1

2 DR. MARÍA NATALIA UMAÑA (Orcid ID : 0000-0001-5876-7720)

3 DR. GABRIEL ARELLANO (Orcid ID : 0000-0003-3990-5344)

4

5

13

14 **Tree seedling trait optimization and growth in response to local-scale soil and light**

15 **variability**

16

17 María Natalia Umaña[1*], Gabriel Arellano[1], Nathan G. Swenson[2], Jenny Zambrano[3]

18

19 [1] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor,

20 Michigan 48109, U.S.A.

21 [2] Department of Biology, University of Maryland, College Park, Maryland 20742, U.S.A.

22 [3] The School of Biological Sciences, Washington State University, Pullman, Washington

23 99164, U.S.A.

24

25 [*] Corresponding author: maumana@gmail.com

26

29

30 **ABSTRACT**

31 At local scales, it has been suggested that high levels of resources lead to increased tree

32 growth via trait optimization (highly peaked trait distribution). However, this contrasts with

33 (i) theories that suggest that trait optimization and high growth occur in the most common
34 resource level and (ii) empirical evidence showing that high trait optimization can be also
35 found at low resource levels. This raises the question of how are traits and growth optimized
36 in highly diverse plant communities? Here, we propose a series of hypotheses about how
37 traits and growth are expected to be maximized under different resource levels (low, the most
38 common, and high) in tree seedling communities from a subtropical forest in Puerto Rico.
39 We studied the variation in the distribution of biomass allocation and leaf traits and seedlings
40 growth rate along four resource gradients: light availability (canopy openness) and soil K,
41 Mg, and N contents. Our analyses consisted of comparing trait kurtosis (a measurement of
42 trait optimization), community trait means, and relative growth rates at three resource levels
43 (low, common, and high). Trait optimization varied across the three resource levels
44 depending on the type of resource and trait, with leaf traits being optimized under high N and
45 in the most common K and Mg conditions, but not at any of the light levels. Also, seedling
46 growth increased at high light conditions and high N and K but was not related to trait
47 kurtosis. Our results indicate that local-scale variability of soil fertility and understory light
48 conditions result in shifts in species ecological strategies that increase growth despite a weak
49 trait optimization, suggesting the existence of alternative phenotypes that achieve similar
50 high performance. Uncovering the links between abiotic factors, functional trait diversity and
51 performance is necessary to better predict tree responses to future changes in abiotic
52 conditions.
53
54 **Keywords:** biomass allocation traits, canopy openness, kurtosis, leaf area, specific leaf area,
55 Puerto Rico, soil nutrients

56 **INTRODUCTION**

57 Understanding how abiotic factors drive functional trait distributions and growth of local
58 communities is important for determining community responses to future changes in
59 environmental conditions (Violle et al. 2007, Estrada et al. 2016, Sakschewski et al. 2016).
60 Trait distributions of plant communities are assumed to be the outcome, to some degree, of
61 environmental conditions exerting selective forces and favoring species that make a good fit
62 for given conditions. In other words, traits are assumed to reflect optimal or, at least,
63 optimized ecological strategies for any given environment (although this set of optimal traits
64 may change due to temporal changes in conditions) (Southwood 1977, Grime 1979, Keddy
65 1992, McGill et al. 2006). As a result, local species composition should cover a relatively
66 narrow range of trait values that fit the requirements of the environment there. However, this

67   expectation contradicts the often-observed pattern of a wide diversity of forms and functions

68   in tropical plant communities and suggests the existence of alternative phenotypes with

69   equivalent performance (Marks and Lechowicz 2006, Worthy et al. 2020).

70   At local scales, the distribution of a given resource is typically unimodal, with some

71   resource values being more frequent than values located at the tails of the distribution (Fig. 1,

72   Appendix S1: Fig. S1) (Abrams 1995, Brigatti et al. 2007). For example, levels of canopy

73   openness (used as a proxy for understory light availability) are often around 10% in tropical

74   forests. However, light availability values, even in a closed forest, can range between < 1%

75   and 35%, with these extreme values being less frequent than mean values (Chazdon and

76   Fetcher 1984). Similarly, soil resources may exhibit a similar peaked hump-shaped

77   distribution, with soils showing low and high levels of fertility towards the tails of the

78   distribution (Appendix S1: Fig. S1). As traits reflect the interaction between the organisms

79   and their environment, local variation in abiotic factors is expected to have an impact on trait

80   distributions in plant communities and on growth. There are at least three potential scenarios

81   describing trait distributions at the community level, and plant growth in response to resource

82   gradients:

83   *Scenario 1: Peaked trait distributions towards common conditions.* In the first

84   scenario, uncommon conditions are too rare to lead to peaked trait distributions –trait

85   optimization– given that resources are not suitable and abundant enough to maintain stable

86   populations that represent a good fit for those conditions, while common conditions represent

87   suitable areas and allow trait optimization (Fig. 1A) (McGill et al. 2006, Violle et al. 2007).

88   These two different levels of trait optimization would imply better performance (e.g., growth)

89   for individuals present in the most common conditions and lower performance of those

90   individuals in places with uncommon resource levels.

91   *Scenario 2: Peaked trait distributions towards rare conditions.* Uncommon

92   conditions that represent extremes of the resource distribution (characterized by either low or

93   high resource levels) could lead to trait optimization due to strong selective forces that

94   operate under these conditions (Fig. 1B). For example, in high-light conditions species that

95   acquire resources fast and efficiently outcompete other species leading to optimization in leaf

96   traits. Similarly, in nutrient-poor soils only a handful of specialized species may persist,

97   representing a (relatively) narrow range of traits. Empirical evidence has shown that trait

98   values are more strongly selected at the extremes of the resource distribution characterized by

99   either low or high resource levels, with trait optimization occurring at these extremes rather

100   than at most common ones (Weiher et al. 1998, Cornwell and Ackerly 2009, de Bello et al.

101   2009, Kraft and Ackerly 2010, Swenson et al. 2011, Bernard-Verdier et al. 2012, Bruelheide

102   et al. 2018). For instance, a previous study found that open sites (i.e., treefall gaps) exert

103   strong selective forces on tree communities allowing only light-demanding species to

104   successfully colonize these forest gaps (trait optimization), while intermediate and low light

105   level sites exhibit greater diversity of life-forms (lower trait optimization) (Hubbell 2005).

106   Other studies have also shown that across environmental gradients, low soil nutrient levels

107   tend to favor stress-tolerant species, resulting in trait optimization towards lower extremes of

108   the resource distribution (Pinho et al. 2018). These patterns in trait distributions have been

109   well documented at the landscape and regional scales (Cornwell and Ackerly 2009, Enquist

110   et al. 2015, Šímová et al. 2015). At local scales, similar trends are expected if extreme abiotic

111   conditions select for particular traits that maximize organisms' performance (e.g., high

112   growth) (Fig. 1B).

