1 **Running Head:** Traits and performance landscapes

2

3 **Alternative designs and tropical tree seedling growth performance landscapes**

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23 **Abstract**

24   The functional trait values that constitute a whole-plant phenotype interact with the

25 environment to determine demographic rates. Current approaches often fail to explicitly consider

26 trait-trait and trait-environment interactions, which may lead to missed information that is

27 valuable for understanding and predicting the drivers of demographic rates and functional

28 diversity. Here, we consider these interactions by modeling growth performance landscapes that

29 span multidimensional trait spaces along environmental gradients. We utilize individual-level

30 leaf, stem and root trait data combined with growth data from tree seedlings along soil nutrient

31 and light gradients in a hyper-diverse tropical rainforest. We find that multiple trait combinations

32 in phenotypic space (i.e. alternative designs) lead to multiple growth performance peaks that

33 shift along light and soil axes such that no single or set of interacting traits consistently results in

34 peak growth performance. Evidence from these growth performance peaks also generally

35 indicates frequent independence of above and below ground resource acquisition strategies.

36 These results help explain how functional diversity is maintained in ecological communities and

37 question the practice of utilizing a single trait or environmental variable, in isolation, to predict

38 the growth performance of individual trees.

39

40 Key Words: Demographic Rate, Forest Ecology, Functional Traits, Growth, Seedlings, Tropical

41 Forest

42 **Introduction**

43   The diversity and dynamics of communities are driven by differential demographic rates

44 that largely arise from how phenotypes interact with the environment (Fonseca et al. 2000,

45 Ackerly 2003, Cavender-Bares et al. 2004, HilleRisLambers et al. 2012, Anderson 2016). The

46 links between functional traits, demographic rates, and population and community structure form

47 the basis of trait-based community ecology (McGill et al. 2006). In this regard, two analytical

48 approaches are common: quantifying the relationships between single traits and demographic

49 rates, and quantifying the relationships between traits and environmental gradients (Wright and

50 Westoby 1999, Poorter et al. 2008, Enquist et al. 2015, Jager et al. 2015, Costa et al. 2017). The

51 first approach generally operates under the implicit assumption that trait-demographic rate

52 relationships are consistent across environments (Wright et al. 2004, Poorter et al. 2008, Kraft et

53 al. 2010, Adler et al. 2014). For example, a low wood density confers fast growth (e.g. Chave et

54 al. 2009, Kraft et al. 2010). The second approach implicitly assumes the optimal value for a

55 given trait changes across an environmental gradient. Thus, the two approaches appear to be

56 inconsistent, with the first searching for a single global optimum and the second searching for a

57 shifting optimum across an environmental gradient (Laughlin et al. 2018).

58   The functional diversity in ecological communities can potentially be explained by the

59 existence of alternative designs, *i.e.*, different phenotypic trait combinations that lead to similar

60 demographic performance in a given environment (Marks and Lechowicz 2006). Alternative

61 designs arise when the relationship between a trait and performance is dependent upon an

62 interaction with another trait. These trait-trait interactions can be demonstrated using

63 performance landscapes where one can visualize expected performance along two trait axes (Fig.

64 1). While performance landscapes are rarely utilized in functional trait-based ecology,

65 evolutionary biologists have long utilized these landscapes beginning with Wright's adaptive

66 landscape of gene frequencies (Wright 1931, Wright 1932, Wright 1945), progressing from

67 Simpson's phenotypic landscape (Simpson 1944) to adaptive landscapes (Arnold et al. 2001).

68 Despite this existing literature and the recognition for decades that plant functional trait-based

69 ecology should focus more intently on trait-trait interactions (Ackerly et al. 2000, Marks and

70 Lechowicz 2006, Dwyer and Laughlin 2017a, D'Andrea et al. 2018), performance landscapes

71 have been largely ignored (but see Laughlin and Messier 2015, Dwyer and Laughlin 2017b) as

72 has a focus on individual-level positions on these landscapes over that of species means.

73   Functional diversity within a community can be further promoted if the shape of

74 performance landscapes shifts along local-scale environmental gradients. In other words, the

75 alternative phenotypic designs that perform best on one end of a local-scale environmental

76 gradient will not necessarily be those expected to perform best on the other end thereby

77 increasing the diversity of traits and trait combinations performing well within a community

78 (Fig. 1). Thus, not only do trait-trait interactions need to be considered when modeling individual

79 performance, but a simultaneous investigation of the interactions among multiple traits and

80 environmental gradients may be necessary to understand how traits drive performance and plant

81 community diversity.

82   Theory indicates that trait-trait and trait-environment interactions are essential for

83 understanding how traits relate to whole-plant performance, influence population level

84 parameters, and drive community structure and dynamics (Marks and Lechowicz 2006, Enquist

85 et al. 2015). However, we currently lack clear empirical evidence that multiple phenotypic

86 optima exist in a given environment and that these optima change across an environmental

87 gradient. Ideally, such evidence would be gathered using individual-level trait, demographic and

88 environmental information to account for the importance of intraspecific trait variation (Yang et

89 al. 2018, Swenson et al. 2020). Here, we determined whether interactions between multiple

90 functional traits and environmental gradients impacted tropical tree seedling growth rates.

