

#### Widespread variation in functional trait-vital rate relationships in tropical tree seedlings across a precipitation and soil phosphorus gradient

Browne, Luke ; Markesteijn, Lars; Manzané-Pinzón, Eric; Wright, S. Joseph; Bagchi, Robert; Engelbrecht, Bettina; Jones, F. Andrew; Comita, Liza S.

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1	<b>Title:</b> Widespread variation in functional trait-vital rate relationships in tropical
2	tree seedlings across a precipitation and soil phosphorus gradient
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4	Luke Browne <sup>1</sup> , Lars Markesteijn <sup>2,3,4</sup> , Eric Manzané-Pinzón <sup>2</sup> , S. Joseph Wright <sup>2</sup> , Robert Bagchi <sup>5</sup> ,
5	Bettina M. J. Engelbrecht <sup>2,6</sup> , F. Andrew Jones <sup>2,7</sup> , Liza S. Comita <sup>1,2</sup>
6	
7	Affiliations:
8	<sup>1</sup> School of the Environment, Yale University, New Haven, CT, USA 06511
9	<sup>2</sup> Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, Panama
10	<sup>3</sup> Departamento de Biología y Geología, Física y Química inorgánica. ESCET, Universidad Rey
11	Juan Carlos, C/Tulipán s/n, Móstoles, C.P. 28933, Madrid, Spain
12	<sup>4</sup> School of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2DG United Kingdom
13	<sup>5</sup> Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT USA
14	06269
15	<sup>6</sup> Department of Plant Ecology, Bayreuth Center of Ecology and Environmental Research
16	(BayCEER), University of Bayreuth, 95440 Bayreuth, Germany
17	<sup>7</sup> Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331
18	USA
19	
20	
21	Running head: Variable trait-rate relationships in tropical seedlings
22	*Corresponding author: Luke Browne, <a href="https://www.lukembrowne@gmail.com">lukembrowne@gmail.com</a>
23	
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- 34

## 35 **Competing Interests Statement**

- 36 The authors declare no competing interests.
- 37

# 38 Author Contributions

- 39 LSC and LB conceived the study. RB, SJW, and LM contributed to study design and
- 40 establishment. LM, LSC, EM-P, and LB participated in data collection. LB performed data
- 41 analysis with input from LSC. LB wrote the first draft of the manuscript, and all authors
- 42 contributed to interpretation and writing. All authors approve of the submitted version of the
- 43 manuscript.
- 44

# 45 Data availability

- 46 Full model code, data, and instructions to reproduce statistical analyses in this study will be
- 47 made available on a public repository (*e.g.*, figshare, Dryad) following publication. Model code
- 48 is available for the review process at -
- 49 https://anonymous.4open.science/r/FE\_Repo\_For\_Review-4511.
- 50

#### 51 Abstract

52 A fundamental assumption of functional ecology is that functional traits are related to 53 interspecific variation in performance. However, the relationship between functional traits and 54 performance is often weak or uncertain, especially for plants. A potential explanation for this 55 inconsistency is that the relationship between functional traits and vital rates (e.g., growth and mortality) is dependent on local environmental conditions, which would lead to variation in trait-56 57 rate relationships across environmental gradients. In this study, we examined trait-rate 58 relationships for six functional traits (seed mass, wood density, maximum height, leaf mass per 59 area, leaf area, and leaf dry matter content) using long-term data on seedling growth and survival 60 of woody plant species from eight forest sites spanning a pronounced precipitation and soil 61 phosphorus gradient in central Panama. For all traits considered except for leaf mass per area-62 mortality, leaf mass per area-growth, and leaf area-mortality relationships, we found widespread variation in the strength of trait-rate relationships across sites. For some traits, trait-rate 63 64 relationships showed no overall trend but displayed wide site-to-site variation. In a small subset 65 of cases, variation in trait-rate relationships were explained by soil phosphorus availability. Our results demonstrate that environmental gradients have the potential to influence how functional 66 67 traits are related to growth and mortality rates, though much variation remains to be explained. 68 Accounting for site-to-site variation may help resolve a fundamental issue in trait-based ecology 69 - that traits are often weakly related to performance - and improve the utility of functional traits 70 for explaining key ecological and evolutionary processes.

71

72 Keywords: soil nutrients, forest dynamics, Panama, rainfall gradient, tropics

#### 73 Introduction

Trait-based ecology assumes that functional traits influence fitness via their effects on 74 75 vital rates including recruitment, growth, and survival (Violle et al., 2007). These functional 76 trait-vital rate relationships (hereafter trait-rate relationships) provide the basis for understanding 77 and predicting fundamental ecological and evolutionary processes such as species coexistence. 78 community assembly, response to environmental change, and ecosystem functioning (Cadotte et 79 al., 2011; Kraft et al., 2015; Lavorel & Garnier, 2002; McGill et al., 2006). While a number of 80 studies have found some consistency in trait-rate relationships (Poorter et al., 2008; Visser et al., 81 2016; Wright et al., 2010), the relationship between functional traits and vital rates in plants is 82 often weak or non-existent (Paine et al., 2015; Poorter et al., 2018; Worthy & Swenson, 2019), 83 calling into question one of the foundational assumptions of trait-based ecology and limiting the 84 utility of trait-based approaches (Swenson et al., 2020; Yang et al., 2018). A potential 85 explanation for this inconsistency is that phenotypes and vital rates interact with local 86 environmental conditions. This in turn would lead to variation in trait-rate relationships across 87 environmental gradients that would obscure and weaken general patterns within and among plant 88 species (Li et al., 2022; Swenson et al., 2020; Yang et al., 2018). Thus, resolving the degree to 89 which trait-rate relationships vary across environmental gradients will likely help improve the 90 use of functional traits as a paradigm to explain ecological and evolutionary processes (Laughlin, 91 2018; Yang et al., 2018).

92

93 Because of tradeoffs in resource allocation, only a subset of all possible life history 94 strategies are likely to provide fitness advantages in a given environment (Stearns, 1992). This 95 variation in life history strategies among species can potentially be correlated with a relatively 96 small number of functional traits, which is especially useful in species-diverse tropical tree 97 communities, where detailed information on demography and life history is typically lacking for 98 most species (Díaz et al., 2016; Laughlin, 2014; Worthy & Swenson, 2019). For example, 99 species with high wood density, high leaf mass per unit area, and high leaf dry matter content 100 tend to have a more resource-conservative strategy along the fast-slow life-history continuum 101 that prioritizes defense and storage, with greater investment in the physical protection of leaves, 102 lower respiration rates, greater stress tolerance, and a longer leaf life span (Alvarez-Clare & 103 Kitajima, 2007; Chave et al., 2009; Poorter, 2009; Poorter & Rozendaal, 2008; Reich, 2014;

104 Weiher et al., 1999; Wright et al., 2004; Wright & Westoby, 2002). Trees with higher maximum 105 height and larger leaves tend to have above average growth and survival rates and lower 106 recruitment rates for individuals > 1 cm DBH (diameter at breast height), but lower seedling 107 survival and growth (Kohyama et al., 2003; Rüger et al., 2018, 2020), representing a tradeoff 108 between growth and survival with tree stature, known as the 'stature-recruitment' axis. Seed 109 mass is positively correlated with seedling recruitment rates and greater stress tolerance at early 110 life stages (Moles & Westoby, 2006; Muller-Landau, 2010). Despite the wealth of research into 111 the general relationships between functional traits, life history strategies, and plant performance, 112 the role of environmental context in driving these relationships remains underexplored (Ackerly, 113 2003; Laughlin, 2018; Laughlin & Messier, 2015).

