences in biotic and abiotic conditions result in a great phenotypic

75 variation to cope the local demands (Fajardo and Siefert 2019). Alternatively, if strong

76 constraints operate at the species level maintaining species identities over their entire range,

77 trait variation within species should not exceed the variance across species.

78   Trait responses to local conditions might or might not be consistent across species.

79 The magnitude of trait variation should be related to the strength of trade-offs that operate

80 among traits (Armbruster and Schwaegerle 1996, Armbruster 2016). For example, if few

81 fundamental trade-offs operate consistently across species (e.g. biophysical constraints to

82 achieve a given physiological function), then trait variance at the level of individuals and

83 populations (across ecological scales) should be consistent across species. However,

84 alternative explanations propose that co-occurring species might achieve functional

85 equivalence through different combination of traits resulting in different patterns of variance

86 structure across species (Marks and Lechowicz 2006, Marks 2007). In this case, traits will be

87 connected through complex networks of trade-offs that do not necessary result in the same

88 (obligate) trait combinations across species. In fact, past studies have suggested that variance

89 structure is highly idiosyncratic for species in temperate forests (Albert et al. 2010, Kumordzi

90 et al. 2015).

91   Given that the phenotype of an individual is an assemblage of traits that together

92 achieve the vital functions of organisms (Lewontin 1978), and as a whole, organisms respond

93 to local environments, it is necessary to understand the multidimensional integration of the

94 phenotype to predict species responses to climatic changes (Laughlin and Messier 2015).

95 Covariance in traits has been widely studied in the past (Grime 1979, 1997, Felsenstein 1988,

96 Armbruster and Schwaegerle 1996, Reich et al. 1998, 1999, Ackerly and Reich 1999,

97 Santiago et al. 2004b, 2004a, Wright et al. 2004), and, in the case of plants, main trait spectra

98 have been identified (Westoby 1998, Wright et al. 2004, Chave et al. 2009, Díaz et al. 2015).

99 For example, the leaf economic spectrum describes a range of strategies that go from

100 acquisitive to conservative in carbon investment and return and has shown strong correlations

101   at worldwide scale across species (Wright et al. 2004) and within species (Martin et al. 2007,

102   Vasseur et al. 2012, Fajardo and Siefert 2018). However, the generality of this pattern across

103   spatial scales has been questioned by studies that have found weak or non-existent trait

104   correlations at local scales (Cornwell and Ackerly 2009, Wright and Sutton-Grier 2012,

105   Grubb 2016, Messier et al. 2017). These contradictory results suggest that filtering forces

106   leading to trait correlations along environmental gradients might not determine trait

107   correlations at other ecological scales. Whether the patterns of trait covariation found along

108   environmental gradients across species are equally strong within broadly distributed species,

109   remains understudied (but see, Anderegg *et al.* 2018).

110   Although trait variation within species is recognized, there is controversy regarding

111   over whether trait variation within species is comparable in magnitude to that of the species

112   level, and whether this variation mirrors that found at the community level. Here, we were

113   interested in characterizing variation in leaf traits for species that are broadly distributed

114   along an elevation gradient in Puerto Rico. The elevation gradient studied exhibits a

115   variation in annual rainfall of 1300 mm from the lowest to the highest sampled sites and a

116   difference in mean annual temperature of 4°C. We examined four ecological scales:

117   elevation, species, population (group of individuals of the same species at each sampled

118   elevation) and individuals, and we focused on leaf traits that represent a significant portion

119   of functional differentiation in plants that reflect resource acquisition strategies, plant

120   structure and design as well as water transport (Tilman et al. 1997, Westoby et al. 2002,

121   Wright et al. 2004, Poorter and Rozendaal 2008). The resource acquisition traits are mainly

122   defined by the leaf economic spectrum (LES) and the N stable isotope ratio ($\delta^{15}N$). The LES

123   is described as the range of strategies from low carbon rate acquisition and release to high

124   carbon rates. The N isotope relates to N availability in soil and is affected by climate and

125   mycorrhizal fungi (Martinelli et al. 1999, Dawson et al. 2002, Santiago et al. 2004b, Craine et

126   al. 2009). The architectural design trait is related to leaf display for carbon gain and is

127   represented by leaf area (Poorter and Rozendaal 2008). The third dimension is related to

128   water use efficiency and water availability represented by C Isotope ($\delta^{13}C$). Based on this