91 Specifically, we modeled the growth of 1,559 individual tree seedlings from 122 species in a

92 Chinese tropical rainforest using an unprecedented dataset of individual-level leaf, root, and stem

93 trait data and detailed light and soil nutrient data. We asked two main questions: 1) Do

94 alternative phenotypic designs have similar demographic outcomes within an environment?, and

95 2) how do the peaks and ridges of growth performance landscapes change across environmental

96 gradients? We focus on seedlings because differential demographic rates at the seedling stage

97 have large and lasting impacts on tropical forest structure and dynamics (Metz et al. 2010; Paine

98 et al. 2012; Green et al. 2014; Umaña et al. 2016).

99

100 **Methods**

101 *Study Site*

102   This study was conducted in a tropical rainforest in Xishuangbanna, which is in the

103 Chinese province of Yunnan (101°34′E, 21°36′N). The climate for this region is monsoonal with

104 a mean annual temperature of 21.8°C, mean annual precipitation of 1,493 mm, and soil pH

105 between 4.5 and 5.7 (Cao et al. 2008). There are two seasons in this forest, differentiated by

106 precipitation patterns, where the dry season starts in November and ends in April and 85% of the

107 precipitation occurs between May and October (Cao et al. 2008).

108

109 *Seedling Plot Establishment and Monitoring*

110   Across 2-ha of forest, 215 1 × 1 m^2 seedling plots were installed in a regular grid. All

111 seedlings from germination to 50 cm in height were tagged, identified, and monitored for 1 year

112 from 2013 to 2014. Seedlings were monitored for survival monthly, but height was measured

113 twice, once at the beginning and once at the end of the census period. During our study, the

114 average temperature was 22.4°C and the total rainfall was 1,590 mm. At the end of the year-long

115 monitoring, all surviving seedlings were harvested for functional trait measurement. In total,

116 there were 1,559 seedlings of 122 species distributed across the 215 plots. The number of

117 seedlings varied from one to 33 across the plots with a mean number of 7.25 individuals and 1.76

118 species per plot.

119

120 *Functional Traits*

121   Seven functional trait measurements were taken on each individual seedling in the study

122 (Appendix S1: Table S1). The organ-level traits measured were leaf mass per unit area (LMA)

123 and mean leaf thickness, which were measured on one to three leaves for each individual. The

124 biomass allocation traits measured in this study were leaf area ratio (LAR; total plant leaf area

125 divided by whole plant dry mass), leaf mass fraction (LMF; total leaf dry mass divided by whole

126 plant dry mass), root mass fraction (RMF; total root mass divided by whole plant mass), stem

127 mass fraction (SMF; total stem dry mass divided by whole plant dry mass), and stem specific

128 length (SSL; stem length divided by dry stem mass), all according to (Poorter et al. 2012) and

129 previously reported in (Umaña et al. 2015). Leaves, roots and stems were manually separated in

130 the lab using hand pruners and dried in the oven for 72 h at 70 °C. These traits were chosen for

131 measurement because they represent major allocation tradeoffs at the organ and whole plant

132 levels that should impact growth performance. Specifically, LMA represents the leaf economics

133 spectrum (Reich et al. 1997, Wright et al. 2004) where species with high LMA have a

134 conservative strategy with long leaf lifespans, but lower mass-based photosynthetic rates and

135 species with low LMA values have a more acquisitive strategy with short leaf life spans and

136 higher mass-based photosynthetic rates. Leaf thickness is measured to indicate leaf mechanical

137 resistance to damage (Onoda et al. 2011). LAR and LMF reflect relative allocation to leaf tissue

138 and combined with LMA are often used in models of plant growth in functional ecology (Garnier

139 1991, Enquist et al. 2007, Poorter et al. 2012). RMF, SMF and SSL are indicative of allocation to

140 non-photosynthetic tissue. RMF and LMA were of particular interest to us as previous work has

141 indicated that they both are highly responsive to soil nutrient and light gradients (Freschet et al.

142 2015). Higher RMF and higher LMA values indicate an allocation pattern that maximizes soil

143 resource gain relative to light resource gain. Thus, we might expect high RMF and LMA values

144 for individuals in poor soils and/or in shade tolerant individuals and the opposite pattern in

145 nutrient rich soils and/or in high light environments.

146

147 *Environmental Variables*

148 Local environmental conditions were characterized by measuring soil nutrients and light

149 availability for each plot. Prior research has shown that these environmental variables vary

150 significantly, even at local scales (Hubbell et al. 1999; Baldeck et al. 2013; Umaña et al. 2018).

151 Percent canopy openness, measured using hemispherical photographs taken systemically with a

152 Nikon FC-E8 lens and a Nikon Coolpix 4500 camera, was used to determine light availability.

153 We do note that these measurements only capture canopy openness and, therefore, do not capture

154 individual plant light environments or changes in light environments through time, but they do

155 offer a quick and pragmatic approach for estimating the average light environment in a sample

156 plot. Photographs were taken with the camera 1 m above the ground before sunrise with cloudy

157 conditions between March and April 2014 for each seedling plot. The images were analyzed

158 using Gap Light Analyser software (http://www.caryinstitute.org/science-program/our-

159 scientists/dr-charles-d-canham/gap-light-analyzer-gla) (Appendix S1: Table S2).