114

115 Resource availability within and across environments may be an important factor 116 influencing trait-rate relationships. For example, in high resource environments, traits that 117 maximize carbon gain are advantageous and can result in relatively high growth rates, whereas 118 the same strategy can be disadvantageous in low resource environments and result in relatively 119 low growth rates, due to tradeoffs between growth and stress resistance (Fig. 1a) (Coley et al., 120 1985; Grime, 1977; Kobe, 1999; Reich, 2014; Russo et al., 2005). Across a resource availability 121 gradient, the strength of trait-growth rate relationships may then show a predictable pattern 122 where correlations between traits and growth rates are weakest in low resource environments and 123 strongest in high resource environments (Fig. 1a). Conversely, for mortality rates, trait-mortality 124 correlations would be strongest in low resource environments and weakest in high resource 125 environments (Fig. 1b). Evidence of these relationships have been found within a Bornean rain 126 forest, where Russo et al. (2007) demonstrated that resource-acquisitive species suffered higher 127 mortality in low resource soils compared to more fertile soils. Variation in light availability also 128 leads to similar interactions between vital rates and local environment (Bloor & Grubb, 2003; 129 Kobe, 1999; Walters & Reich, 1996; Wright et al., 2010). While recent studies have found in 130 some cases that explicitly accounting for trait by environment interactions improves models of 131 plant performance (Jiang & Jin, 2021; Laughlin et al., 2018; Li et al., 2022; Worthy et al., 2020; 132 Yang et al., 2021), resolving the degree to which local environment influences trait-rate 133 relationships is a key research priority for the field of functional ecology to understand the 134 contexts in which functional traits are strong or weak predictors of fitness.

136 In this study, we tested the hypothesis that trait-rate relationships vary with local 137 environmental context. We combined functional trait data with long-term monitoring of growth 138 and mortality rates of tropical seedling communities across a strong precipitation and soil 139 nutrient gradient in central Panama. The severity of the annual dry season varies widely across 140 the Isthmus of Panama (Fig. 2), with forests on the Caribbean side experiencing less severe dry 141 seasons than forests on the Pacific side (Condit et al., 2013). Additionally, there is a strong 142 variation in soil nutrients, particularly soil phosphorus availability (Condit et al., 2013). Both dry 143 season severity and soil phosphorus availability are important predictors of seedling performance 144 and species distributions across central Panama and other tropical regions (Alvarez-Clare et al., 145 2013; Condit et al., 2013; Gaviria et al., 2017; Wright et al., 2011; Zalamea et al., 2016). We 146 focused on seedling communities because the understory dynamics at these early life stages 147 influence future patterns of forest structure and diversity (Green et al., 2014; Poorter, 2007) and 148 relatively little is known about trait-rate relationships in tropical seedling communities (but see Umaña et al., 2017). Specifically, we asked the following questions: (1) Across all sites, do we 149 150 observe relationships between functional traits and growth and mortality rates (Table 1)? (2) 151 Does the strength of the trait-rate relationships vary among sites? And (3) If so, is that variation 152 predicted by local dry season severity and/or soil phosphorus availability (Table 1)?

153

154 Based on previous studies in both adults and seedlings (Alvarez-Clare & Kitajima, 2007; 155 Chave et al., 2009; Kohyama et al., 2003; Moles & Westoby, 2006; Muller-Landau, 2010; 156 Poorter, 2009; Poorter & Rozendaal, 2008; Reich, 2014; Rüger et al., 2018, 2020; Weiher et al., 157 1999; Wright et al., 2004; Wright & Westoby, 2002), we predicted that growth rates would be 158 negatively related to wood density, leaf mass per unit area, leaf dry matter content, maximum 159 height, seed mass, and leaf area and that the strength of this negative relationship would be 160 stronger in high resource environments compared to low resource environments (Table 1). We 161 predicted that mortality rates would be negatively related to wood density, leaf mass per unit 162 area, leaf dry matter content, and seed mass, with the strength of this relationship being weaker 163 in high resource compared to low resource environments (Table 1). Finally, we predicted that 164 mortality rates would be positively related to maximum height and leaf area, with the strength of 165 this relationship increasing in high resource compared to low resource environments (Table 1).

#### 167 Materials and Methods

168

#### 169 Study area and seedling censuses

170 This study was conducted in eight 1-ha plots in seasonally moist tropical forests across the 171 Isthmus of Panama (Fig. 2). These plots span a relatively short 65-km gradient, where mean 172 annual precipitation ranges from ~3,200 mm to ~1,600 mm. Plant-available soil phosphorus 173 levels (hereafter soil phosphorus levels) also vary strongly among sites and range from 3.0 to 22.8 mg / kg (Condit et al., 2013). Within each 1-ha plot, 400  $1-m^2$  seedling plots were 174 established from September-December 2013, where within each  $1-m^2$  plot, all woody seedlings  $\geq$ 175 176 200 mm in height and < 1 cm DBH (diameter at 1.3m above ground) were tagged, identified, and 177 measured following Comita et al. (2007). Seedling plots were re-censused annually near the 178 beginning of the annual dry season (November-February). The maximum stem height of all 179 marked seedlings was measured, and all seedlings were evaluated whether they were alive or 180 dead. Any new seedlings that recruited into the size criterion ( $\geq 200$  mm height) were entered 181 into the census. Seedlings without a definitive species identification (n = 519 individuals) and 182 lianas were excluded from analyses. Due to limited access, one site, Oleoducto, in 2019 or 2020, 183 and another site, Panamá Pacifico, in 2018, were not censused. The last census included in this 184 study occurred in 2021, for a total of 7 annual census intervals. The overall dataset, before 185 filtering based on trait availability, included 28,303 observations of 9,267 individuals belonging 186 to 358 tree species.