129   varied arrangement of leaf traits, we asked the following questions: (1) is the magnitude of

130   trait variation across species comparable to that occurring within species broadly

131   distributed across environmental gradients (i.e. across populations located in different sites

132   along the gradient or across individuals within the same site)? We predict that if species

133   adjust to local conditions, then the variance structure at the population- and species-levels

134   should be comparable. Alternatively, if species traits confer high tolerances to stressful

135   conditions along the entire gradient or these traits are not strongly selected across the

136   elevation, then species would have lower trait variation at the population-level than at the

137   species-level. (2) Do species have similar trait variance structure? We expect that if species

138   use similar pathways to adjust to local conditions, we should find similar trait variance

139   structure across species indicating that fundamental trade-offs operate strongly across

140   ecological scales. If species achieve functional adjustments through independent

141   arrangements of traits, then, trait variance structure should be different across species. (3)

142   How do the strengths of the correlations between pairs of traits vary across and within

143   broadly distributed species? We propose four different scenarios that describe sets of traits

144   correlations at gradient- and within-species-levels (Fig. 1). At the gradient level,

145   differences across species are ignored and we focus on differences across elevation zones.

146   If environmental factors select similar traits along the gradient of elevation and species are

147   also coordinated in their responses (either through plastic, genetic or biophysical reasons),

148   then we should expect to find strong correlations between traits at the gradient and within-

149   species level (Fig. 1A). If there are biophysical constraints that govern trait correlations, but

150   the environment does not act as a strong selective force on the traits, then we should expect

151   a strong correlation between traits at the within-species level, but not at the gradient level

152   (Fig. 1B). If the environment is a main selective force shaping the functional structure of

153   communities, but species achieve their functional requirements through alternative

154   combinations of traits (Marks and Lechowicz 2006), then the correlation between traits

155   should be significant at the gradient level but not at the within-species level (Fig. C). This

156   result would indicate that abiotic factors act as a strong filter on the phenotype, but that

157   species responses to the environment are highly idiosyncratic by modifying a different

158   combination of traits (Fig. 1C). If the traits are not strongly linked, we should not see

159   strong correlations at any level (Fig. 1D).

160

161   **Methods**

162   The study area is located in North Eastern Puerto Rico, in El Yunque National Forest

163   (18°19.60' N, 65°49.40' W). This is a subtropical wet forest that ranges from 250 to 1075

164   m in elevation. At the lowest elevation, the annual rainfall is 2300 mm, the mean annual

165   temperature is 24.5°C and the forest is characterized by a premontane rainforest tropical

166   vegetation dominated by a palm (*Prestoea acuminata* (Willd.) H.E. Moore) and the tabonuco

167   tree (*Dacryodes excelsa* Vahl*)* (Thompson et al. 2002). At the highest elevation, the annual

168   precipitation is 3600 mm, the mean annual temperature is 20.0°C and the vegetation is typical

169   of a tropical cloud forest. During 2001 and 2002, 16 0.1-ha permanent plots were established

170   along the elevation gradient from 250 to 1000 m and were separated by 50 m in elevation.

171   Within each plot, all individuals with a diameter at breast height (DBH) greater than 1 cm

172   where tagged and 99% of individuals could be identified to species. Despite the short

173   elevation range, the gradient presents a conspicuous community turnover in traits and species

174   (Swenson et al. 2011).

175

176   *Species selection*

177   Based on the abundance distribution of species found across the 16 permanent plots 0.1-ha in

178   area, we selected all tree species that were present in at least eight plots and that were

179   abundant where they appear (more than 10 individuals per 0.1 ha with DBH > than 7cm). A

180   total of six species met the criteria: *Cecropia schreberiana* Miq subspecies *schreberiana*

181   (Urticaceae) (hereafter referred to as CECSCH), *Cordia borinquensis* Urb. (Boraginaceae)

182   (hereafter referred to as CORBOR), *Dacryodes excelsa* Vahl (Burseraceae) (hereafter

183   referred to as DACEXC)*, Henriettea squamulosa* (Cogn.) Judd (Melastomataceae) (hereafter

184   referred to as CALSQU), *Micropholis garciniifolia* Pierre (Sapotaceae*) (hereafter referred to

185   as MIRGAR) and *Sloanea berteroana* Choisy ex DC (Elaeocarpaceae) (hereafter referred to

186   as SLOBER).