160 We also measured soil nutrients for each of the plots due to prior research showing

161 relationships between soil nutrients, habitat associations and demography (Itoh et al. 2003;

162 Palmiotto et al. 2004; Russo et al. 2005; John et al. 2007; Russo et al. 2008). To analyze soil

163 nutrients, 50 g of topsoil (0-10 cm in depth) was collected from each of the corners of the plot.

164 After being air dried and sifted, the cation availability was determined using the Mehlich III

165 extraction method and atomic emission inductively coupled plasma spectrometry (AE-ICP).

166 Total nitrogen (N) and carbon (C) content were determined by total combustion using auto-

167 analyzer and pH measured with a pH meter. All soil analyses were conducted at the

168 Biogeochemical Laboratory at Xishuangbanna Tropical Botanical Garden (Appendix S1: Table

169 S2).

170 All functional trait and environmental variables were natural log-transformed and scaled

171 to a mean of 0. The dimensionality of the soil data was reduced using a principal component

172 analysis (PCA) (Appendix S1: Fig. S1). The first three orthogonal axes, explaining 78% of the

173 total soil variation, were used for further analyses (Appendix S1: Table S3). PC1 scores were

174 negatively associated with K, Mg and Zn, which are known to play major roles in

175 photosynthesis, growth, as well as seed and stem maturation (Terry and Ulrich 1974; Holste et al.

176 2011; Broadley et al. 2007). PC2 scores were negatively associated with Ca and P. Soil

177 phosphorous is the major limitation of these two elements as phosphorous deficiency is known to

178 have negative impacts on plant growth (Wissuwa 2003; Wright et al. 2004). PC3 scores were

179 negatively associated with C and N. Soil N is of particular interest as N is a key component of

180 RuBisCO and, therefore, a resource that can limit photosynthesis (Evans and Clarke 2019).

181

182 *Quantifying Growth Rates*

183 To determine the relative growth rate (RGR) of each seedling, the change in log-

184 transformed height was calculated for each individual as:

185 $$RGR = (\log(M_{t+\Delta t}) - \log(M_t))/\Delta t$$

186   The variable M is the height at successive time steps t (Hoffmann and Poorter 2002). A

187 value of 1 was added to all observed RGR values and then the data were natural log-transformed

188 and scaled to a mean of 0 to approximate normality (Appendix S1: Table S1).

189

190 *Linear Mixed-Effects Model Description*

191   We built linear mixed-effects models of growth using a Bayesian approach ranging in

192 complexity from a single term to having a three-way interaction with a focus on addressing the

193 biological question of whether trait-trait, trait-environment or trait-trait-environment interactions,

194 which are frequently not considered, influence growth rates. Models were run for all pairwise

195 combinations of the seven functional traits and environmental variables for a total of 84 models.

196 In all models, RGR followed a lognormal distribution:

197 $$\log RGR_i \sim N(z_i, \sigma_z)$$

198 where z_i was the relative growth rate of each individual, σ_z was the variance, and i was each

199 individual. First, individual linear models were fit where RGR was a function of a single trait and

200 initial seedling size, where z_i was the relative growth rate of each individual, α was the model

201 intercept, $\beta 1_p$ and $\beta 2_j$ were the plot and species random effects, respectively, β3 was the effect

202 of a trait, β4 was the effect of initial size.

203 $$z_i = \alpha + \beta 1_p + \beta 2_j + \beta 3 \times \text{trait} + \beta 4 \times \text{initial size} \qquad (1)$$

204 These simple linear models highlight a common method used to link functional traits,

205 demographic rates, and population and community structure in the functional trait literature. In

206 rare instances, a functional trait and the environment have been combined in models to include

207 their interactive effect as both impact plant performance (Laughlin and Messier 2015, Dwyer and

208 Laughlin 2017b; Blonder et al. 2018). To mimic these models, we modeled the linear predictor,

209 RGR, using mixed-effects models including a two-way interaction between a functional trait and

210 an environmental variable. Models were of the general form,

211 $$z_i = \alpha + \beta 1_p + \beta 2_j + \beta 3 \times \text{trait} + \beta 4 \times \text{environment} + \beta 5 \times \text{initial size} + \beta 6$$

212 $$\times \text{trait} \times \text{environment} \qquad (2)$$

213 where z_i was the relative growth rate of each individual, α was the model intercept, $\beta 1_p$ and $\beta 2_j$

214 were the plot and species random effects, respectively, β3 was the effect of a trait, β4 was the

215   effect of the environmental variable, β5 was the effect of initial seedling size, and β6 was the

216   effect of the interaction between the trait and the environmental variable on RGR.

217   Lastly, we modeled RGR using a linear mixed-effects model including a three-way

218   interaction between two functional traits and an environmental variable. The three-way

219   interaction term in these models is included to represent a relationship between a functional trait

220   and growth performance dependent upon another functional trait and the environment. In this

221   model, RGR of each individual was modelled using the general form,

222           $z_i = α + β1_p + β2_j + β3 × trait_1 + β4 × trait_2 + β5 × environment + β6 ×$

223   $trait_1 × trait_2 + β7 × trait_1 × environment + β8 × trait_2 × environment + β9 × trait_1 ×$

224           $trait_2 × environment + β10 × initial\ size$ (3)

225   where z_i was the relative growth rate of each individual, α was the model intercept, $β1_p$ and $β2_j$

226   were the plot and species random effects, respectively, β3 was the effect of trait1, β4 was the

227   effect of trait2, β5 was the effect of the environmental variable, β6 was the effect of the

228   interaction between trait1 and trait2, β7 was the effect of the interaction between trait1 and the

229   environment, β8 was the effect of the interaction between trait2 and the environment, β9 was the

230   effect of the three-way interaction between trait1, trait2 and the environment, and β10 was the

231   effect of the initial seedling size on RGR.