187

#### 188 Trait data

189 We focused on six widely available, species-level traits from Wright et al. (2010) that are related 190 to both the fast-slow and stature-recruitment axes of life history variation: wood density  $(g / cm^3)$ , 247 species), LMA (leaf mass per unit area,  $g/m^2$ , 184 species), leaf dry matter content (g/g, 191 192 184 species), maximum height (m, 186 species), seed mass (g, 180 species), and leaf area (cm<sup>2</sup>, 193 184 species. A full description of the methods of trait data collection are available in Wright et 194 al. (2010). Briefly, wood density data was collected from ~5 adult individuals per species within 195 15 km of the Barro Colorado Island (BCI) 50-ha forest dynamics plot, which is located near the 196 center of the rainfall gradient. Leaf traits were collected from leaves receiving indirect sunlight

197 from six of the smallest individuals of each species at the BCI 50-ha plot. Maximum height was 198 estimated as the mean height of the six individuals with the largest DBH in the 50-ha plot on BCI 199 and a nearby 38.4 ha plot (King et al., 2006; Wright et al., 2010). Seed mass is the mean dry 200 mass that includes the endosperm and embryo only, measured from 1-11 individuals and 1-139 201 seeds per species. Pairwise correlations among traits ranged from Pearson's r = 0.01 to 0.57 (Fig. 202 S1). It is also important to note that the trait data used in this study was obtained from a single 203 population of each species and from adults rather than seedlings (trait data from seedling life stages was not available at the time of this study), which fails to capture potentially important 204 205 trait variation across individuals, life stages and populations (Dayrell et al., 2018; Havrilla et al., 206 2021; Palow et al., 2012; Umaña & Swenson, 2019).

207

#### 208 Environmental data

209 We characterized annual drought at each site using dry season severity, defined as the most 210 extreme cumulative rainfall deficit of evapotranspiration exceeding precipitation reached during 211 the annual dry season, with lower values indicating more severe dry seasons (Condit et al., 212 2013). Long-term dry season severity estimates (1961-1990 average) at each site were obtained 213 from Browne et al. (2021). Soil phosphorus levels were obtained from Condit et al. (2013), 214 where soil resin phosphorus levels were estimated using anion-exchange membranes placed in 215 the upper 10 cm of the soil profile during the wet season. We log transformed soil phosphorus 216 levels prior to analysis. While we acknowledge that light available is a major drive of understory 217 dynamics in tropical forests, we were not able to quantify variation in light availability across 218 sites in this study.

219

#### 220 Growth and mortality model formulation

To estimate the relationships between functional traits and growth and mortality rates for the seedling communities in this study, we fit separate hierarchical Bayesian models for growth and mortality that had similar structures in terms of predictor variables and random effects. We quantified growth using relative growth rates (RGR):

225 
$$RGR = \frac{ln(Height_2) - ln(Height_1)}{(t_2 - t_1)}$$

226 where  $t_2$  = time two,  $t_1$  = time one,  $Height_2$  = height at time 2,  $Height_1$  = height at time 1. We 227 used a Box-Cox transformation (lambda = 0.15) to reduce skewness and normalize the 228 distribution of growth rates (Condit et al., 2017). This reduced the number of model divergences 229 as well. RGR values were back-transformed to the original scale for presentation in all figures. 230 While our choice of growth metric (relative growth rate of stem height) provides valuable 231 information on the vertical position of the stem in the understory, which influences access to 232 light and competitive dynamics, it fails to account for other types of growth such radial growth, 233 biomass increase, or below ground growth. To reduce noise in growth measurements, we focused 234 only on positive growth rates in this study, though including negative growth rates (due to stem 235 breakage or measurement error) produced qualitatively similar results (results not shown). 236 In growth models, the response variable (RGR) was assumed to be Normally distributed for each 237 individual observation *i*: 238  $RGR_i \sim Normal(\hat{y}_i, \sigma)$ 239 In mortality models, the response variable (1 = dead, 0 = alive) was assumed to be Bernoulli 240 distributed and adjusted to account for varying census intervals (time):  $Mortality_i \sim Bernoulli(logit(\hat{y}_i)^{time})$ 241 242 243 We estimated overall (*i.e.*, across sites) trait-rate relationships using a model (Model 1) where 244 trait-rate relationships were not allowed to vary across sites: 245 246 Model 1: Trait-rates fixed across sites  $\hat{y}_i \sim \alpha 0 + \alpha 1_{spp} + \alpha 2_{c,s} + \alpha 3_p + \beta 1 \cdot InitialHeight_i + \beta 2 \cdot Trait_i$ 247  $\alpha 1_{spp} \sim \text{Normal}(0, \sigma^2)$ 248  $\alpha 2_{c.s} \sim \text{Normal}(0, \sigma^2)$ 249  $\alpha 3_p \sim \text{Normal}(0, \sigma^2)$ 250 251 where  $\hat{y}_i$  is either Box-cox-transformed RGR or mortality status (1 = dead, 0 = alive) for 252 253 observation *i*,  $\alpha 0$  is the overall intercept,  $\alpha 1_{spp}$  is a species-level (*spp*) random intercept,  $\alpha 2_{c,s}$ 

is a random effect predicted separately for each census-site combination,  $\alpha 3_p$  is a plot-level

255 random effect for each 1x1 m seedling plot p,  $\beta$ 1 estimates the effect of height at the previous

256 census on either RGR or mortality, and  $\beta$ 2 estimates each overall trait-rate relationship across all

sites. Trait data for LMA, leaf dry matter content, seed mass, and leaf area were log-transformed

prior to standardization. We then standardized all trait data such that mean = 0 and standard

deviation = 1. Original mean and standard deviation values of traits are available in Table S1.

260 We log-transformed and standardized initial seedling height within each species such that mean

261 = 0 and standard deviation = 1 to account for differences in mean seedling height across species.

262

To estimate how trait-rate relationships varied across sites, we fit an additional model (Model 2) where  $\beta 2$  was estimated separately for each site *s*:

265

#### 266 Model 2: Trait-rates variable across sites

267

 $\hat{y}_i \sim \alpha 0 + \alpha 1_{spp} + \alpha 2_{c,s} + \alpha 3_p + \beta 1 \cdot InitialHeight_i + \beta 2_s \cdot Trait_i$ 

268  $\beta 2_s \sim Normal(\alpha, \sigma)$ 

269

270 In this case,  $\beta 2_s$  estimates the site-specific slope of a trait on either growth or mortality. To 271 assess whether trait-rate relationships varied substantially across sites, we compared models 272 where  $\beta 2$  was allowed to vary across sites (*i.e.*, Model 2) to the model where  $\beta 2$  was fixed 273 across sites (i.e., Model 1) using LOOIC (leave-one-out information criterion) (Vehtari et al., 274 2017). LOOIC is a robust estimate of pointwise out-of-sample prediction accuracy from a fitted 275 Bayesian model based on log-likelihood scores that is on the same scale as other information 276 criteria (e.g. deviance information criterion, Akaike's information criterion – AIC (Vehtari et al., 277 2017). We considered models within 2 LOOIC units of each other to be equally supported by the 278 data and a model with the lowest LOOIC that was > 2 LOOIC units from the next best model to 279 be best fit to the data (following Eisaguirre et al., 2019; Lindenmayer et al., 2022; Ravindran et 280 al., 2021). To calculate LOOIC in this comparison, we used the log-likelihood scores based on 281  $RGR_i$  or Mortality<sub>i</sub>, depending on whether it was a growth or mortality model. If the LOOIC 282 score was lower for any model where  $\beta_{trait}$  was allowed to vary across sites compared to the

283 model where  $\beta$ 2 was fixed across sites, we considered this as evidence that trait-rate 284 relationships varied across sites.