187

188   *Trait collection*

189   For adult individuals of each species at each elevation, we collected branches from the top-

190   half section of the crown. The total number of individuals by species and ranges of elevation

191   used for this study are shown in Table 1. Most of the individuals collected were present in

192   the permanent 0.1-ha plots, but some of them were collected from nearby individuals that

193   were at the same elevation. We measured seven leaf traits on fully expanded and non-

194   senescent leaves, at the distal portion of all branches because these had the greatest

195   exposure to sunlight. The traits measured were: leaf nitrogen content (LNC, reported on

196   mass basis) is correlated photosynthetic capacity because nitrogen forms part of the rubisco

197   enzyme that is involved in the carbon fixation (Schulze et al. 1994). Leaf carbon content

198   (LCC, reported on mass basis) reflects the investment in leaves' structure and defense

199   against herbivory (Bryant et al. 1983, Niinemets 2007). Foliar carbon stable isotope content

200   (δ^{13}C, reported relative to V-PDB, ‰) represents the balance between CO_2 diffusion

201   (stomatal conductance) and atmospheric CO_2 uptake and is related to water use efficiency

202   (Farquhar et al. 1989). Foliar nitrogen stable isotope content (δ^{15}N, reported relative to AIR,

203 ‰) is related to high nitrogen availability in the soil and low precipitation (Dawson et al.

204 2002, Amundson et al. 2003, Santiago et al. 2004b, Ma et al. 2012) . In addition, recent

205 studies have shown that δ^{15}N varies with mycorrhizal fungi composition and is an indicator

206 of nitrogen cycling (Amundson et al. 2003, Craine et al. 2009). Although the mechanisms

207 underlying these shifts in δ^{15}N are not well understood, previous literature indicates

208 significant responses to environmental gradients in tropical systems (Santiago et al. 2004b)

209 making it of interest to those studying patterns of trait variation within and across species.

210 Specific leaf area (SLA, $cm^2 g^{-1}$), calculated as the ratio between leaf area and dry mass is

211 one of the leaf economic traits (Wright et al. 2004). Leaf thickness (μm) reflects mechanical

212 resistance and is linked to leaf life-span (Onoda et al. 2011). Leaf area (LA, cm^2) is

213 considered an architectural trait and although it is not directly related to physiological

214 functions, it reflects leaf light capture strategies and light competition (Poorter and Rozendaal

215 2008). The measurements of these traits followed standardized methodology (Cornelissen et

216 al. 2003, Onoda et al. 2011) and for chemical traits, all leaves were analyzed at the Cornell

217 University Stable Isotope Lab. We log-transformed LA, SLA, and leaf thickness to correct

218 for skewness.

219

220 *Analyses*

221 To compare the patterns of variation in traits across ecological levels (question 1) we

222 calculated how variance was partitioned across 4 nested levels (elevation, species,

223 population, and tree) for each trait by fitting linear mixed-effects models following the

224 same procedure described by Messier et al. (2010). The population scale refers to

225 individuals of the same species within the same elevation. We performed random

226 resampling of the individuals in the data matrix (700 permutations) and performed the same

227 analyses to estimate 95% credible intervals. In addition, to address the second question and

228 to examine whether species exhibit similar variance structure, we calculated variance

229 partitioning across populations and individuals for each species independently. Next, we

230 conducted Pearson correlation tests between variances at the population- and individual-

231 level for all species pairs.

232   To evaluate trait covariance and potential mechanisms constraining trait variation

233 and to test predictions presented in Fig. 1 (question 3), we performed Pearson correlations

234 across all pairs of traits at two different levels: across-species along the gradient and

235 within-species along the gradient (hereafter referred to as the gradient and the within-

236 species levels respectively). For the trait correlations at the gradient-level, we calculated the