113   *Scenario 3: Low peaked trait distributions occur in both common and rare resource*

114   *levels.* Alternatively to these two scenarios, traits might not be strongly optimized towards a

115   single or a narrow range of values. Instead, plants may display contrasting phenotypes that

116   constitute alternative solutions for the given local conditions (Marks and Lechowicz 2006,

117   Muscarella and Uriarte 2016, Worthy et al. 2020). For example, Hirose and Werger (1995)

118   found that in a tropical forest different species of trees exhibit contrasting strategies for

119   capturing light that result in similar performance. In this case, we should observe a lack of

120   trait optimization across different resource levels, yet species may still achieve high

121   performance anywhere along the local gradient of conditions.

122   Here, we examine both biomass allocation and non-biomass allocation traits. Biomass

123   allocation traits represent a group of traits that have shown great variation within species and

124   reflect the amount of biomass that plants allocate to a particular organ depending on the

125   resources that are the most limiting for plant growth (Bloom, Chapin, & Mooney, 1985;

126   Poorter et al., 2012; Umaña, Zhang, Cao, Lin, & Swenson, 2018). For example, according to

127   optimal allocation theory, strong limitation in soil nutrient content should result in increased

128   biomass allocation to roots at the expense of lower biomass allocation to leaves and stems

129   (Bloom et al. 1985). Another group includes non-biomass allocation traits, such as specific

130   leaf area or leaf area, which have shown strong responses to shifts in a variety of abiotic

131   factors (Chapin, 1980; Craine, Froehle, Tilman, Wedin, & Chapin, 2001; Oksanen, Fretwell,

132   Arruda, & Niemela, 1981; Reich, Walters, & Ellsworth, 1997; Wright et al., 2004). For

133   example, environments with low resource levels tend to be dominated by species with

134   conservative traits such as low specific leaf area and low leaf area (Le Bagousse-Pinguet et

135   al. 2017). Combined, biomass allocation and non-biomass allocation traits capture a wide

136   range of species responses to local-scale resource variation.

137   We study trait optimization in response to local-scale resource variation and how that

138   results in differences in seedling growth in a subtropical forest. We use growth and trait

139   information collected from all individuals present in 200 seedling plots (~1800 individuals)

140   in combination with local-scale abiotic information on soil nutrient content (K, Mg, and N)

141   and canopy openness (a proxy for light availability in the forest understory) (Appendix S1:

142   Fig. S1). While most trait-based studies have used species' mean traits values, which assumes

143   that all individuals within a species are identical in their traits, here, we have trait and

144   seedling growth information for all individuals. With this information, we can accurately

145   study trait and growth distributions across local-scale resource gradients. Specifically, we ask

146   the following questions:

147

148   1. How does trait optimization differ in extreme vs. common resource levels? We propose to

149   examine the three alternative scenarios described above by quantifying trait optimization

150   under different resource levels.

151

152   2. How do community mean trait values change across resource levels? We expect changes in

153   trait means across different resource levels depending on the type of trait. Specifically, we

154   expect biomass allocation traits to vary according to the optimal allocation theory (i.e., higher

155   allocation towards most limiting resources), while non-biomass allocation traits will be more

156   conservative (e.g. low SLA and LA) towards the most limiting extremes of resource levels.

157

158   3. How does seedling growth vary between extreme vs. common resource levels? Does trait

159   optimization lead to high seedling growth? We predict variation in seedling growth across

160   common and extreme levels of soil nutrient and light conditions, with at least two potential

161   and non-exclusive outcomes: 1) at high resource levels, seedling growth rates are high; 2)

162   seedling growth rates are high in resource levels that show high trait optimization.

163

164   **METHODS**

165   *Field surveys and trait data collection*

166   The study was conducted in El Yunque National Forest, in Puerto Rico (65°47′ W, 18°19′ N).

167   This forest, classified as a subtropical wet forest, has a mean annual rainfall of 3548 mm and

168   an average temperature of 23ºC (Ewel and Whitmore 1973). The vegetation is dominated by

169   the tree species *Dacryodes excelsa* (Burseraceae) and the palm *Prestoea acuminata*

170   (Arecaceae). In 2013, 200 1x1m seedling plots were established to monitor seedling growth

171   for one year. Seedling plots were arranged in a regular grid separated by 10 m. All tree

172   seedlings ≤ 50 cm in height (n = 1771) were measured, tagged, and identified to species

173   (Umaña et al. 2015). Between June and July 2014, all surviving individual seedlings were

174   collected for trait measurements. We measured fresh leaf area (LA in cm^2) for 1-3 fully

175   expanded leaves. The leaves were then dried and weighed to calculate specific leaf area (SLA

176   = LA/dry mass; cm^2/g). Roots were cleaned and separated from the main stem. Leaves and

177   roots were dried in an oven for 72 hours at 70ºC and measured for dry mass (g) to calculate

178   traits related to biomass allocation. Leaf mass fraction (LMF) was calculated as: LMF = leaf

179   dry mass/total plant dry mass. Root mass fraction (RMF) as: root dry mass/total plant dry

180   mass. Leaf area ratio (LAR) was calculated as: LAR = leaf area/total plant dry mass (Poorter

181   *et al.* 2012). Leaf traits included leaf area (LA) and specific leaf area (SLA). LA reflects the

182   area displayed to capture light (Rozendaal et al. 2006), while SLA describes a range of

183   strategies (conservative to acquisitive) for carbon assimilation (Reich et al., 1997; Wright et

184   al., 2004).

185

186   *Relative growth rate*

187   We defined seedling relative growth rate (RGR) as the change in log-transformed total height

188   (cm) from 2013 to 2014. The total height of each seedling was measured from the base to the

189   most distant part of the main stem. We standardized relative growth values by subtracting the

190   mean of each species and dividing by the standard deviation per species. This allows

191   comparisons across species with different inherent growth rates, as those involved in the

192   survival-growth trade-off (Arellano et al. 2019).

193

194   *Soil nutrient content and canopy openness*

195   Soil samples were extracted below the organic litter layer (0-10 cm depth) in July 2014. Each

196   soil sample consisted of mixed soil from each of the plot corners and from the center of the

197   seedling plots, and we collected a total of 200 soil samples. Soil samples were sent to

198   Brookside Laboratories Inc. (Ohio, USA) for chemical analyses. Magnesium and potassium

199   (Mg, mg/kg; and K, mg/kg) were extracted using the Mehlich-III solution. Magnesium is an

200   essential macronutrient found in the chlorophyll of green plants and potassium is essential for

201   photosynthesis and protein synthesis as well as carbohydrate transport and storage (Maathuis

202   2009). Potassium has been found to limit seedling growth in tropical and temperate forests

203   (Tripler et al. 2006, Wright et al. 2011). Total soil N concentration was obtained using the

204   total combustion method. Nitrogen is an essential constituent of proteins found in chlorophyll

205   and is needed in substantial amounts (Maathuis 2009). While soil P is an important limiting

206   resource for tropical forests, most of the P concentrations in our samples fell below the

207   detection threshold for the method and we could not use it for the present study.

208

209   To assess light conditions, we took hemispherical photographs using a camera Nikon

210   Coolpix5000 with an FC-E8 Nikon fisheye lens. The photographs were taken at 1m height in

211   the center of each seedling plot at uniform light conditions at dawn with homogeneous light

212   conditions (Glatthorn and Beckschäfer 2014). The photographs were analyzed using the Gap

213   Light Analyzer software (GLA) (Frazer et al. 2000) (available at

214   https://www.caryinstitute.org/science-program/our-scientists/dr-charles-d-canham/gap-light-

215   analyzer-gla). Appendix S1: Table S1 reports ranges and mean values for all the studied

216   abiotic variables.