232   In all models, plot ($β1_p$) and species ($β2_j$) were modeled as normally distributed random

233   intercepts to account for species-level differences in RGR that were unrelated to spatial

234   autocorrelation and the traits, respectively. For the hyperparameters of the random effects, we

235   specified diffuse normal priors: N(mean = 0, precision = 0.01). The variance hyperparameters

236   were given diffuse gamma priors: $Gamma$(shape = 0.1, rate = 0.1). We performed variable

237   selection by comparing "full" models, equation (3), with models of all other iterations of

238   variables using deviance information criterion (DIC) to determine the most parsimonious model

239   (Spiegelhalter et al. 2002). Typically, it is thought that DIC is a Bayesian analogue of AIC (Kéry

240   2010). They have a similar justification, but DIC has wider applicability (Spiegelhalter et al.

241   2002). The two main differences between AIC and DIC calculations are that the maximum

242   likelihood estimate is replaced with the posterior mean and the number of parameters is replaced

243   with a data-based bias correction (Gelman et al. 2013). Any model with a DIC value within 5

244   (ΔDIC < 5) of the lowest value for all models was given consideration (Spiegelhalter et al. 2002;

245   Lesaffre and Lawson 2012). Along with evaluating models with DIC, we assessed the fit of the

246   models by checking the posterior predictive distribution of the fit of the actual data with the fit of

247   an "ideal" dataset and computed the Bayesian *p*-value (Gelman et al. 1996). As the Bayesian *p*-

248   value approaches 0.5, simulated data generated from the posteriors should look similar to the

249   observed data indicating a good fit model (Gelman et al. 2013). Evaluating models using DIC

250   and Bayesian *p*-values allowed us to compare less complex, commonly used models, equation

251   (1) for one, to our high-dimensional models (equations 2 and 3) to test for overall model fit

252   (Bayesian *p*-value ~ 0.5) and discover instances where more complex models, those containing a

253   three-way interaction, are more parsimonious (ΔDIC < 5) than more simple models lacking a

254   three-way interaction between two traits and the environment. Pearson's product-moment

255   correlation coefficients showed that some traits were weakly correlated (Appendix S1: Table

256   S4). We checked for multicollinearity between traits using variance inflation factor (VIF)

257   analysis to verify that all trait combinations had a VIF < 10 thereby indicating that we can

258   include them together in our models (Ohlemüller et al. 2006; Hair et al. 2014; Enquist et al.

259   2015) (Appendix S1: Table S4).

260   All models were fit using Markov Chain Monte Carlo (MCMC) sampling techniques in

261   *JAGS* 4.3.0 (Plummer 2003) interfaced with R v3.3.1 programming language using the *rjags*

262   (Plummer 2016) and *runjags* (Denwood 2016) packages (Data S1). We ran six parallel chains

263   with random initial values for 50,000 iterations with a burn-in period of 10,000 iterations.

264   Parameter estimates and 95% credible intervals were obtained from the quantiles of the posterior

265   distribution. Parameters were statistically supported when their credible interval did not overlap

266   zero. Convergence of the MCMC chains was assessed visually in traceplots and using the

267   Gelman-Rubin convergence diagnostic to ensure values were less than 1.1 (Gelman and Rubin

268   1992).

269

270   *Assessing Growth Performance Peaks*

271   Two criteria had to be met in order to declare the presence of alternative designs in a

272   growth performance landscape. First, the two-way (trait-trait, trait-environment) or three-way

273   interaction (trait-trait-environment) term in the model had to be statistically supported with 95%

274   credible intervals around the parameter estimate not overlapping zero. Second, the slope of the

275   relationship between the traits and RGR, computed as the first partial derivative of the fitted

276   model, had to switch signs across the range of the environmental variable (Laughlin 2018,

277   Laughlin et al. 2018). A switch in sign indicates that the partial derivative passed through zero at

278   some point along the environmental gradient. This would be evidence that a "saddle" exists at

279   the intermediate environmental condition, due to the probability surface being pulled downward

280   (Laughlin et al. 2018). To verify that the slope was significantly different from zero, we

281   randomly sampled parameter estimates, with replacement, from the posterior distribution 1000

282   times and calculated the slope for each sample to determine 95% confidence intervals (Appendix

283   S1: Table S5).

284   To understand how the effect of two functional traits on RGR changes across the

285   environmental gradients, simple slopes and intercepts were calculated to visualize partial effects

286   and peaks in growth performance. The minimum and maximum observed values were used as

287   constants for the second trait and environmental variable during the calculation of the simple

288   slopes and intercepts. We also statistically tested for the presence of multiple growth

289   performance peaks at each end of the environmental gradients. We randomly sampled, with

290   replacement, from the posterior distribution 1000 times from each model. We then calculated

291   each of the simple slopes for each of the 1000 samples. We then determined the number of times

292   the slopes were different in sign for the two growth performance peaks at the same end of the

293   environmental gradient. An exact binomial test with a probability of success equal to 0.50 was

294   used to test for significant differences. In all cases, a p value of < 0.05 indicated the presence of

295   two simple slopes, meaning traits were combining in different ways at the same end of the

296   environmental gradient to achieve higher RGR (Appendix S1: Table S6). If the signs of the mean

297   values of the simple slopes were in the same direction for both growth performance peaks in an

298   environment, we were unable to show a statistical presence of one versus two peaks. All analyses

299   were performed in R statistical software version 3.3.1 (R Development Core Team 2016).