237 mean trait values per elevation (averaging trait values of all co-occurring individuals of
238 different species) and then performed Pearson correlations among all pairs of traits. For the
239 correlations within species, we performed Pearson correlations across all pair of traits for
240 each species separately (we used individual-level information). Further, we compared the
241 significance of the correlations and the sign of Pearson's r across the six species and the
242 correlation at the gradient level to examine predictions presented in Fig. 1.
243
244 **Results**
245 In terms of the variance partitioning analyses across the four ecological levels (elevation,
246 species, population, and individual), we found that elevation explained little variance for
247 three traits (leaf thickness, δ^{13} C and only 1% for SLA); that the population- and the species-
248 level variance were comparable for all traits; and for δ^{13} C, δ^{15} N and LNC, variance at the
249 individual-level was similar or higher than at the population-level (Fig. 2, Appendix S1:
250 Table S1). In addition, LNC, LCC, and δ^{15} N had trait variation evenly distributed at the
251 individual-, population- and species-level (Fig.2, Appendix S1: Table S1). Variance
252 explained at the elevation- and population-level was similar for leaf thickness and δ^{13} C, but
253 at the individual-level, the variance explained was higher for δ^{13} C than the variance
254 explained for leaf thickness (Fig. 2, Appendix S1: Table S1). Leaf area had a large
255 percentage of its variance at the population- and species-level (47%) and a small percentage
256 at the individual-level (Fig. 2, Appendix S1: Table S1). SLA had the same amount of
257 explained variance at the species- and population-level (40%), less so at individual-level
258 (19%) and none due to elevation-level (Fig. 2, Appendix S1: Table S1).
259   When examining differences in trait variance structure across species by performing
260 correlations between pairs of species at the population- and individual-level, we found only
261 one significant correlation (between DACEXC and SLOBER). This indicates that species
262 show highly independent patterns in trait variation (Fig. 3, Appendix S1: Fig. S1).
263   For trait covariance, we found that eight out of 20 correlations were significant at the
264 gradient level and three were significant within-species along the gradient (where all the
265 species consistently showed significant correlations) (Fig. 4, Appendix S1: Tables S2-S3).
266 The correlation between SLA and LNC was marginal (P = 0.05) and positive at the gradient
267 level, and only significant for DACEXC and SLOBER (Fig. 4A, Appendix S1: Tables S2-
268 S3). SLA was negatively correlated with leaf thickness and δ^{13} C at within-species and
269 gradient levels (Fig. 4B and C, Appendix S1: Tables S2- S3). The correlation between SLA
270 and δ^{15} N was negative at the gradient level and at the within-species level, DACEXC,

271   MIRGAR, and SLOBER showed positive correlations (Fig. 4D, Appendix S1: Tables S2-S3).

272   Log-transformed leaf thickness and $\delta^{13}C$ were positively correlated at both levels (Fig. 4E,

273   Appendix S1: Tables S2-S3). At the gradient level, log-transformed leaf thickness and $\delta^{15}N$

274   were positively correlated and at the within-species level, DACEXC, and SLOBER showed

275   negative correlations (Fig. 4F, Appendix S1: Tables S2-S3). The correlation between log-

276   transformed leaf thickness and LNC was negative at the gradient level and at the within-

277   species level, CORBOR, DACEXC, and SLOBER showed negative correlations (Fig. 4G,

278   Appendix S1: Tables S2-S3). The correlation between $\delta^{15}N$ and $\delta^{13}C$ was positive at the

279   gradient level and at within-species level, DACEXC, and MIRGAR showed negative

280   correlations (Fig. 4H, Appendix S1: Tables S2-S3). The correlation between log-transformed

281   LA and LNC was positive at the gradient level and at within-species level CECSCH and

282   SLOBER showed positive correlations, while MIRGAR showed a negative correlation (Fig.

283   4I, Appendix S1: Tables S2-S3). In summary, our results show that for traits that were

284   significantly correlated, the most common scenario depicting trait relationships matches Fig.

285   1C.

286

287   **Discussion**

288   In this study, we were interested in characterizing intra- and inter-specific variation in leaf

289   traits for six broadly distributed tree species within a subtropical wet forest. Overall, our

290   results make evident that patterns of trait variation within species do not necessarily reflect

291   inter-specific patterns and their interpretations are highly context-dependent. These results

292   suggest that organisms distributed along different environments have great potential for

293   adjustment. However, these adjustments are idiosyncratic between species, which results in

294   the high diversity of forms and functions at local scales, often observed in tropical

295   communities. Our results question traditional functional approaches that assume a single

296   optimal phenotype matches a given environment and instead, suggest that multiple

297   phenotypes may successfully meet the requirements imposed by the environment potentially

298   due to trait-trait interactions.