217

218   *Plot selection at different resource levels*

219   Our approach consisted of classifying plots into three resource levels (low, common, and

220   high) and then calculating trait kurtosis per each resource level. This approach allows us to

221   use seedling communities large enough at each resource level in order to have robust

222   measurements of kurtosis, otherwise, our plots are too small to have a high number of trait

223   values (seedling abundance range: [1, 39]; mean = 9). Prior to the analyses, we examined

224   correlations between abiotic variables across the 200 plots (Appendix S1: Table S2) and their

225   distribution. All abiotic variables showed unimodal distribution with the most common

226   resource level around the average resource value (Appendix S1: Fig. S1).

227   Next, we calculated the relative frequency of each resource level using a kernel

228   density estimation for each abiotic variable using the R function "density" from package

229   "stats" (R Development Core Team 2017). Given that the density estimation is affected by

230   the bandwidth, we used two methods to select the appropriate bandwidth. The first method is

231   based on a linear diffusion process (Botev et al. 2010), a non-parametric density estimator

232   independent of a normal model and less sensitive to outliers (Botev et al. 2010). This method

233   was implemented by using the function "botev" from the package "provenance" in R

234   (Vermeesch 2020). The second method uses the asymptotic mean integrated squared method

235   error (AMISE) and consists of evaluating the mean integrated squared error of a density

236   estimate based on a normal distribution (see Appendix S2).

237   We classified subsets of plots into "low resource" plots, "high resource" plots, and

238   "the most common resource" plots, for each environmental variable (hereafter referred to as

239   low, high, and common, respectively). The low resource plots corresponded to the 10% with

240   the lowest level of the resource. The high resource plots corresponded to the 10% with the

241   highest level of the resource. The most common resource plots corresponded to the 10%

242   closest to the most frequent conditions, inferred from the location of the peak in the unimodal

243   estimation of density. Since we have some plots with repeated values for the different

244   resources studied, the number of plots selected per resource level varied between 10-16% of

245   the total number of plots; Appendix S1: Table S3 contains the specific number of plots

246   selected per resource level, and Appendix S1: Figure S1 indicates the plots that were selected

247   in each resource level (of the 200 plots established, some were excluded from the analyses to

248   focus on the most extreme and common values). To determine whether our results were

249   sensitive to the number of selected plots for each resource level, we repeated all the analyses

250   using the $p\%$ plots with the lowest, highest, or the most common levels of the resource, p in

251   {5, 6, …, 14, 15}. The results (Appendix S3) were not sensitive to the value of p, except in

252   low ranges (likely due to the low sample size, the inherent variability in the tails and/or the

253   skewed distribution of some of the resources studied).

254

255   *Measurement of trait optimization at each resource level*

256   To examine how trait distribution varied with different resource levels (question 1), we

257   compared trait kurtosis values using information from seedlings located in the low, high, and

258   the most common resource plots. Very peaked distributions (high kurtosis) indicate strong

259   trait optimization, while very flat distributions (low kurtosis) indicate weak trait optimization

260   (Enquist et al. 2015, Le Bagousse-Pinguet et al. 2017). We calculated kurtosis for individual

261   traits per resource level. We choose kurtosis over variance because we are interested in

262   detecting a pointed peak (or lack of it) in trait distributions beyond the information about how

263   spread is the data (Figure S2 in Appendix S1 shows that the degree to which a given

264   distribution is peaked is independent of the spread of the data) (Enquist et al. 2015).

265   Given that kurtosis values are difficult to compare with each other, at least in terms of

266   how much they differ from the expected by chance, we used a more interpretable metric than

267   raw kurtosis, by calculating the Standardized Effect Sizes (SES) for the kurtosis values

268   obtained in all resource level classes, for all environmental variables and traits. To calculate

269   the SES for kurtosis, we created null models where each trait value per individual within a

270   community matrix (including all 200 plots) was randomized 999 times and we re-calculated

271   kurtosis for each resource level for each randomized dataset. We then obtained a mean null

272   value and standard deviation from the null distribution that were used to calculate the kurtosis

273   SES:

274

275
$$SES\ Kurtosis\ = \frac{Observed\ kurtosis - mean\ null\ kurtosis}{SD\ null\ kurtosis}$$

276

277   SES kurtosis values > 1.96 indicate higher than expected kurtosis in a certain trait

278   given the number of seedlings present in plots at each resource level and SES kurtosis values

279   < -1.96 values indicate a lower than expected kurtosis for a certain trait given the number of

280   seedlings present in plots at each resource level.

281

282   *Change in mean trait values in each resource level*

283   To determine how community mean trait values change across resource levels (question 2),

284   we calculated and compared mean community trait values at each resource level. When

285   calculating mean trait values, we used all individual seedlings present at each resource level.

286   To allow comparisons between traits measured in different units, we used standardized trait

287   values at the community level (mean = 0, standard deviation = 1). Next, to determine whether

288   trait means at each resource level differ from zero, we performed a bootstrap sampling with

289   replacement. To do this, we randomly selected seedlings (with different trait values) for each

290   resource level 999 times and calculated the mean per trait. If 95% of the values of the

291   bootstrap distribution overlapped zero, then it was considered not significant. In other words,

292   this test examines whether the trait mean at a given resource level differs from the expected

293   for the species.

294

295   *Variation in seedling growth rates at each resource level*

296   To address how seedling growth varies across resource levels (question 3), we performed a

297   similar analysis from the one used for mean traits, but instead of using functional traits, we

298   used RGR (see raw RGR distributions at each resource level in Appendix S1: Fig. S3). We

299   also performed a bootstrap sampling with replacement to assess the significance of changes

300   in RGR at each resource level (*i.e.* deviations in RGR from the expected for the species).

301   Furthermore, we evaluated if kurtosis was related to mean RGR at each resource level

302   (question 4) using a linear mixed-effects model (function "lmer", package "lme4" (Bates et

303   al. 2015) in R (R Development Core Team 2017)). In these models, the response variable was

304   mean RGR at each resource level. The independent variable was trait kurtosis per resource

305   level; abiotic factors (canopy openness, soil N, Mg, and K) and resource levels (high, low and

306   the most common) were included as intercept-specific random effects, to account for the

307   effects of variation of both variables on growth. The sample size for this model was n = 60.

308   To calculate the marginal and conditional coefficients of determination described by

309   Nakagawa and Schielzeth (2013), we used the function "r2" in the package "performance"

310   (Lüdecke 2020).