285

286 To determine whether variation in trait-rate relationships across sites could be explained by local 287 environmental factors, we used a second-level regression within each mortality and growth 288 model. We linked site-level estimates of trait-rate relationships to Dry Season Severity (DSS, 289 average from 1961-1990, lower numbers indicate more severe dry seasons), and soil phosphorus 290 (SoilP). We fit three separate model formulations that included either DSS (Model 3) and SoilP 291 (Model 4) as predictors of trait-rate variation across sites ( $\beta 2_s$ ), or an intercept only model with 292 no predictor covariates that allows for variation in trait-rates across sites (Model 2, above) and 293 compared these models using LOOIC, with the log-likelihood calculated based on  $\beta 2_s$ . 294 Comparing models with DSS or SoilP as predictors to an intercept only model allowed us to test 295 whether these local environmental factors could explain variation in trait-rate relationships 296 across sites. We did not include both DSS and SoilP in a single model because the high 297 collinearity between DSS and SoilP at our sites (R = -0.74) and low number of sites (n = 8) 298 would lead to reduced power and high uncertainty in parameter estimates when both predictors 299 were used in a single model.

300

301 Model 3: DSS as predictor

302

 $\beta 2_s \sim Normal(\alpha + \beta 3 \cdot DSS_s, \sigma)$ 

303

#### 304 Model 4: Soil Phosphorus as predictor

305

 $\beta 2_s \sim Normal(\alpha + \beta 4 \cdot SoilP_s, \sigma)$ 

306

307 All models were fit using Stan (Carpenter et al., 2017) using the 'rstan' package vs. 2.21.2 (Stan

308 Development Team, 2020). Following the Stan prior choice recommendations (Stan

309 Development Team, 2017), we used weakly-informative priors of Half-Normal(0,1) for

310 variance parameters, Student<sub>t</sub>(5, 0, 2.5) for coefficients in mortality models, and Normal(0, 1)

314 models linking dry season severity or soil phosphorus to growth-trait variation across sites.

311

312

313

315 Using a weakly-informative prior produced qualitatively similar results. For each model, we ran

for coefficients in growth models. To ensure no model divergences, which would indicate an

issue with model estimation (Stan Development Team, 2020), we used a more informative prior

of Half-Normal(0.04, 0.05) for the variance parameter in the second level regression of growth

four independent chains for 3,000 iterations, with 1,500 iterations of burn in. We checked chain

317 convergence visually and by ensuring the potential scale reduction factor statistic ('rhat') was <

318 1.10 (Kéry, 2010). We calculated LOOIC scores using the 'loo' R package v. 2.4.1 (Vehtari et319 al., 2020).

320

#### 321 **Results**

322

#### 323 (1) Overall trait-rate relationships across sites

324 We found overall relationships between traits and growth and mortality rates for most traits 325 considered. Annual relative growth rates decreased most strongly with increasing wood density, 326 LMA, and seed mass (Fig. 3a). Relative growth rates also decreased with increasing leaf dry 327 matter content, but the strength of the relationship between growth rates, maximum height, and 328 leaf area was close to 0 (Fig. 3a). Average mortality rates decreased strongly with increasing wood density, increasing LMA, and increasing leaf dry matter content and increased strongly 329 330 with increasing maximum height (Fig. 3b). The strength of mortality rate-trait relationships was 331 weaker for leaf area and seed mass (Fig. 3b).

332

#### 333 (2) Variation in trait-rate relationships across sites

334 Trait-growth and trait-mortality relationships were variable across sites for most trait-rate 335 combinations considered, as indicated by  $\Delta$ LOOIC scores > -2 units for models that allowed sites 336 to vary in their trait-rate relationships than models where trait-rate relationships were fixed 337 across sites (Table 2). The exceptions were LMA-growth, LMA-mortality and leaf area-mortality 338 relationships, where models with trait-rate relationships variable across sites were all within 2 339 LOOIC units of models with trait-rate relationships fixed across sites (Table 2).

# 341 (3) Dry season severity and soil phosphorus predicting variation in trait-rate relationships 342 across sites

- 343 Variation in trait-growth or trait-mortality relationships was not predicted by dry season severity
  344 in any of the 12 comparisons made, but variation was predicted by soil phosphorus in 2/12
- 345 comparisons (Fig. 4, 5), as indicated by  $\Delta$ LOOIC scores within 2 units for models with soil
- 346 phosphorus as a predictor vs. intercept-only models with no environmental predictors (Table 3).
- 347

348 Variation in trait-growth relationships for wood density, leaf dry matter content, LMA,

- 349 maximum height, seed mass, and leaf area was not explained by variation in either dry season
- 350 severity or soil phosphorus across sites (Fig. 4, Table 3). In general, there was large uncertainty
- in these estimates due to the limited number of sites (Table S2).
- 352

Wood density-mortality relationships were more strongly negative (higher wood density associated with lower mortality) and maximum height-mortality relationships were more strongly positive (with higher maximum height associated with higher mortality rates) in sites with higher soil phosphorus levels, but neither showed a relationship with dry season severity (Fig. 5). Neither dry season severity nor soil phosphorus explained variation in trait-mortality relationships for LMA, leaf dry matter content, seed mass, or leaf area (Fig. 5, Table 3).

359

#### 360 Discussion

361 The relationships between functional traits and vital rates in plants are often weak or 362 inconsistent, and the underlying drivers of this pattern are currently unresolved (Paine et al., 363 2015). In this study, we found widespread evidence that trait-rate relationships varied for 364 seedlings across eight sites along the Isthmus of Panama for a set of common functional traits 365 related to major axes of life history variation. We found limited support for the hypothesis that 366 local resource availability drives variation in trait-rate relationships. Environmental variables 367 related to water and soil nutrient availability failed to explain site-to-site variation in trait-rate 368 relationships for the majority of cases. In a small subset of cases, soil phosphorus levels 369 explained variation in trait-mortality relationships. These results demonstrate that site-level 370 factors modulate the interaction between functional trait strategies and demographic outcomes, which may explain why trait-rate relationships are inconsistent and weak at broad scales whenthese factors are not considered.

373

#### 374 (1) Overall trait-rate relationships across sites

375 The first goal of our study was to determine whether general trait-rate relationships existed for 376 seedlings across the eight study sites included in this study. Consistent with previous studies in 377 tropical forests (Poorter et al., 2008; Wright et al., 2010), we found general relationships in the 378 expected direction for most trait-rate relationships we considered in this study, despite using trait 379 data collected from adults. We found that species with high wood density, LMA, and leaf dry 380 matter content showed lower growth rates and lower mortality rates, following the well-381 established leaf and wood economics spectrums (Chave et al., 2009; Wright et al., 2004). For 382 seed mass, we found that larger seeds were generally associated with decreased growth rates but 383 contrary to our expectations, were not strongly associated with mortality rates, with the 95% 384 credible interval including 0. The lack of a strong relationship between seed mass and seedling 385 mortality is partly in contrast to previous studies that have found increased seed mass is related 386 to increased seedling establishment and survival; however, this relationship can decouple as 387 seedlings age and rely less on the resources provided by the seed (Dalling & Hubbell, 2002; 388 Moles & Westoby, 2006; Westoby et al., 2002). The 200 mm minimum height cutoff used in this 389 study encompasses a range of seedling ages, most of which may be beyond the point of relying 390 on the seed for sustenance, which could explain the absence of a negative relationship between 391 seed mass and mortality rates. We found that higher trait values of maximum height were 392 associated with increased mortality rates but not strongly associated with growth rates, while leaf 393 area was not strongly associated with either growth or mortality rates. These results are partially 394 consistent with previous studies that have found that species with high maximum height ('long-395 lived pioneers') tend to have lower seedling performance (Rüger et al., 2018). The lack of a 396 general relationship for maximum height, leaf area, and growth rates could be explained by wide 397 site-to-site variation in these trait-rate relationships across our eight sites (see below).