299

300   *Substantial intraspecific variation and highly idiosyncratic trait variance structure across*

301   *species*

302   The high trait variation at population level suggests that organisms have a substantial level of

303   adjustment to variable environmental conditions, a pattern that is consistent with previous

304   community-level studies (Albert et al. 2010, Messier et al. 2010, De Bello et al. 2011,

305 Fajardo and Piper 2011, Siefert et al. 2015). This population-level trait variation was

306 equivalent to the species-level for all traits, indicating that differences in leaf traits across

307 species might be surpassed by differences within species when broad variation in the

308 environment is considered. The high intraspecific leaf trait variation is consistent with

309 previous findings obtained for smaller spatial scales (Hulshof and Swenson 2010, Messier et

310 al. 2010, 2017) and stresses the context-dependent aspect of leaf traits (see also Messier *et al.*

311 2010; Jung *et al.* 2010; Lepš *et al.* 2011; Anderegg *et al.* 2018). Thus, applying averaged leaf

312 trait values for broadly distributed species should be carefully interpreted when inferring

313 ecological mechanisms leading community assembly (Ames et al. 2016).

314   In addition to the population-level variation, our results show a considerable amount

315 of individual-level variation (Fig. 2) that is likely related to micro-environmental variability

316 (Albert *et al.* 2010). These traits are highly sensitive to the local scale variation and could be

317 important for understanding interactions among co-occurring individuals. For example, leaf

318 δ^{15}N is believed to be highly influenced by environmental conditions such as soil and

319 mycorrhizal composition that often exhibits substantial variation at local scales (Vitousek et

320 al. 1989, Hobbie and Högberg 2012). However, these interpretations should be considered

321 carefully since changes in δ^{15}N could be influenced by additional factors and our mechanistic

322 understanding of the drivers of δ^{15}N variation is still underdeveloped (Evans 2001).

323 Furthermore, this result indicates that local-scale (i.e. within population) environmental

324 gradients, that frequently go unmeasured, are very important for determining trait

325 distributions (Fajardo and Siefert 2018, 2019).

326   At the elevation-level, only leaf thickness, δ^{13}C and SLA showed sensitivity to this

327 scale (Fig. 2), suggesting that these traits could be useful for inferring processes operating at

328 large scales. In agreement with this result, previous studies have found that leaf thickness and

329 δ^{13}C vary broadly across environmental gradients (for leaf thickness, Billings and Mooney

330 1968, Körner and Diemer 1987; for δ^{13}C, Vitousek et al. 1990, Marshall and Zhang 1994).

331 Although for SLA, the elevation-level variance was minor (only 1% of the variance was

332 explained at elevation), previous studies have found high sensitive for large-scale variation

333 for LMA (inverse of SLA) (Liu et al. 2010, Messier et al. 2017).

334   In terms of the trait variance structure, we found idiosyncratic patterns across traits

335 despite that some of these traits should be highly correlated given that participate in common

336 functions (i.e., LNC and SLA) (Fig. 2). A potential explanation for the lack of similarity in

337 variance structure across most of the leaf traits is that similarity in the variance structure

338 across traits might not be tightly related to the strength of the trait correlation, instead, there

339 should be a minimum limit in dissimilarity in variance structure for highly correlated traits
340 (Messier et al. 2017). In other words, dissimilarity in trait variation for highly related traits
341 should be limited by a minimum but not by a maximum threshold, allowing considerable
342 independence among traits. In addition, we found that species showed poor consistency in
343 trait variance patterns (Fig. 3), which suggest that there is a considerable level of
344 independence in leaf traits that allows species to individualistically fulfill ecological
345 requirements imposed by the environment through the differential alteration of traits (see also
346 Albert et al. 2010, Fajardo and Siefert 2018). A further consequence of this is that alternative
347 arrangements of traits might be good solutions for a given environment (Marks and
348 Lechowicz 2006; Marks 2007).