311

312   **RESULTS**

313   *Variation in trait distributions with different resource levels (question 1)*

314   Observed kurtosis patterns based on different traits showed a variation across the different

315   studied resource levels (low, common, and high), but the patterns were resource- and trait-

316   specific (Appendix S1: Fig. 2). For canopy openness, observed kurtosis values for all traits

317   did not differ from a random expectation, but there was a generalized trend for higher SES

318   kurtosis in the most common light conditions, except for RMF (Fig. 2). For soil K content,

319   SLA had higher than expected kurtosis at high resource values while LAR had higher than

320   expected kurtosis at the most common level, the rest of the traits had kurtosis that was not

321   significantly different than expected by the null model. For soil Mg content, LAR had higher

322   than expected kurtosis at the most common resource level, indicating trait optimization and

323   RMF had higher than expected kurtosis at the low resource level. The rest of the traits had

324   kurtosis levels that were not significantly different from the null expectation for soil Mg. For

325   soil N content, SLA, LAR, and LMF had a higher than expected kurtosis at the high resource

326   level indicating trait optimization at high N levels. The rest of the traits had kurtosis that was

327   not significantly different than expected by the null model for soil N. Results obtained using

328   the AMISE method were largely consistent with the results described above, especially for

329   results based on canopy openness and soil N (Appendix S2). For Mg and K, kurtosis values

330   of LAR, LMF, and SLA were less consistent (Appendix S2).

331

332   *Variation in mean trait values with different resource levels (question 2)*

333   In addition to the kurtosis analyses, we also examined shifts in mean trait values across the

334   three resource levels. For canopy openness, LA and LAR were significantly higher at high

335   light levels, and LAR, RMF, and SLA were significantly lower at the most common resource

336   level. The means of the rest of the traits were not significantly different from their

337   community-wide means at any level of canopy openness (Fig. 3). For soil K content, LA was

338 significantly higher at low and high resource levels but it was significantly lower at the most
339 common resource level. Also, LAR was significantly higher when soil K was high. The rest
340 of the traits showed means that were not significantly different from the mean community
341 value for soil K (Fig. 3). For soil Mg content, RMF and LA were significantly higher, while
342 SLA was significantly lower at the most common resource level. The rest of the traits showed
343 means that were not significantly different from the mean community value for soil Mg (Fig.
344 3). For soil N content, LAR and LMF were significantly higher at the low resource level,
345 while LMF and LAR were significantly lower and RMF was significantly high at the most
346 common resource level, and LA, RMF, and LAR were significantly higher at the high
347 resource level. The rest of the traits showed means that were not significantly different from
348 the mean community value for soil N (Fig. 3).
349
350 *Community growth rates in three resource levels (question 3)*
351 Mean seedling relative growth rate (RGR) was significantly higher at high levels of canopy
352 openness, soil N, and K content (Fig. 4). For the rest of the resource levels, standardized
353 RGR showed no significant differences. In addition, in the linear mixed-effects model
354 relating trait kurtosis and growth, the kurtosis had virtually no effect on RGR (coefficient =
355 0.01, 95% CI: [-0.01, 0.03]); the model had a low fit (marginal R^2 = 0.02 and conditional R^2
356 = 0.53).
357
358 **DISCUSSION**
359 Understanding how resource variation at local scales determines trait distributions and plant
360 performance remains a major question in ecology. To examine this question, we combined
361 individual trait and growth information collected from tropical seedling communities along
362 local-scale light and soil fertility gradients. We found that trends in trait optimization are not
363 generalizable across soil and light gradients. Specifically, trait optimization was observed for
364 the most common levels of K and Mg as well as in high soil N sites, while traits were not
365 particularly optimized at any level of canopy openness. Variation in growth rates was also
366 resource-specific, with seedling growth being the highest when canopy openness and soil K
367 and N content were high but was not related to trait optimization. Overall, these findings
368 suggest that peaked trait distributions do not necessarily match the most common resource
369 levels nor lead to an increase in growth as it is commonly assumed for local-scales studies.
370 Further, we show that seedling growth can increase despite a lack of trait optimization.
371 Below, we discuss in more detail our findings.

372

Traits are optimized under low, high and common resource levels

We observed a strong variation of trait optimization across three resource levels. However, these shifts in trait optimization were highly dependent on the type of resource and studied trait. For instance, LA, LMF, and LAR showed peaked distributions when soil N content was high supporting the scenario showed in Fig. 1B. Similar results have been reported in studies including broader environmental gradients than the one included in this study, in which high soil fertility leads to high trait kurtosis (Enquist et al. 2015, Le Bagousse-Pinguet et al. 2017). However, when considering soil Mg or K content, peaks in trait distributions (for LAR) were found at sites with the most common resource level, supporting the scenario showed in Fig. 1A and suggesting strong selecting forces on trait distributions under the most common conditions. These results are concordant with previous theoretical studies predicting a high frequency of trait values under the most common conditions (Austin 1986, McGill et al. 2006, Enquist et al. 2015), yet empirical evidence has remained scarce. Surprisingly, we also found a lack of trait optimization for any of the studied traits when considering canopy openness that can be related to high temporal variability in light conditions. Overall, the discrepancies in trait distributions across different resource levels suggest that selective forces operate with variable intensity at different resource availabilities and may even result in a prevalence of low peaked trait distributions. These results are consistent with another study of tree communities across the entire island of Puerto Rico that examined the variation in community weighed mean trait values with shifts in species occurrence to test for trait optimization (Muscarella and Uriarte 2016). Their results showed that while some traits support the optimization hypothesis (LMA, wood density, and maximum height), there were many other cases where trait optimization was not found.

Mean trait values are more acquisitive under high resource levels

We expected a variation in mean trait values in response to different resource levels (Fig. 3). Specifically, we predicted acquisitive strategies (i.e., high SLA and LA) to be predominant at high resource levels and increased biomass allocation to organs involved in the acquisition of limited resources (low resource levels). For leaf allocation traits, our results did not follow the expected trend and instead, showed that seedlings tend to allocate a greater area to leaves (LAR) rather than allocating biomass to roots in habitats experiencing high light levels. These findings contradict the optimal allocation theory in which plants are expected to allocate greater leaf biomass in low light conditions than at higher light availability (Mooney

406 1972, Bloom et al. 1985). However, for non-biomass allocation leaf traits, our results were
407 consistent with our expectations with LA increasing with high understory light availability
408 and indicating that seedling communities located in more open environments are
409 characterized by acquisitive traits. These findings are concordant with previous studies
410 conducted at a Neotropical forest where species displayed high leaf sizes values at high light
411 levels contributing to their carbon gain (Lambers and Poorter 1992, Poorter and Rozendaal
412 2008). It is important to note that similar trends observed for LAR and LA can be also
413 explained by the correlation between both traits (Fig. S4, Appendix S1).

414 By taking together results of mean and kurtosis trait values for variable light
415 conditions, we infer that trait distributions across the three light levels show to some degree
416 shifts in mean functional strategies, yet under each light level, there is no evidence of trait
417 optimization. This indicates that trait selection operates differently across low, most common,
418 and high light levels but within each resource level there is a substantial variation in
419 phenotypes that result in platykurtic trait distributions. This agrees with results from a
420 previous study from the El Yunque forest that showed that during the seed-to seedling
421 transition, functional divergence tends to be higher than expected by chance (Umaña et al.,
422 2016).