398

#### 399 (2) Variation in trait-rate relationships across sites

400 Our second question focused on whether the strength of trait-rate relationships varied

401 substantially among our study sites. We found strong support for the hypothesis that trait-rate

402 relationships vary among sites, with all functional traits analyzed except for LMA-growth, LMA-403 mortality, and leaf area-mortality relationships showing evidence of variation across sites. While 404 a goal of this study was to test whether resource availability could explain variation in trait-rate 405 relationships across sites, differences in species composition could also lead to variation in trait-406 rate relationships, especially if compositional differences across sites are due to species turnover 407 rather than nestedness. In our dataset, the majority of species (59%) occurred in at least two sites 408 and our statistical models included a species-level random intercept that in theory would help 409 control for differences in species composition across sites, especially in cases where species 410 turnover is not complete. However, in our study area, there is a significant level of species 411 turnover across sites related to differences in both precipitation and soil phosphorus (Pyke et al., 412 2001; Umaña et al., 2021), which may contribute to the variation in functional trait-rate 413 relationships across sites we observed.

414

415 In some cases, such as wood density-mortality relationships, the slope estimates remained 416 consistently in the same direction across all sites, though the magnitude of the slope estimate 417 varied on a site-by-site basis. In contrast, for maximum height-growth, leaf area-growth, and leaf 418 dry matter content-growth relationships, slope estimates varied between positive, negative, or 419 close to 0 across sites, obscuring a general pattern in trait-rate relationships for these traits. 420 Taken together, these results suggest that at least for some traits, a single-site study is unlikely to 421 fully capture the potential variability or even accurately estimate the general direction of a trait-422 rate relationship. Therefore, care must be taken when extrapolating the results from single sites 423 to other communities in different environmental contexts. Additionally, a general relationship 424 between functional traits and a vital rate does not preclude the existence of considerable site-by-425 site variation that may be explained by site-level factors. Conversely, the lack of a general trait-426 rate relationship may arise due to wide site-to-site variation and thus weak overall trait-rate 427 relationships do not imply that a given trait is not relevant for vital rates at a particular site. 428

# 429 (3) Dry season severity and soil phosphorus predicting variation in trait-rate relationships 430 across sites

For our third question, we tested the hypothesis that variation in local resource availability
explains variation in trait-rate relationships across sites, with the expectation that lower resource

environments would lead to weaker trait-growth relationships and stronger trait-mortality
relationships (Fig. 1). We found limited support for this hypothesis. Overall, we found limited
statistical support that models including dry season severity or soil phosphorous performed better
than a more parsimonious model that did not use environmental predictors to explain variation in
trait-rate relationships across sites. Altogether, none of the trait-growth and trait-mortality
relationships were predicted by dry season severity or and 2/6 trait-mortality relationships were
predicted by soil phosphorus, and neither of those cases were in the predicted direction (Table 1).

441 Contrary to our expectations that trait-mortality relationships would be strongest at sites 442 with low soil phosphorus (Fig. 1b), we found more strongly negative wood density-mortality 443 relationships and more strongly positive maximum height-mortality relationships in sites with 444 high soil phosphorus, indicating that species with low wood density and higher maximum height 445 suffered relatively high mortality at high phosphorus sites compared to low phosphorus sites. A 446 potential explanation for these unexpected results is that herbivory tends to be higher at sites 447 with high levels of soil phosphorus, which also tend to be drier sites (Muehleisen et al., 2020; 448 Weissflog et al., 2018). Furthermore, experimental studies have shown that phosphorus addition 449 increases herbivory pressure on seedlings, implicating phosphorus as a causal mechanism driving 450 herbivory (Santiago et al., 2012). Taking this into account, any potential benefits to competitive 451 ability of low wood density or high maximum height at sites with high soil phosphorus may be 452 offset by higher rates of herbivory, suggesting that herbivory may be a limiting factor for vital 453 rates of seedlings at these sites, though future experimental work is needed to confirm this 454 hypothesis.

455

#### 456 Conclusion

In summary, we showed through a long-term demographic study of thousands of seedlings across the Isthmus of Panama that there is widespread variation in trait-rate relationships across sites, that some of this variation was explained by site-level differences in soil phosphorus, but mostly remains unexplained. Future studies that assess a wider range of environmental covariates, including variation in light and ecological processes like herbivory, along with considering variation in traits across individuals, life stages, and populations, will likely improve the amount of variation in trait-rate relationships explained across environmental gradients. More

- 464 broadly, accounting for site-to-site variation and acknowledging the context-dependent nature of
- 465 trait-rate relationships may help resolve a fundamental issue in trait-based ecology that many
- 466 studies show weak to non-existent relationships between functional traits and vital rates.

#### 467 **References**

- 469 Ackerly, D. D. (2003). Community assembly, niche conservatism, and adaptive evolution in
- 470 changing environments. *International Journal of Plant Sciences*, 164(S3), S165–S184.
- 471 https://doi.org/10.1086/368401
- 472 Alvarez-Clare, S., & Kitajima, K. (2007). Physical defence traits enhance seedling survival of
- 473 neotropical tree species. *Functional Ecology*, 21(6), 1044–1054.
- 474 https://doi.org/10.1111/j.1365-2435.2007.01320.x
- 475 Alvarez-Clare, S., Mack, M. C., & Brooks, M. (2013). A direct test of nitrogen and phosphorus
- 476 limitation to net primary productivity in a lowland tropical wet forest. *Ecology*, 94(7),
- 477 1540–1551. https://doi.org/10.1890/12-2128.1
- 478 Bloor, J. M. G., & Grubb, P. J. (2003). Growth and mortality in high and low light: trends among
- 479 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology*, 91(1), 77–85.
- 480 https://doi.org/10.1046/j.1365-2745.2003.00743.x
- 481 Browne, L., Markesteijn, L., Engelbrecht, B. M. J., Jones, F. A., Lewis, O. T., Manzané-Pinzón,
- 482 E., Wright, S. J., & Comita, L. S. (2021). Increased mortality of tropical tree seedlings
- 483 during the extreme 2015-16 El Niño. *Global Change Biology*, 27(20), 5043–5053.
- 484 https://doi.org/10.1111/gcb.15809
- 485 Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: functional diversity
- 486 and the maintenance of ecological processes and services. *Journal of Applied Ecology*,
- 487 48(5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x
- 488 Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker,
- 489 M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language.
- 490 *Journal of Statistical Software*, 76(1), 1–32. https://doi.org/10.18637/jss.v076.i01