300

301   **Results**

302   The models in this study were designed based on biological interactions of functional

303   traits and the environment that are known or predicted in the literature (Wright et al. 2004,

304   Baraloto et al. 2010, Fortunel et al. 2012, Adler et al. 2014, Reich et al. 2014, Freschet et al.

305   2015, Liu et al. 2016). Eight models, out of 84 total, had evidence of multiple growth

306   performance peaks indicated by a significant three-way interaction in the model and a slope that

307 changed sign along the environmental gradient (Appendix S2). Five models, each with a

308 different three-way interaction term, were the most parsimonious or equally parsimonious based

309 on comparison of DIC values between each "full" model (equation 3) and simpler versions of

310 each model (Appendix S2: Tables S1-S5). For the remaining three models, the "full" model was

311 not the most parsimonious overall after variable selection, based on DIC, but was more

312 parsimonious than commonly used models, trait-growth rate and trait $\times$ environment-growth

313 rate (Appendix S2: Tables S6-S8). All eight of these models had appropriate Bayesian *p*-values

314 (~ 0.5) indicating model fit and that values calculated from the simulated data are distributed

315 around the observed values (Appendix S2).

316

317 *Comparison of Model Types*

318   Each model was built to evaluate commonly used modeling methods (single trait-growth

319 rate models and trait $\times$ environment-growth rate models) with high dimensional models

320 containing a three-way interaction between two functional traits and the environment. Below we

321 present an extended comparison between simple models and the "full" model for one of the eight

322 different significant three-way interactions found (LMA $\times$ RMF $\times$ light). We then present just

323 the interpretation of the "full" model for the remaining seven three-way interactions.

324   The "full" model, which contained the three-way interaction LMA $\times$ RMF $\times$ light, had

325 equally the highest support (lower DIC) than all iterations of variables of this "full" model

326 (Appendix S2: Table S1). We compared the "full" model with the simplest, commonly used

327 models that fit linear mixed-effects models with relative growth rate (RGR) as a function of each

328 trait. We found significant negative relationships between leaf mass per area (LMA) and RGR

329 (Appendix S1: Table S7) as well as between root mass fraction (RMF) and RGR (Appendix S1:

330 Table S7). However, neither of these models was as well supported as the "full" model based on

331 DIC (Appendix S2: Table S1). Next, we included a trait by environment interaction into the

332 linear mixed-effects models. The interaction between LMA and light was not significant (Fig.

333 2a) so the first criteria for evidence of growth performance peaks was not met (Fig. 2b).

334 However, the interaction between RMF and light was significant (Fig. 2c), but the slope of the

335 relationship between RMF and RGR had only a few individuals cross zero along the light

336 gradient suggesting a weak interaction. There was one obvious peak in RGR for individuals

337 when they had low RMF in high light environments, however some individuals did occupy an

338   alternative peak where individuals had high RMF in low light environments (Fig. 2d). Despite

339   these models with two-way interactions showing evidence of growth peaks, they had higher DIC

340   values (less support) than the "full" model that contained the three-way interaction (Appendix

341   S2: Table S1). Furthermore, the single term and two-way interaction term models afforded less

342   interpretation of the effects of the model variables on growth because they lack the three-way

343   interaction term between two traits and the environment.

344   This "full" model contained a significant interaction between LMA, RMF, and light and

345   had equally the highest support (lowest DIC) following variable selection of the model (Fig. 3a;

346   Appendix S2: Table S1). The slope of the relationship between LMA and RGR at different

347   values of RMF changed sign along the light gradient indicating multiple growth performance

348   peaks which allows for the effect of the three-way interaction term on growth to be examined. In

349   low light environments, there were two growth performance peaks for individuals, one when

350   they had low LMA and high RMF and one when they had high LMA and low RMF (Fig. 3b). In

351   high light environments, there were also two growth performance peaks for individuals, one

352   when they had both high LMA and RMF and one when they had both low LMA and RMF (Fig.

353   3b).

354

355   *Evidence of Multiple Growth Performance Peaks*

356   The following three models had a three-way interaction term that was significant in the

357   model and had a slope that changed sign along the environmental gradient (i.e. multiple growth

358   performance peaks present). Variable selection was performed on each model separately using

359   DIC. For each of these models, the "full" model was not the best supported overall, but had

360   higher support than commonly used trait-growth rate and trait × environment-growth rate

361   models (Appendix S2: Tables S6-S8). For each of these three models, the best supported model

362   was a complex model highlighting the inability of simple models to reflect the effects of the

363   traits and the environment on growth (Appendix S2: Tables S6-S8).