423 Mean trait values also varied in response to soil resource levels. We expected greater
424 biomass allocation to roots in poor soil conditions as suggested by the optimal allocation
425 theory (Bloom et al., 1985; Garnier, 1991; Marschner, Kirkby, & Cakmak, 1996; Santiago et
426 al., 2012; Wright et al., 2011) and an increase in SLA as soils become more fertile (Ordoñez
427 et al. 2009). However, these expectations were not supported in this study as we found no
428 general trends for patterns of biomass allocation or distribution of leaf-related acquisitive
429 strategies. One potential explanation is that patterns of biomass allocation and trait variation
430 depend on the interaction of multiple abiotic factors (Blonder et al. 2018). For example, root
431 biomass responds to both soil fertility and water availability that does not always covary at
432 the local scales included here and may result in conflicting trait responses. Another potential
433 explanation is that trait-trait correlations may potentially mask plant responses to variation in
434 resource availability. For example, the significant correlation between leaf and root mass
435 fractions may limit the ability to identify and separate the responses of below and
436 aboveground traits (Fig. S4).

437

438 *Seedling growth increases under high light and high soil N and K content but is not related to*
439 *trait optimization*

440   We expected that seedling growth would increase in areas of high resource levels and/or in
441   areas of high trait optimization (high trait kurtosis). Our results show that high light
442   availability and soil N and K content resulted in high seedling growth rates (Fig. 4); however,
443   growth was not related to trait optimization. Our findings related to light suggest that
444   understory light conditions are a key limiting factor in this forest and that at high understory
445   light availability, plants might enhance their growth in the absence of a trait optimization.
446   Our results are concordant with results from other plant community studies that have shown
447   species exhibiting contrasting phenotypes that increase plant performance and conform
448   alternative phenotypes under particular resource conditions (Hirose and Werger 1995, Pistón
449   et al. 2019, Worthy et al. 2020). Our results also agree with previous studies conducted in the
450   studied forest showing light as a key factor influencing performance at early ontogenetic
451   stages (Comita et al. 2009, Uriarte et al. 2018).
452
453   For soil nutrients, the direct effects of soil N and K should be carefully interpreted as both
454   variables were significantly correlated making it difficult to determine the independent
455   contribution of each factor to seedling growth ($r = 0.56$, $p < 0.001$, Table S2 in Appendix S1).
456   Although it has been suggested that soil N should not be considered as a limiting factor for
457   tropical forests (Hedin et al. 2009), previous studies in tropical regions have found that soil N
458   may have positive significant effects on plant biomass accumulation and productivity
459   (Vitousek and Sanford 1986, Mirmanto et al. 1999, LeBauer and Treseder 2008, Graefe et al.
460   2010, Santiago et al. 2012). Similarly, soil K has shown significant effects on seedling
461   growth, as found in our study (Santiago et al. 2012, Wright 2019).
462

463   *Conclusion*
464   Our findings suggest that high plant growth does not necessarily result from trait
465   optimization. Furthermore, we did not find support for the expectation that the most common
466   resource level translates into highly peaked trait distributions and high seedling growth.
467   Instead, we found that seedling growth at the Luquillo forest is limited by light, soil K, and N
468   content and that increase in growth can be the outcome from co-occurring contrasting
469   phenotypes. Overall, our study suggests that the high functional diversity found in tropical
470   forests partially results from a variety of phenotypic designs that perform well under given
471   resource levels. Also, an important portion of the trait variation observed in our study comes
472   from within species and highlights the need to incorporate this level of information in future

473   studies to gain a better understanding of community responses to local-scale resource

474   gradients.

475

476   **Acknowledgments** We are grateful to Roxy Cruz-de-Hoyos and Carrie Barker for their

477   assistance in collecting data; John Bithorn for help with field species identification; Seth

478   Rifkin and Samuel Matta for assistance in locating filed sites. Cecilia Prada provided

479   insightful discussion. Two anonymous reviewers provided insightful comments that largely

480   improved the manuscript. Authors' contributions: MNU designed the study. MNU and NGS

481   designed the fieldwork. MNU conducted fieldwork. MNU analyzed the data with input from

482   GA and NGS. MNU wrote the manuscript with input from GA, NGS, and JZ.

483

484   **Supporting Information**

485   Additional supporting information may be found online at: [link to be added in production]

486

487   **Data Availability**

488   Data is available from the Dryad Digital Repository (Umaña et al. 2021):

489   https://doi.org/10.5061/dryad.sqv9s4n29

490

491   **References**

492   Abrams, P. A. 1995. Monotonic or unimodal diversity-productivity gradients: What does

493   competition theory predict? Ecology 76:2019–2027.

494   Arellano, G., N. G. Medina, S. Tan, M. Mohamad, and S. J. Davies. 2019. Crown damage

495   and the mortality of tropical trees. New Phytologist 221:169–179.

496   Austin, M. P. 1986. The theoretical basis of vegetation science. Trends in Ecology and

497   Evolution 1:161–164.

498   Le Bagousse-Pinguet, Y., N. Gross, F. T. Maestre, V. Maire, F. de Bello, C. R. Fonseca, J.

499   Kattge, E. Valencia, J. Leps, and P. Liancourt. 2017. Testing the environmental filtering

500   concept in global drylands. Journal of Ecology 105:1058–1069.

501   Bates, D., M. Maechler, B. M. Bolker, and S. Walker. 2015. lme4: Linear mixed-effects

502   models using Eigen and S4. Version 1.1-12.

503   de Bello, F., W. Thuiller, J. Leps, P. Choler, J.-C. Clément, P. Macek, M.-T. Sebastià, and S.

504   Lavorel. 2009. Partitioning of functional diversity reveals the scale and extent of trait

505   convergence and divergence. Journal of Vegetation Science 20:475–486.

506   Bernard-Verdier, M., M. L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012.

507 Community assembly along a soil depth gradient: Contrasting patterns of plant trait

508   convergence and divergence in a Mediterranean rangeland. Journal of Ecology

509   100:1422–1433.

510 Blonder, B., R. E. Kapas, R. M. Dalton, B. J. Graae, J. M. Heiling, and Ø. H. Opedal. 2018.

511   Microenvironment and functional-trait context dependence predict alpine plant

512   community dynamics. Journal of Ecology 106:1323–1337.

513 Bloom, A. J., F. S. Chapin, H. a. Mooney, F. S. Chapin III, and H. a. Mooney. 1985. resource

514   limitation in plants-an economic analogy. Annual Review of Ecology and Systematics

515   16:363–392.