- 491 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009).
- 492 Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366.
   493 https://doi.org/10.1111/j.1461-0248.2009.01285.x
- 494 Coley, P. D., Bryant, J. P., & Chapin, F. S., 3rd. (1985). Resource availability and plant
- 495 antiherbivore defense. *Science*, *230*(4728), 895–899.
- 496 https://doi.org/10.1126/science.230.4728.895
- 497 Comita, L. S., Aguilar, S., Pérez, R., Lao, S., & Hubbell, S. P. (2007). Patterns of woody plant
  498 species abundance and diversity in the seedling layer of a tropical forest. *Journal of*
- 499 *Vegetation Science*, *18*(2), 163. https://doi.org/10.1658/1100-
- 500 9233(2007)18[163:powpsa]2.0.co;2
- 501 Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R., & Turner, B. L. (2013). Species
- 502 distributions in response to individual soil nutrients and seasonal drought across a
- 503 community of tropical trees. *Proceedings of the National Academy of Sciences of the*
- 504 United States of America, 110(13), 5064–5068. https://doi.org/10.1073/pnas.1218042110
- 505 Condit, R., Pérez, R., Lao, S., Aguilar, S., & Hubbell, S. P. (2017). Demographic trends and
- 506 climate over 35 years in the Barro Colorado 50 ha plot. *Forest Ecosystems*, 4(1), 17.
- 507 https://doi.org/10.1186/s40663-017-0103-1
- Dalling, J. W., & Hubbell, S. P. (2002). Seed size, growth rate and gap microsite conditions as
   determinants of recruitment success for pioneer species. *Journal of Ecology*, 90(3), 557–
- 510 568. https://doi.org/10.1046/j.1365-2745.2002.00695.x
- 511 Dayrell, R. L. C., Arruda, A. J., Pierce, S., Negreiros, D., Meyer, P. B., Lambers, H., & Silveira,
- 512 F. A. O. (2018). Ontogenetic shifts in plant ecological strategies. *Functional Ecology*,
- 513 *32*(12), 2730–2741. https://doi.org/10.1111/1365-2435.13221

514	Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M.,
515	Wirth, C., Prentice, I. C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.
516	B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., Gorné, L. D. (2016). The
517	global spectrum of plant form and function. Nature, 529(7585), 167–171.
518	https://doi.org/10.1038/nature16489
519	Eisaguirre, J. M., Auger-Méthé, M., Barger, C. P., Lewis, S. B., Booms, T. L., & Breed, G. A.
520	(2019). Dynamic-parameter movement models reveal drivers of migratory pace in a
521	soaring bird. Frontiers in Ecology and Evolution, 7.
522	https://doi.org/10.3389/fevo.2019.00317
523	Gaviria, J., Turner, B. L., & Engelbrecht, B. M. J. (2017). Drivers of tree species distribution
524	across a tropical rainfall gradient. Ecosphere, 8(2), e01712.
525	https://doi.org/10.1002/ecs2.1712
526	Green, P. T., Harms, K. E., & Connell, J. H. (2014). Nonrandom, diversifying processes are
527	disproportionately strong in the smallest size classes of a tropical forest. Proceedings of

- *the National Academy of Sciences*, *111*(52), 18649–18654.
- 529 https://doi.org/10.1073/pnas.1321892112
- 530 Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its
- 531 relevance to ecological and evolutionary theory. *The American Naturalist*, *111*(982),
- 532 1169–1194. https://doi.org/10.1086/283244
- 533 Havrilla, C. A., Munson, S. M., Yackulic, E. O., & Butterfield, B. J. (2021). Ontogenetic trait
- shifts: Seedlings display high trait variability during early stages of development.
- 535 *Functional Ecology*, *35*(11), 2409–2423. https://doi.org/10.1111/1365-2435.13897

- Jiang, F., & Jin, G. (2021). Functional traits influence plant survival depending on environmental
  contexts and life stages in an old-growth temperate forest. *Journal of Plant Ecology*,
- 538 14(5), 981–994. https://doi.org/10.1093/jpe/rtab049
- 539 Kéry, M. (2010). Introduction to WinBUGS for Ecologists. Academic Press.
- 540 https://doi.org/10.1016/B978-0-12-378605-0.00022-3
- 541 King, D. A., Wright, S. J., & Connell, J. H. (2006). The distribution of maximum tree heights in
- tropical vs. temperate forests: Cause or consequence of tropical diversity. *Journal of Tropical Ecology*, 22, 11–24.
- 544 Kobe, R. K. (1999). Light gradient partitioning among tropical tree species through differential
- 545 seedling mortality and growth. *Ecology*, 80(1), 187–201. https://doi.org/10.1890/0012546 9658(1999)080[0187:lgpatt]2.0.co;2
- 547 Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T., & Kubo, T. (2003). Tree species
- 548 differentiation in growth, recruitment and allometry in relation to maximum height in a
- 549 Bornean mixed dipterocarp forest. *Journal of Ecology*, *91*(5), 797–806.
- 550 https://doi.org/10.1046/j.1365-2745.2003.00810.x
- 551 Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015).
- 552 Community assembly, coexistence and the environmental filtering metaphor. *Functional*

553 *Ecology*, 29(5), 592–599. https://doi.org/10.1111/1365-2435.12345

- Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to
- community assembly. *Journal of Ecology*, *102*(1), 186–193.
- 556 https://doi.org/10.1111/1365-2745.12187
- Laughlin, D. C. (2018). Rugged fitness landscapes and Darwinian demons in trait-based ecology.
- 558 The New Phytologist, 217(2), 501–503. https://doi.org/10.1111/nph.14908

- Laughlin, D. C., & Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic
- adaptive landscapes. *Trends in Ecology & Evolution*, *30*(8), 487–496.
- 561 https://doi.org/10.1016/j.tree.2015.06.003
- 562 Laughlin, D. C., Strahan, R. T., Adler, P. B., & Moore, M. M. (2018). Survival rates indicate that
- 563 correlations between community-weighted mean traits and environments can be
- 564 unreliable estimates of the adaptive value of traits. *Ecology Letters*, 21(3), 411–421.
- 565 https://doi.org/10.1111/ele.12914
- 566 Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem
- 567 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16(5), 545–
- 568 556. https://doi.org/10.1046/j.1365-2435.2002.00664.x
- Li, Y., Jiang, Y., Zhao, K., Chen, Y., Wei, W., Shipley, B., & Chu, C. (2022). Exploring trait-
- performance relationships of tree seedlings along experimentally manipulated light and
  water gradients. *Ecology*, e3703. https://doi.org/10.1002/ecy.3703
- 572 Lindenmayer, D., Blanchard, W., Bowd, E., Scheel, B., Tyrone, F. C. L., & David, M. L. B.
- 573 (2022). Rapid bird species recovery following high-severity wildfire but in the absence of
- 674 early successional specialists. *Diversity and Dis*. https://doi.org/10.1111/ddi.13611
- 575 McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology
- from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185.
- 577 https://doi.org/10.1016/j.tree.2006.02.002
- 578 Moles, A. T., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle.
- 579 *Oikos*, *113*(1), 91–105. https://doi.org/10.1111/j.0030-1299.2006.14194.x