349

350 *Within-species trait covariation was highly dependent on the species and generally not*
351 *consistent with gradient-level patterns*
352 Most of the trait correlations were not consistent across species (Fig. 4). For instance, the
353 correlation between log-transformed SLA and $\delta^{15}N$ was positive and significant only for
354 three species and the trend at the gradient-level was negative. Similarly, the correlation
355 between log-transformed thickness and $\delta^{15}N$ was negative for two species, but the trend at
356 the gradient-level was positive and not significant for the other four species. This mismatch
357 in correlations across ecological scales and across species suggests that species may meet the
358 physiological requirements imposed by the environment using variable combinations of traits
359 (Marks and Lechowicz 2006) and that there might be additional traits that exhibit strong
360 responses to environmental stresses along gradients (i.e. plant height) (Fajardo et al. 2018). In
361 plants, leaves represent key organs where suits of traits interact in order to satisfy plant's
362 water and carbon economies. These traits may interact in different ways that not always
363 respond to a single trade-off (Marks and Lechowicz 2006). In fact, previous studies have
364 shown that plant species achieve similar requirements through alternative routes, for
365 example, while tall species have advantages for capturing light, understory species are more
366 efficient at using their biomass to capture light (Hirose and Werger 1995). In the case of the
367 elevational gradient, investing in thicker leaves to avoid damage for high radiation, also
368 increases costs of construction, therefore, plants may invest in alternative routes to mitigate
369 effects imposed by high elevation conditions. These results are compatible with the variance
370 partitioning analyses that show weak associations in trait variance structure across species,
371 suggesting high independence in species responses to conditions imposed by the
372 environment. Combined, the distinct phenotypes arrangements of species along

373 environmental gradients should result in rugged landscapes instead of typically considered
374 unimodal landscapes (Laughlin 2018). Unfortunately, in the present study we cannot provide
375 evidence of demographic performance or fitness. Thus, we cannot fully test the ideas
376 proposed by previous authors (Marks and Lechowicz 2006, Laughlin 2018) regarding how
377 different trait combinations can lead to similar performance along an environmental gradient
378 and we look forward to future work that can address this research gap.

379   A further consequence of the observed idiosyncratic trait covariance patterns across
380 species is that species would respond differentially to potential climatic changes. Those
381 species with trait covariance patterns that track the environmental changes would have better
382 chances to succeed, given that their trait variation will allow them to tolerate broader range of
383 conditions, while species with a trait covariance that does not follow the climatic changes
384 will exhibit a more restricted capacity to tolerate climatic changes (see Fajardo and Siefert
385 2019). Similar ideas have been discussed previously by Laughlin and Messier (2015) as
386 dynamic adaptive landscapes and these could be readily applied in future studies in
387 combination with demographic data.

388   In addition, trait covariance within species was usually weak and not significant. This
389 result is surprising given the known linkage between traits involved in carbon gain (Wright et
390 al. 2004). For example, SLA and LNC are often tightly correlated across species and
391 involved in photosynthesis (Reich et al. 1998, Larcher 2003, Wright et al. 2004, Lambers et
392 al. 2008). However, our results show that although this correlation was significant across the
393 gradient, the results were not always significant within-species. A similar trend for leaf
394 economic traits in a soil nutrient gradient in Chile showed that trait correlations within
395 species tended to be weaker, but still significant, than across species (Fajardo and Siefert
396 2018). Our findings question the generality of previously reported leaf trait economics and
397 are in agreement with previous studies that also found weak correlations among LES traits at
398 local scales (Wright and Sutton-Grier 2012, Funk and Cornwell 2013, Messier et al. 2017,
399 Anderegg et al. 2018). One reason for these weak correlations could be related to the range of
400 variation in leaf life-span (Messier et al. 2017, Osnas et al. 2018). Funk and Cornwell (2013)
401 suggested that the trait covariance for LES traits depends on the variation in leaf lifespan and
402 that the strength of the correlation among LES traits would be contingent on the range in leaf
403 life-span values. In our study, the range of variation in leaf lifespan covered by a single
404 species might not be large enough to make evident the trade-offs between LES traits. Thus,
405 our results not only emphasize the fact that traditional trait correlation patterns in community-
406 wide studies may not agree with species-level patterns, but that interpretations of trade-offs

407 among traits should be carefully considered when evaluating intraspecific patterns.

408   At the gradient-level, eight trait correlations were significant. Most of these
409 correlations involve traits that are not tightly biophysically linked (i.e. LA and LNC or leaf
410 thickness and δ^{15}N). Thus, we infer from these results that the observed trait correlations may
411 emerge as a result of strong selective forces exerted by the environment and suggest a key
412 role of environment in selecting functional composition and structure along variable
413 conditions (Berg 1960, Armbruster et al. 2014). At both levels, gradient- and within-species-
414 level, only three correlations were significant (Fig. 1A and Fig. 4B, C and E). These
415 correlations involved SLA, leaf thickness, and δ^{13}C, three traits that showed sensitivity to
416 elevation-level scale in the variance partitioning analyses. Although these traits do not
417 constitute the core of the LES, they all are involved in carbon and water processing (Farquhar
418 et al. 1989, Reich et al. 1998, Lucas et al. 2000) that usually vary along altitudinal and aridity
419 gradients (Cordell et al. 1998, Hultine and Marshall 2000, Liu et al. 2010). The strong link
420 between traits at different ecological scales suggests that environmental and biophysical
421 constraints simultaneously are responsible for the patterns observed.