364   The first of these three models had a significant three-way interaction between LMA,

365   stem mass fraction (SMF) and light (Appendix S1: Fig. S2a; Appendix S2: Table S6). For

366   individuals to achieve a growth performance peak across the light gradient, they combined LMA

367   and SMF in different manners (Appendix S1: Fig. S2b). In low light environments, there were

368   two growth performance peaks for individuals, one when they have both low LMA and SMF and

369 one when they have both high LMA and SMF. In high light environments, there were also two

370 growth performance peaks for individuals, one when they have low LMA and high SMF and one

371 when they have high LMA and low SMF. The last two models involved three-way interactions

372 with the soil PC2 environmental variable, which was negatively associated with soil Ca and P.

373 The first involved an interaction between LMA, RMF and soil PC2 (Appendix S1: Fig. S3a;

374 Appendix S2: Table S7). When soil PC2 was low, indicating high levels of Ca and P, plants with

375 high LMA and low RMF or low LMA and high RMF grew faster (Appendix S1: Fig. S3b). In

376 high soil PC2 environments, indicating low levels of Ca and P, plants with either low LMA and

377 low RMF or high LMA and high RMF performed best (Appendix S1: Fig. S3b). Finally, there

378 was a significant interaction between leaf area ratio (LAR) and leaf mass fraction (LMF)

379 (Appendix S1: Fig. S4a; Appendix S2: Table S8). We found that the effect of LAR on growth

380 rates along the soil PC2 gradient was dependent on LMF (Appendix S1: Fig. S4b). In order for

381 individuals to be on a growth performance peak in low soil PC2 environments, meaning high Ca

382 and P, they had high LAR and low LMF or high LAR and high LMF (Appendix S1: Fig. S4b).

383 However, we were unable to statistically show each of these peaks separately because the slopes

384 for each peak were the same sign since LAR was high for both peaks. In high soil PC2

385 environments, individuals with high LAR and high LMF or low LAR and low LMF exhibited

386 peak growth performance (Appendix S1: Fig. S4b).

387   The "full" model of the remaining four models had the best support or equal support

388 (ΔDIC < 5) after variable selection (Appendix S2: Table S2-S5). These models also had support

389 for multiple growth performance peaks (i.e. they had a slope that switched sign along the

390 environmental gradient). Three of these models had significant interactions of traits with soil

391 PC1, which was negatively associated with Mg, K, and Zn (Appendix S1: Table S3). The first

392 interaction was between LMA and RMF (Appendix S1: Fig. S5a; Appendix S2: Table S2). In

393 low soil PC1 environments, indicating high levels of Mg, K and Zn, individuals had high LMA

394 and low RMF or low LMA and high RMF (Appendix S1: Fig. S5b). In high soil PC1

395 environments, individuals with high LMA and high RMF or low LMA and low RMF exhibited

396 peak growth performance (Appendix S1: Fig. S5b). The second interaction was between leaf

397 thickness and RMF (Appendix S1: Fig. S6a; Appendix S2: Table S3). In order for individuals to

398 be on a growth performance peak in low soil PC1 environments, they had high leaf thickness and

399 low RMF or low leaf thickness and high RMF (Appendix S1: Fig. S6b). In high soil PC1

400　environments, individuals with high leaf thickness and high RMF or low leaf thickness and low

401　RMF exhibited peak performance (Appendix S1: Fig. S6b). The next interaction was between

402　leaf thickness and SMF (Appendix S1: Fig. S7a; Appendix S2: Table S4). Two performance

403　peaks were found when soil PC1 is low and when soil PC1 is high (Appendix S1: Fig. S7b).

404　When soil PC1 was low, indicating high levels of Mg, K and Zn, individuals with low leaf

405　thickness and low SMF or high leaf thickness and high SMF exhibited the highest RGR

406　(Appendix S1: Fig. S7b). When soil PC1 was high, indicating low values of Mg, K, and Zn,

407　individuals with low leaf thickness and high SMF or high leaf thickness and low SMF exhibited

408　peak growth performance (Appendix S1: Fig. S7b). The final model had a significant interaction

409　between leaf thickness, SSL, and soil PC2 (Appendix S1: Fig. S8a; Appendix S2: Table S5). For

410　this interaction of traits, peak growth performance in low soil PC2 environments occurred for

411　individuals that had high leaf thickness with high SSL or had low leaf thickness with low SSL

412　(Appendix S1: Fig. S8b). To perform well in high soil PC2 environments, plants with low leaf

413　thickness and high SSL or high leaf thickness and low SSL had faster growth (Appendix S1: Fig.

414　S8b).

415

416　**Discussion**

417　　　Here, we have provided empirical evidence of multiple peaks in growth rate, a strong

418　determinant of long-term plant performance, across phenotypic space in a diverse tropical

419　seedling community thereby indicating the presence of multiple successful alternative designs. In

420　other words, multiple trait combinations can lead to similar growth performance. The location of

421　growth performance peaks in phenotypic space shifts across local-scale light and soil gradients

422　such that no single or set of interacting traits resulted in a peak in growth across these

423　environmental gradients. These results help to demonstrate how functional diversity can be

424　maintained in ecological communities and question the practice of utilizing a single trait or

425　environmental variable in isolation to predict the growth performance of individual trees.