580	Muehleisen, A. J., Engelbrecht, B. M. J., Jones, F. A., Manzané-Pinzón, E., & Comita, L. S.
581	(2020). Local adaptation to herbivory within tropical tree species along a rainfall
582	gradient. Ecology, 101(11), e03151. https://doi.org/10.1002/ecy.3151
583	Muller-Landau, H. C. (2010). The tolerance-fecundity trade-off and the maintenance of diversity
584	in seed size. Proceedings of the National Academy of Sciences of the United States of
585	America, 107(9), 4242–4247. https://doi.org/10.1073/pnas.0911637107
586	Paine, C. E. T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H.,
587	Daïnou, K., de Gouvenain, R. C., Doucet, JL., Doust, S., Fine, P. V. A., Fortunel, C.,
588	Haase, J., Holl, K. D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., Hector, A.
589	(2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do
590	not know why. Journal of Ecology, 103(4), 978–989. https://doi.org/10.1111/1365-
591	2745.12401
592	Palow, D. T., Nolting, K., & Kitajima, K. (2012). Functional trait divergence of juveniles and
593	adults of nine Inga species with contrasting soil preference in a tropical rain forest.
594	Functional Ecology, 26(5), 1144-1152. https://doi.org/10.1111/j.1365-
595	2435.2012.02019.x
596	Poorter, L. (2007). Are species adapted to their regeneration niche, adult niche, or both? The
597	American Naturalist, 169(4), 433-442. https://doi.org/10.1086/512045
598	Poorter, L. (2009). Leaf traits show different relationships with shade tolerance in moist versus
599	dry tropical forests. The New Phytologist, 181(4), 890-900.
600	https://doi.org/10.1111/j.1469-8137.2008.02715.x

601	Poorter, L.,	Castilho,	C. V.,	, Schietti, J.,	Oliveira,	R. S., &	Costa, F. I	R. C. (2018).	Can traits
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- 602 predict individual growth performance? A test in a hyperdiverse tropical forest. *The New*603 *Phytologist*, 219(1), 109–121. https://doi.org/10.1111/nph.15206
- Poorter, L., & Rozendaal, D. M. A. (2008). Leaf size and leaf display of thirty-eight tropical tree
  species. *Oecologia*, 158(1), 35–46. https://doi.org/10.1007/s00442-008-1131-x
- 606 Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., Harms, K.
- 607 E., Licona, J. C., Martínez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Peña-Claros,
- 608 M., Webb, C. O., & Wright, I. J. (2008). Are functional traits good predictors of
- demographic rates? Evidence from five neotropical forests. *Ecology*, 89(7), 1908–1920.
- 610 https://doi.org/10.1890/07-0207.1
- 611 Pyke, C. R., Condit, R., Aguilar, S., & Lao, S. (2001). Floristic composition across a climatic
- 612 gradient in a neotropical lowland forest. *Journal of Vegetation Science: Official Organ of*
- 613 *the International Association for Vegetation Science*, *12*(4), 553–566.
- 614 https://doi.org/10.2307/3237007
- 615 Ravindran, S., Froy, H., Underwood, S. L., Dorrens, J., Seeker, L. A., Watt, K., Wilbourn, R. V.,
- 616 Pilkington, J. G., Harrington, L., Pemberton, J. M., & Nussey, D. H. (2021). The
- 617 association between female reproductive performance and leukocyte telomere length in
- 618 wild Soay sheep. *Molecular Ecology*. https://doi.org/10.1111/mec.16175
- Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: a traits manifesto.

620 *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

- 621 Rüger, N., Comita, L. S., Condit, R., Purves, D., Rosenbaum, B., Visser, M. D., Wright, S. J., &
- 622 Wirth, C. (2018). Beyond the fast-slow continuum: demographic dimensions structuring

- 623 a tropical tree community. *Ecology Letters*, 21(7), 1075–1084.
- 624 https://doi.org/10.1111/ele.12974
- 625 Rüger, N., Condit, R., Dent, D. H., DeWalt, S. J., Hubbell, S. P., Lichstein, J. W., Lopez, O. R.,
- 626 Wirth, C., & Farrior, C. E. (2020). Demographic trade-offs predict tropical forest
- 627 dynamics. *Science*, *368*(6487), 165–168. https://doi.org/10.1126/science.aaz4797
- 628 Russo, S. E., Brown, P., Tan, S., & Davies, S. J. (2007). Interspecific demographic trade-offs and
- 629 soil-related habitat associations of tree species along resource gradients: Demographic
- trade-offs on habitat gradients. *The Journal of Ecology*, 96(1), 192–203.
- 631 https://doi.org/10.1111/j.1365-2745.2007.01330.x
- Russo, S. E., Davies, S. J., King, D. A., & Tan, S. (2005). Soil-related performance variation and
- distributions of tree species in a Bornean rain forest. *Journal of Ecology*, 93(5), 879–889.
  https://doi.org/10.1111/j.1365-2745.2005.01030.x
- 635 Santiago, L. S., Wright, S. J., Harms, K. E., Yavitt, J. B., Korine, C., Garcia, M. N., & Turner, B.
- 636 L. (2012). Tropical tree seedling growth responses to nitrogen, phosphorus and potassium
- 637 addition. Journal of Ecology, 100(2), 309–316. https://doi.org/10.1111/j.1365-
- 638 2745.2011.01904.x
- 639 Stan Development Team. (2017). *Prior Choice Recommendations*. Stan Wiki.
- 640 https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations
- 641 Stan Development Team. (2020). *RStan: the R interface to Stan* (2.21.2) [Computer software].
  642 http://mc-stan.org/
- 643 Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.
- 644 Swenson, N. G., Worthy, S. J., Eubanks, D., Iida, Y., Monks, L., Petprakob, K., Rubio, V. E.,
- 645 Staiger, K., & Zambrano, J. (2020). A reframing of trait–demographic rate analyses for

646 ecology and evolutionary biology. *International Journal of Plant Sciences*, 181(1), 33–

647 43. https://doi.org/10.1086/706189

648 Umaña, M. N., Condit, R., Pérez, R., Turner, B. L., Wright, S. J., & Comita, L. S. (2021). Shifts

649 in taxonomic and functional composition of trees along rainfall and phosphorus gradients

650 in central Panama. Journal of Ecology, 109(1), 51–61. https://doi.org/10.1111/1365-