516 Botev, Z. I., J. F. Grotowski, and D. P. Kroese. 2010. Kernel density estimation via diffusion.

517   Annals of Statistics 38:2916–2957.

518 Brigatti, E., J. S. Sá Martins, and I. Roditi. 2007. Evolution of biodiversity and sympatric

519   speciation through competition in a unimodal distribution of resources. Physica A:

520   Statistical Mechanics and its Applications 376:378–386.

521 Bruelheide, H., J. Dengler, O. Purschke, J. Lenoir, B. Jiménez-Alfaro, S. M. Hennekens, Z.

522   Botta-Dukát, M. Chytrý, R. Field, F. Jansen, J. Kattge, V. D. Pillar, F. Schrodt, M. D.

523   Mahecha, R. K. Peet, B. Sandel, P. van Bodegom, J. Altman, E. Alvarez-Dávila, M. A.

524   S. Arfin Khan, F. Attorre, I. Aubin, C. Baraloto, J. G. Barroso, M. Bauters, E.

525   Bergmeier, I. Biurrun, A. D. Bjorkman, B. Blonder, A. Čarni, L. Cayuela, T. Černý, J.

526   H. C. Cornelissen, D. Craven, M. Dainese, G. Derroire, M. De Sanctis, S. Díaz, J.

527   Doležal, W. Farfan-Rios, T. R. Feldpausch, N. J. Fenton, E. Garnier, G. R. Guerin, A. G.

528   Gutiérrez, S. Haider, T. Hattab, G. Henry, B. Hérault, P. Higuchi, N. Hölzel, J. Homeier,

529   A. Jentsch, N. Jürgens, Z. Kącki, D. N. Karger, M. Kessler, M. Kleyer, I. Knollová, A.

530   Y. Korolyuk, I. Kühn, D. C. Laughlin, F. Lens, J. Loos, F. Louault, M. I. Lyubenova, Y.

531   Malhi, C. Marcenò, M. Mencuccini, J. V. Müller, J. Munzinger, I. H. Myers-Smith, D.

532   A. Neill, Ü. Niinemets, K. H. Orwin, W. A. Ozinga, J. Penuelas, A. Pérez-Haase, P.

533   Petřík, O. L. Phillips, M. Pärtel, P. B. Reich, C. Römermann, A. V. Rodrigues, F. M.

534   Sabatini, J. Sardans, M. Schmidt, G. Seidler, J. E. Silva Espejo, M. Silveira, A. Smyth,

535   M. Sporbert, J.-C. Svenning, Z. Tang, R. Thomas, I. Tsiripidis, K. Vassilev, C. Violle,

536   R. Virtanen, E. Weiher, E. Welk, K. Wesche, M. Winter, C. Wirth, and U. Jandt. 2018.

537   Global trait–environment relationships of plant communities. Nature Ecology &

538   Evolution 2:1906–1917.

539 Chapin, F. S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and

540   Systematics 11:233–260.

541 Chazdon, R. L., and N. Fetcher. 1984. Light environments of tropical forests. Pages 27–36 *in*
542   E. Medina, H. A. Mooney, and C. Vázquez-Yánes, editors. Physiological ecology of
543   plants of the wet tropics. Springer Netherlands.

544 Comita, L. S., M. Uriarte, J. Thompson, I. Jonckheere, C. D. Canham, and J. K. Zimmerman.
545   2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical
546   forest. Journal of Ecology 97:1346–1359.

547 Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait
548   distributions across an environmental gradient in coastal California. Ecological
549   Monographs 79:109–126.

550 Craine, J. M., J. Froehle, D. G. Tilman, D. A. Wedin, and F. S. Chapin. 2001. The
551   relationships among root and leaf traits of 76 grassland species and relative abundance
552   along fertility and disturbance gradients. Oikos 93:274–285.

553 Daniel Lüdecke. 2020. Package "performance": Assessment of regression models
554   performance.

555 Enquist, B. J., J. Norberg, S. P. Bonser, C. Violle, C. T. Webb, A. Henderson, L. L. Sloat,
556   and V. M. Savage. 2015. Scaling from traits to ecosystems: developing a general trait
557   driver theory via integrating trait-based and metabolic scaling theories. Advances in
558   Ecological Research 52:249–318.

559 Estrada, A., I. Morales-Castilla, P. Caplat, and R. Early. 2016. Usefulness of species traits in
560   predicting range shifts. Trends in Ecology and Evolution 31:190–203.

561 Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the
562   U.S.Virgin Islands. Page USDA Forest Service Research, Institute for Tropical Forestry,
563   Rio Piedras, Puerto Rico.

564 Frazer, G. W., C. D. Canham, and K. P. Lertzman. 2000. Gap Light Analyzer (GLA), version
565   2.0. Page Technological tools.

566 Garnier, E. 1991. Resource capture, biomass allocation and growth in herbaceous plants.
567   Trends in Ecology and Evolution 6:126–131.

568 Glatthorn, J., and P. Beckschäfer. 2014. Standardizing the protocol for hemispherical
569   photographs: Accuracy assessment of binarization algorithms. PLoS ONE 9:1–19.

570 Graefe, S., D. Hertel, and C. Leuschner. 2010. N, P and K limitation of fine root growth
571   along an elevation transect in tropical mountain forests. Acta Oecologica 36:537–542.

572 Grime, J. P. 1979. Primary strategies in plants. Transactions of the Botanical Society of
573   Edinburgh 43:151–160.

574 Hedin, L. O., E. N. J. Brookshire, D. N. L. Menge, and A. R. Barron. 2009. The Nitrogen

575   Paradox in Tropical Forest Ecosystems. Annual Review of Ecology, Evolution, and

576   Systematics 40:613–635.

577 Hirose, T., and M. J. A. Werger. 1995. Canopy structure and photon flux partitioning among

578   species in a herbaceous plant community. Ecology 76:466–474.

579 Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional

580   equivalence. Functional Ecology 19:166–172.

581 Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community

582   ecology. Journal of Vegetation Sciences 3:157–164.

583 Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of

584   community assembly across spatial scales in an Amazonian forest. Ecological

585   Monographs 80:401–422.

586 Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants:

587   A search for physiological causes and ecological consequences. Advances in Ecological

588   Research 23:187–261.

589 LeBauer, D. S., and K. Treseder. 2008. Nitrogen limitation of net primary productivity.

590   Ecology 89:371–379.

591 Maathuis, F. J. 2009. Physiological functions of mineral macronutrients. Current Opinion in

592   Plant Biology 12:250–258.

593 Marks, C. O., and M. J. Lechowicz. 2006. Alternative designs and the evolution of functional

594   diversity. The American Naturalist 167:55–66.

595 Marschner, H., E. A. Kirkby, and I. Cakmak. 1996. Effect of mineral nutritional status on

596   shoot-root partitioning of photoassimilates and cycling of mineral nutrients. Journal of

597   Experimental Botany 47:1255–1263.

598 McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community

599   ecology from functional traits. Trends in Ecology & evolution 21:178–85.

600 Mirmanto, E., J. Proctor, J. Green, L. Nagy, and Suriantata. 1999. Effects of nitrogen and

601   phosphorus fertilizations in a lowland evergreen rainforest. Journal of the Philippine

602   Medical Association 354:1825–1829.

603 Mooney, H. A. 1972. The carbon balance of plants. Annual Review of Ecology and

604   Systematics 3:315–346.

605 Muscarella, R., and M. Uriarte. 2016. Do community-weighted mean functional traits reflect

606   optimal strategies? Proceedings of the Royal Society B 283:20152434.

607 Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from

608   generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

609   Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation Ecosystems in

610   Gradients of Primary Productivity. The American Naturalist 118:240–261.

611   Ordoñez, J. C., P. M. Van Bodegom, J. P. M. Witte, I. J. Wright, P. B. Reich, and R. Aerts.

612   2009. A global study of relationships between leaf traits, climate and soil measures of

613   nutrient fertility. Global Ecology and Biogeography 18:137–149.

614   Pinho, B. X., F. P. L. de Melo, V. Arroyo-Rodríguez, S. Pierce, M. Lohbeck, and M.

615   Tabarelli. 2018. Soil-mediated filtering organizes tree assemblages in regenerating

616   tropical forests. Journal of Ecology 106:137–147.