422

423 *Conclusion*
424 In conclusion, we show that species distributed along environmental gradients have the
425 potential to exhibit considerable variation in leaf traits, equivalent to variation across species.
426 These results challenge a functional trait paradigm were inter-specific differences should be
427 more pronounced than intraspecific differences and have consequences on the inferences of
428 ecological mechanisms and species responses to climate change. In addition, the highly
429 idiosyncratic trait variation and weak intraspecific trait coordination for most of the traits
430 implies that species may track environments using different combinations of traits that
431 ultimately provide equivalent performance outcomes. This result has important implications
432 in that predictions of species movements with changing climates cannot reliably be made
433 upon the basis of one, or even a few, trait values and even when multiple traits and their
434 combinations can be considered, species average trait values may often be misleading
435 (Laughlin and Messier 2015). In sum, functional trait-based ecology needs to more seriously
436 consider how many traits interact to determine demographic outcomes on the individual-level
437 in varying environmental contexts and the degree to which this is achieved via plasticity
438 versus local adaptation.

439

440 **Acknowledgments**

446

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669   DATA AVAILABILITY

670   Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6505nf4

671

672   **Table 1.** Elevation range for six tree species included in the present study. Species names are
673   abbreviated as follows: *Henriettea squamulosa* (Cogn.) Judd (CALSQU), *Cecropia*
674   *schreberiana* Miq subspecies schreberiana (CECSCH), *Cordia borinquensis* Urb.
675   (CORBOR), *Dacryodes excelsa* Vahl (DACEXC), *Micropholis garciniifolia* Pierre
676   (MIRGAR), *Sloanea berteroana* Choisy ex DC (SLOBER).

677

Species	Range of elevations (m)	Total individuals
CALSQU	600-1000	66
CECSCH	600-1000	60
CORBOR	400-900	86
DACEXC	300-650	68
MIRGAR	500-1000	97
SLOBER	250-650	85

678

679 **Figure legends**

680 **Fig. 1.** Schematic representation of potential scenarios of trait covariation at various

681 ecological scales. A) Correlations among traits at the species level mirror those across the

682 environmental gradient. B) No correlation across the environmental gradient but positive

683 correlations at the species level. C) Correlations at the environmental gradient and weak and

684 variable correlations at the species level. D) No significant correlations at any level.

685 **Fig. 2.** Variance partitioning for seven traits across four nested ecological levels (elevation,

686 species, population, and individual). See methods' section for all abbreviations. The numbers

687 refer to the percentage of variance explain at a given level for each trait. 13C — foliar carbon

688 stable isotope content; 15N — foliar nitrogen stable isotope content; LCC — leaf carbon

689 content; LNC — leaf nitrogen content; LA — leaf area; SLA — specific leaf area.

690 **Fig. 3.** Pairwise correlations of fractions of variance explained at the population-level of leaf

691 traits for all species pairs. The values refer to the Pearson's correlation coefficient. Each

692 square represents a correlation between values of variance explained at the population-level

693 of all traits for one species with the values of variance explained for another species. The

694 significance level for all correlations was 5 % (alpha =0.05), all correlations except one

695 (DACEXC and SLOBER, indicated with *) were non-significant. Species codes are the same

696 than in Table 1.

697 **Fig. 4**. Pearson's correlations between pairs of traits at gradient and within-species levels.

698 Black dots and lines show the correlations at the gradient level. Color dots and lines show

699 correlations for each species. Symbols: two black asterisks in the top right corner of each plot

700 indicate that correlations were significant for the gradient level and all species. Colored

701 asterisks indicate significant correlation for a given species. Species codes are the same than

702 in Table 1.

Legend:
— Environmental Gradient
--- Species

A — Trait B vs Trait A
B — Trait B vs Trait A
C — Trait B vs Trait A
D — Trait B vs Trait A

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