426　　Through a step-wise process of increasing model complexity, we have shown that including

427　interactions between two functional traits and the environment and visualization of growth

428　performance landscapes leads to a better overall indication of how functional traits and the

429　environment affect individual seedling growth performance. Specifically, we provide five

430　separate instances where multiple growth performance peaks are found in best supported (ΔDIC

431 < 5) high-dimensional models containing a three-way interaction (Fig. 3, Appendix S1: Figs. S5-
432 S8).

433   Based on fast-slow plant economics theory (Reich 2014), it may be expected that single
434 growth performance peaks relating to a combination of acquisitive values may be found in areas
435 with higher resource levels. For example, species with relatively more leaf mass investment and
436 lower leaf mass per area (LMA) may be expected in high light environments (Lusk et al. 2008).
437 Similarly, combinations of conservative traits (e.g. low root mass investment and high LMA),
438 may be expected to have superior growth in resource poor (e.g. low light) environments. This
439 expectation is only partially supported by our results. For example, we did find a growth
440 performance peak for plants with acquisitive traits (i.e. relatively high root investment and low
441 LMA) in high soil nutrient environments (Appendix S1: Fig. S3, Fig. S5). However, we also
442 have several instances where multiple growth performance peaks occur at a given point on light
443 or soil gradients and many of these peaks combine an acquisitive below ground strategy and a
444 conservative above ground or leaf level strategy. For instance, at the high end of the soil PC1
445 gradient, meaning low levels of Mg, K, and Zn, growth performance peaked at either high LMA
446 with high root mass fraction (RMF), which reflect a more conservative leaf strategy and
447 acquisitive root strategy, respectively, or low LMA with low RMF, which reflect a more
448 acquisitive leaf strategy and conservative root strategy (Appendix S1: Fig. S5). For the soil
449 nutrient gradients, we found multiple growth performance peaks at both ends of the gradients.
450 The high ends of the soil PC1 and PC2 gradients were associated with low levels of K, Mg, Zn
451 (PC1) and Ca and P (PC2), nutrients known to play major roles in photosynthesis, growth, as
452 well as seed and stem maturation (Terry and Ulrich 1974; Wissuwa 2003; Wright et al. 2004;
453 Broadley et al. 2007; Holste et al. 2011). Soil moisture may have also contributed to peaks
454 associated with soil nutrients, but we were unable to measure this environmental axis.

455   This modulation of root and leaf resource acquisition may indicate a fourth interaction
456 between light and soil nutrient levels (Freschet et al. 2015). We did not explicitly test for
457 interactions between environmental gradients here, however, our results generally indicate that
458 above ground resource levels (i.e. light) and below ground resource levels (i.e. soil nutrients) can
459 vary independently such that mixtures of conservative and acquisitive leaf and root strategies can
460 be selected independently in a forest depending on the resource that is most limiting. Indeed, soil
461 and light variables are very weakly correlated in this study, which likely promotes a greater

462   diversity of trait combinations in the community (Appendix S1: Table S8). We do note that leaf

463   and root traits, at the plant level, are not independent of one another, given that plants only have

464   a finite amount of resources to invest in each. However, we have shown that plants can express

465   acquisitive leaf traits while their root traits are conservative, which may allow us to see

466   disassociation of leaf and root traits at the population or community level. Thus, our results often

467   did not indicate superior growth arising from either conservative or acquisitive strategies at the

468   whole plant scale and this is likely due to the independence of the selective environments above

469   and below ground in the system. In other systems where resource levels above and below ground

470   co-vary, a whole plant coordination of plant functional spectra may be more common (e.g.

471   Freschet et al. 2015). The results also coincide with evidence in the literature that indicates major

472   functional spectra (e.g. leaf and wood economics spectra (e.g. Baraloto et al. 2010); leaf and root

473   economics spectra (e.g. Fortunel et al. 2012)) are generally weakly correlated in adult trees in

474   tropical forests as is the case in the present study for tropical seedlings (Appendix S1: Table S4).

475   All other significant interactions were similar in that multiple growth performance peaks and

476   frequent independence of above and below ground strategies were evident (Appendix S1: Figs.

477   S2-S8).

478   Functional trait-based studies of plant community assembly and structure often focus on

479   abiotic selection for optimal trait values. For example, community weighted mean trait values are

480   expected to shift predictably across abiotic gradients (Muscarella and Uriarte 2016), and the

481   stress gradient hypothesis (Keddy 1992) emphasizes that the expected variation around this trait

482   optimum should decrease in more abiotically stressful conditions (Dwyer and Laughlin 2017b).

483   Correlative studies of plant functional traits and demographic rates implicitly assume that a

484   single trait value will lead to a similar demographic outcome across environments (Laughlin

485   2018; but see Westerband and Horvitz 2017). This is because of their use of a linear model

486   regressing a trait on a rate using data from many environments or datasets. We have shown

487   empirically that multiple growth performance peaks associated with different trait combinations

488   can occur at multiple points along an environmental gradient. Multiple growth performance

489   peaks were found on both ends of the environmental gradients, indicating that in extreme ends of

490   an environmental gradient, multiple trait combinations can lead to high demographic

491   performance. Importantly, we show the performance of a single trait value is dependent upon

492   other trait values. Combined, the trait-trait and trait-environment interactions, the context

493　dependencies of trait-performance relationships, and the ability of multiple trait combinations to

494　give rise to similar performance outcomes indicate why single functional traits often fail to

495　predict tree demographic rates (Poorter et al. 2008; Paine et al. 2015, Yang et al. 2018; Swenson

496　et al. 2020) and how trait diversity can be maintained in ecological communities.