617   Pistón, N., F. de Bello, A. T. C. Dias, L. Götzenberger, B. H. P. Rosado, E. A. de Mattos, R.

618   Salguero-Gómez, and C. P. Carmona. 2019. Multidimensional ecological analyses

619   demonstrate how interactions between functional traits shape fitness and life history

620   strategies. Journal of Ecology:2317–2328.

621   Poorter, H., K. J. Niklas, P. B. Reich, J. Oleksyn, P. Poot, and L. Mommer. 2012. Biomass

622   allocation to leaves, stems and roots: meta-analyses of interspecific variation and

623   environmental control. New Phytologist 193:30–50.

624   Poorter, L., and D. M. A. Rozendaal. 2008. Leaf size and leaf display of thirty-eight tropical

625   tree species. Oecologia 158:35–46.

626   R Development Core Team. 2017. R: A language and environment for statistical computing

627   R Development Core Team. R Foundation for Statistical Computing.

628   Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: Global

629   convergence in plant functioning. Ecology 94:13730–13734.

630   Rozendaal, D. M. A., V. H. Hurtado, and L. Poorter. 2006. Plasticity in leaf traits of 38

631   tropical tree species in response to light; relationships with light demand and adult

632   stature. Functional Ecology 20:207–216.

633   Sakschewski, B., W. Von Bloh, A. Boit, L. Poorter, M. Peña-Claros, J. Heinke, J. Joshi, and

634   K. Thonicke. 2016. Resilience of Amazon forests emerges from plant trait diversity.

635   Nature Climate Change 6:1032–1036.

636   Santiago, L. S., S. J. Wright, K. E. Harms, J. B. Yavitt, C. Korine, M. N. Garcia, and B. L.

637   Turner. 2012. Tropical tree seedling growth responses to nitrogen, phosphorus and

638   potassium addition. Journal of Ecology 100:309–316.

639   Šímová, I., C. Violle, N. J. B. Kraft, D. Storch, J. C. Svenning, B. Boyle, J. C. Donoghue, P.

640   Jørgensen, B. J. McGill, N. Morueta-Holme, W. H. Piel, R. K. Peet, J. Regetz, M.

641   Schildhauer, N. Spencer, B. Thiers, S. Wiser, and B. J. Enquist. 2015. Shifts in trait

642   means and variances in North American tree assemblages: Species richness patterns are

643 loosely related to the functional space. Ecography 38:649–658.

644 Southwood, T. R. E. 1977. Habitat the Templet for Ecological Strategies? Journal of Animal
645 Ecology 46:336–365.

646 Swenson, N. G., P. Anglada-Cordero, and J. A. Barone. 2011. Deterministic tropical tree
647 community turnover: evidence from patterns of functional beta diversity along an
648 elevational gradient. Proceedings of the Royal Society B: Biological Sciences 278:877–
649 884.

650 Tripler, C. E., S. S. Kaushal, G. E. Likens, and M. Todd Walter. 2006. Patterns in potassium
651 dynamics in forest ecosystems. Ecology Letters 9:451–466.

652 Umaña, M. N., J. Forero-Montaña, R. Muscarella, C. J. C. J. Nytch, J. Thompson, M. Uriarte,
653 J. K. Zimmerman, and N. G. Swenson. 2016. Interspecific functional convergence and
654 divergence and intraspecific negative density dependence underlie the seed-to-seedling
655 transition in tropical trees. The American Naturalist 187:99–109.

656 Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2015. Commonness, rarity,
657 and intraspecific variation in traits and performance in tropical tree seedlings. Ecology
658 Letters 18:1329–1337.

659 Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2018. Quantifying the role of
660 intra-specific trait variation for allocation and organ-level traits in tropical seedling
661 communities. Journal of Vegetation Science 29:276–284.

662 Umaña, M. N., G. Arellano, N. Swenson, and J. Zambrano. 2021. Tree seedling trait
663 optimization and growth in response to local-scale soil and light variability. Dryad, data
664 set. https://doi.org/10.5061/dryad.sqv9s4n29

665 Uriarte, M., R. Muscarella, and J. K. Zimmerman. 2018. Environmental heterogeneity and
666 biotic interactions mediate climate impacts on tropical forest regeneration. Global
667 Change Biology 24:e692–e704.

668 Vermeesch, P. 2020. Package 'provenance': statistical Toolbox for Sedimentary Provenance
669 Analysis.

670 Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007.
671 Let the concept of trait be functional! Oikos 116:882–892.

672 Vitousek, P. M., and R. L. Sanford. 1986. Nutrient Cycling in Moist Tropical Forest. Annual
673 Review of Ecology and Systematics 17:137–167.

674 Weiher, E., G. D. P. Clarke, and P. a. Keddy. 1998. Community Assembly Rules,
675 Morphological Dispersion, and the Coexistence of Plant Species. Oikos 81:309.

676 Worthy, S. J., D. C. Laughlin, J. Zambrano, M. N. Umaña, C. Zhang, L. Lin, M. Cao, and N.

677   G. Swenson. 2020. Alternative designs and tropical tree seedling growth performance

678   landscapes. Ecology.

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

680   Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J.

681   Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L.

682   Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov,

683   C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The

684   worldwide leaf economics spectrum. Nature 428:821–827.

685   Wright, S. J. 2019. Plant responses to nutrient addition experiments conducted in tropical

686   forests. Ecological Monographs 89:1–18.

687   Wright, S. J., J. B. Yavitt, N. Wurzburger, B. I. Turner, E. V. J. Tanner, E. J. Sayer, L. S.

688   Santiago, M. Kaspari, L. O. Hedin, K. E. Harms, M. N. Garcia, and M. D. Corre. 2011.

689   Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production

690   in a lowland tropical forest. Ecology 92:1616–1625.

691

692   FIGURE LEGENDS

693   **Figure 1.** Conceptual diagram depicting changes in trait distributions (kurtosis) between rare

694   and the most common resource levels. In the center, the plot depicts the variation in a given

695   resource that describes a unimodal distribution with values at the two extremes being less

696   frequent than the values in the central section. Based on these three resource levels, we show

697   two scenarios (A and B) of how trait distribution is expected to vary between rare and

698   common resource levels.

699

700   **Figure 2**. SES kurtosis of trait values for three resource levels (low, common, and high).

701   Positive SES values above indicate kurtosis values higher than expected by chance. Negative

702   SES values below indicate significantly lower than the expected kurtosis in a given

703   community. Dashed horizontal lines represent +/-1.96 indicating significantly higher/lower

704   kurtosis than expected by chance. Color codes represent individual traits. LA– leaf area,

705   SLA– specific leaf area, LAR–leaf area ratio, LMF–Leaf mass fraction, RMF– root mass
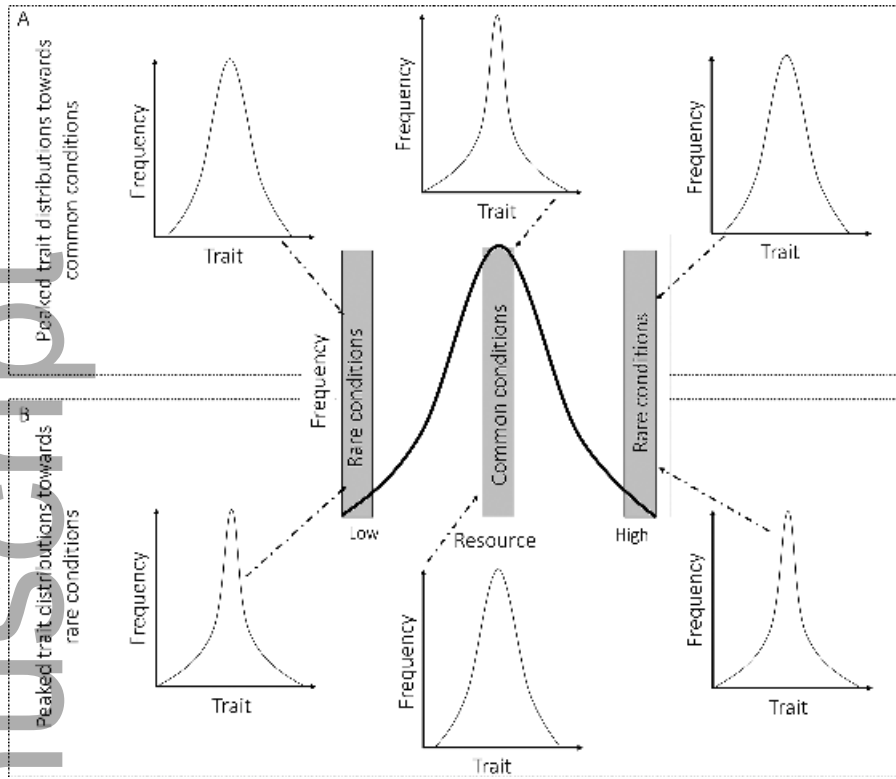
706   fraction.

707

708   **Figure 3**. Differences in mean trait values for three resource levels (low, common, and high).

709   All traits were standardized at the community level (mean = 0, standard deviation = 1) to

710   make them comparable. Positive values indicate that for a given resource level, mean traits

711   are higher than the whole-community mean. Negative values indicate that for a given

712   resource level, mean traits are lower than the whole-community mean. Triangles indicate

713   95% confidence intervals not overlapping zero when estimating the distribution of the mean

714   after 999 bootstrap resampling, while circles represent 95% confidence intervals that overlap

715   zero. Color codes represent individual traits. Acronyms for traits are the same as in Fig. 2.

716

717   **Figure 4.** Differences in mean seedling relative growth rates (RGR standardized at the

718   species level) for three resource levels (low, common, and high). Color codes represent

719   resources (canopy openness and three soil nutrients). Positive values indicate that mean RGR

720   at a given resource level is higher than the whole-community mean. Negative values indicate

721   that mean RGR at a given resource level is lower than the whole-community mean. Triangles

722   indicate that 95% confidence intervals of bootstrap sampling do not overlap zero, circles

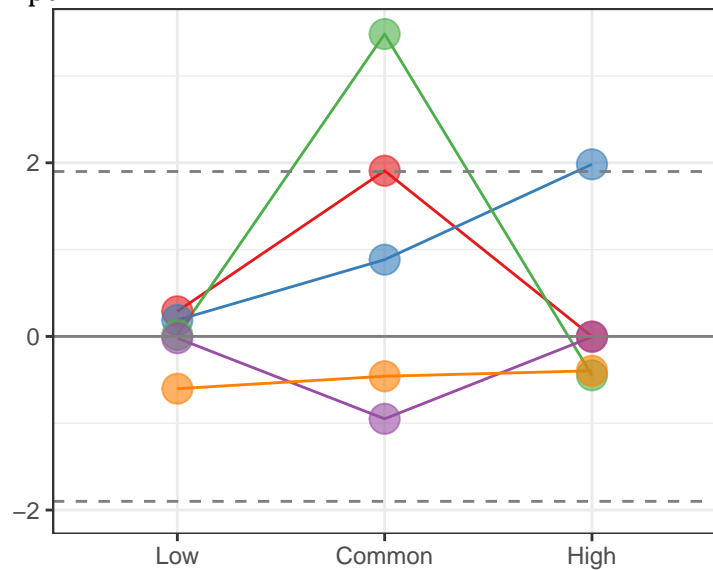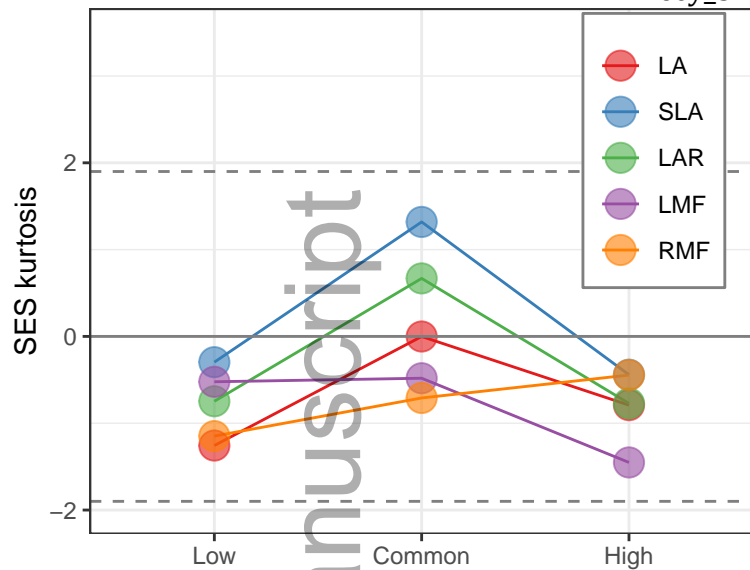723   indicate that the 95% confidence intervals overlap zero.

ecy_3252_f1.tif
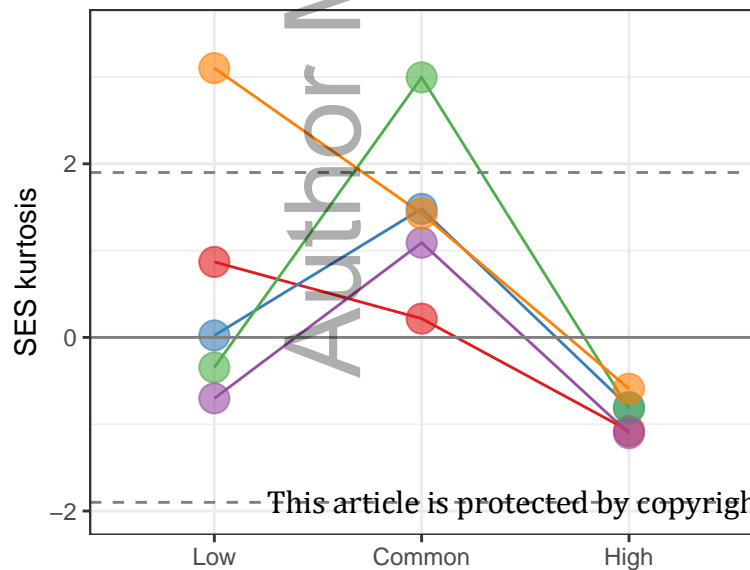
ecy_3252_f4.tif