497　　　　High-dimensional trait-based trade-offs have been hypothesized as being important for

498　promoting species co-existence and maintaining community diversity (e.g. Adler et al. 2013,

499　Kraft et al. 2015). Our results support this hypothesis by showing that the relationship between

500　traits, the environment, and demographic outcomes is complex and can lead to alternative

501　phenotypic designs. While we find evidence in this study from multiple models of multiple

502　growth performance peaks, we understand that performance will vary across years and that

503　growth isn't the only metric of performance. We also know that the number of peaks we found is

504　relatively small compared to the number of species in our study system with only eight of 84

505　models having evidence of multiple growth performance peaks. This raises several new

506　questions that should be addressed in the future. First, how densely occupied are growth

507　performance peaks? Specifically, if multiple peaks exist in phenotypic space, are some more

508　densely occupied by individuals and species in the system and, if so, why? Second, are growth

509　performance peaks mitigated or eroded by other demographic outcomes (e.g. low survival rates,

510　recruitment or reproductive output) at the same or later life stages such that ultimately a single

511　peak is produced from a given environment? Answering these two questions is critical for our

512　understanding of why trait distributions in tropical forests often have only one or two modes (e.g.

513　Swenson et al. 2012). Final outstanding questions are: how do species that occupy the same

514　growth performance peak co-exist? Are intra-specific interactions (e.g. shared enemies,

515　competition) strong enough to permit the co-existence of multiple species on a given growth

516　performance peak? Do species occupying the same peak spatially or temporally segregate the

517　environment? These questions are all large foundational questions in trait-based community

518　ecology and our results should re-focus this literature towards a stronger consideration of

519　performance landscapes and multiple alternative phenotypic designs.

520

521　**Conclusions**

522　　　　Here we have explored the possibility that multiple growth performance peaks occur in

523　the phenotypic space found in a diverse tropical seedling community using detailed individual

524 level trait and growth rate data. We find evidence for multiple peaks in phenotypic space and that

525 these peaks shift across environmental gradients. Further, we found evidence that above and

526 below ground functional strategies often combine to produce optimal growth performance in

527 such a way that acquisitive above ground strategies can align with conservative below ground

528 strategies and vice versa. Combined, these results show that there are multiple trait combinations

529 possible in phenotypic space that will lead to increased growth performance in a diverse

530 community, which lead to the promotion and maintenance of functional diversity. The results

531 also caution against focusing on single trait analyses in functional trait-based community ecology

532 and the aggregation of individual level trait variation to the species level. In particular, complex

533 trait-trait and trait-environment interactions are realized at the individual-level in communities

534 and performance landscapes should be empirically quantified and conceptualized using

535 individual-level data (Liu et al. 2016, Umaña et al. 2018, Swenson et al. 2020). Lastly, future

536 research will be needed to uncover the mechanisms that allow multiple species in a community

537 to occupy the same performance peaks in multidimensional phenotypic space and how above and

538 below ground resource levels interact to influence performance landscapes across systems.

539

540 **Acknowledgments**

552

553

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750 **Data Availability**

751 All code and data associated with this study are available from

752 http://doi.org/10.5281/zenodo.3382271

753

754 **Figure Legends**

755 **Figure 1.** Conceptual model of a theoretical performance landscape of an individual along two

756 trait axes at (a) the low end of an environmental gradient and (b) at the high end of an

757 environmental gradient. Note the multiple performance peaks within an environment and the

758 shift in location of these performance peaks across the environmental gradient.

759 **Figure 2**. Models including two-way interactions between leaf mass per area (LMA) and light (a,

760 b) and between root mass fraction (RMF) and light (c, d). a,c) Standardized regression

761 coefficients where circles indicate posterior mean values, lines indicate 95% credible intervals,

762 and filled circles represent significant effects. b) Simple slopes and intercepts visualizing the

763 partial effects of LMA on RGR when light is held constant at its minimum (0.66) and maximum

764 values (10.10). d) Simple slopes and intercepts visualizing the partial effects of RMF on RGR

765 when light is held constant at its minimum (0.66) and maximum (10.10) values. All variables

766 were natural log-transformed and scaled to unit variance. Values on the axes have been back

767 transformed.

768 **Figure 3.** Model including three-way interaction between leaf mass per area (LMA), root mass

769 fraction (RMF), and light. a) Standardized regression coefficients where circles indicate posterior

770 mean values, lines indicate 95% credible intervals, and filled circles represent significant effects.

771   b) Simple slopes and intercepts visualizing the partial effects of LMA on RGR when RMF and

772   light are held constant at combinations of their minimum (RMF = 0.04, Light = 0.66) and

773   maximum (RMF = 0.93, Light = 10.10) values. All variables was scaled and natural log-

774   transformed. Values on the axes have been back transformed. In low light environments, there

775   are two growth performance peaks for individuals, one when they have low LMA and high RMF

776   and one when they have high LMA and low RMF. In high light environments, there are two

777   performance peaks for individuals, one when they have low LMA and low RMF and one when

778   they have high LMA and high RMF.

779

780   Figure 1

781

(a) Low end of environmental gradient

(b) High end of environmental gradient

782

783

784   Figure 3