651 2745.13442

- Umaña, M. N., & Swenson, N. G. (2019). Intraspecific variation in traits and tree growth along
  an elevational gradient in a subtropical forest. *Oecologia*, *191*(1), 153–164.
- 654 https://doi.org/10.1007/s00442-019-04453-6
- Umaña, M. N., Zhang, C., Cao, M., Lin, L., & Swenson, N. G. (2017). A core-transient
- 656 framework for trait-based community ecology: an example from a tropical tree seedling
  657 community. *Ecology Letters*. https://doi.org/10.1111/ELE.12760
- 658 Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T., & Gelman, A.
- 659 (2020). *loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models* (R
  660 package version 2.4.1) [Computer software]. https://mc-stan.org/loo/
- 661 Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-
- one-out cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413–1432.
- 663 https://doi.org/10.1007/s11222-016-9696-4
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007).
- Let the concept of trait be functional! *Oikos*, *116*(5), 882–892.
- 666 https://doi.org/10.1111/j.0030-1299.2007.15559.x
- 667 Visser, M. D., Bruijning, M., Wright, S. J., Muller-Landau, H. C., Jongejans, E., Comita, L. S.,
- 668 & de Kroon, H. (2016). Functional traits as predictors of vital rates across the life cycle

- of tropical trees. *Functional Ecology*, *30*(2), 168–180. https://doi.org/10.1111/13652435.12621
- Walters, M. B., & Reich, P. B. (1996). Are shade tolerance, survival, and growth linked? Low
- 672 light and nitrogen effects on hardwood seedlings. *Ecology*, 77(3), 841–853.
- 673 https://doi.org/10.2307/2265505
- 674 Weiher, E., Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999).
- 675 Challenging Theophrastus: A common core list of plant traits for functional ecology.
  676 *Journal of Vegetation Science*, *10*(5), 609–620. https://doi.org/10.2307/3237076
- 677 Weissflog, A., Markesteijn, L., Lewis, O. T., Comita, L. S., & Engelbrecht, B. M. J. (2018).
- 678 Contrasting patterns of insect herbivory and predation pressure across a tropical rainfall
  679 gradient. *Biotropica*, 50(2), 302–311. https://doi.org/10.1111/btp.12513
- 680 Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological
- 681 strategies: some leading dimensions of variation between species. *Annual Review of*
- 682 *Ecology and Systematics*, *33*(1), 125–159.
- 683 https://doi.org/10.1146/annurev.ecolsys.33.010802.150452
- Worthy, S. J., Laughlin, D. C., Zambrano, J., Umaña, M. N., Zhang, C., Lin, L., Cao, M., &
- 685 Swenson, N. G. (2020). Alternative designs and tropical tree seedling growth
- 686 performance landscapes. *Ecology*, e03007. https://doi.org/10.1002/ecy.3007
- Worthy, S. J., & Swenson, N. G. (2019). Functional perspectives on tropical tree demography
  and forest dynamics. *Ecological Processes*, 8(1), 1. https://doi.org/10.1186/s13717-0180154-4
- 690 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-
- 691 Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P.

- 692 K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R.
- 693 (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827.
- 694 https://doi.org/10.1038/nature02403
- 695 Wright, I. J., & Westoby, M. (2002). Leaves at low versus high rainfall: coordination of
- 696 structure, lifespan and physiology. *The New Phytologist*, 155(3), 403–416.
- 697 https://doi.org/10.1046/j.1469-8137.2002.00479.x
- 698 Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R.,
- Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P.,
- 700 Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits
- and the growth-mortality trade-off in tropical trees. *Ecology*, *91*(12), 3664–3674.
- 702 https://doi.org/10.1890/09-2335.1
- 703 Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. L., Tanner, E. V. J., Sayer, E. J., Santiago,
- 704 L. S., Kaspari, M., Hedin, L. O., Harms, K. E., Garcia, M. N., & Corre, M. D. (2011).
- 705 Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production
- 706 in a lowland tropical forest. *Ecology*, 92(8), 1616–1625. https://doi.org/10.1890/10-
- 707 1558.1
- Yang, J., Cao, M., & Swenson, N. G. (2018). Why functional traits do not predict tree

demographic rates. *Trends in Ecology & Evolution*, *33*(5), 326–336.

- 710 https://doi.org/10.1016/j.tree.2018.03.003
- 711 Yang, J., Song, X., Zambrano, J., Chen, Y., Cao, M., Deng, X., Zhang, W., Yang, X., Zhang, G.,
- 712 Tang, Y., & Swenson, N. G. (2021). Intraspecific variation in tree growth responses to
- neighbourhood composition and seasonal drought in a tropical forest. *The Journal of*
- 714 *Ecology*, *109*(1), 26–37. https://doi.org/10.1111/1365-2745.13439

715 Z	Zalamea, P0	C., Turner	, B. L.	, Winter, K	, Jones, F	. A., S	Sarmiento,	С.,	& Dalling, J.	W.	(2016).
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- 716
   Seedling growth responses to phosphorus reflect adult distribution patterns of tropical
- 717 trees. *The New Phytologist*, 212(2), 400–408. https://doi.org/10.1111/nph.14045

719	Tables and Figures	
720		
721	Table 1	
722	Expected predictions of directionality of growth and mortality rates in seedlings and six	
723	functional traits. Shown are both the overall relationship ( <i>i.e.</i> , averaged across sites) and how the	
724	strength of the relationship is expected to change going form low to high resource environments.	
725	'-' indicates an expected negative relationship and '+' indicates an expected positive	
726	relationship. A representative graphical depiction of these relationships is shown in Figure 1.	
727		
	Growth Mortality	

			1101 tunty			
Trait	Overall relationship	Change from low to high resources	Overall relationship	Change from low to high resources		
Wood density	_	_	_	+		
LMA	_	_	_	+		
Leaf dry matter content	_	_	_	+		
Max height	_	_	+	_		
Seed mass	_	_	_	+		
Leaf area	_	_	+	-		

# 730 **Table 2**

Comparisons of models where trait-rate relationships were either held constant across sites ('not variable across sites') or allowed to vary across sites ('variable across sites') for functional traits and separate growth and mortality models. LOOIC is the leave-one-out information criterion, and lower values indicate better model fit.  $\Delta$ LOOIC is the difference in LOOIC values between the model where trait-rate relationships varied across sites compared to a model where trait-rate relationships were fixed across sites. Values in bold indicate  $\Delta$ LOOIC values < -2, where the model with variable trait-rate relationships was the better fit.



Vital rate	Trait	Not variable across sites	Variable across sites	ΔLOOIC
		LOOIC (Model 1)	LOOIC (Model 2)	
Growth	Wood density	26779.84	26749.18	-30.66
	LMA	17644.97	17644.65	-0.32
	Leaf dry matter content	17684.52	17663.03	-21.49
	Max height	17739.11	17730.37	-8.74
	Seed mass	23333.84	23327.05	-6.79
	Leaf area	17684.58	17673.17	-11.41
Mortality	Wood density	14099.40	14092.81	-6.59
	LMA	7927.00	7927.01	0.01
	Leaf dry matter content	7965.31	7953.73	-11.58
	Max height	8028.38	8021.09	-7.29
	Seed mass	12746.35	12737.86	-8.49
	Leaf area	7971.50	7970.46	-1.04

#### 740 **Table 3**

741 Comparisons of models of how dry season severity (Model 3) and soil phosphorus (Model 4)

explain variation in trait-rate relationships for functional traits and growth and mortality models.

743 The 'Dry season severity' and 'Soil phosphorus' models contain each environmental factor as a

single covariate, while the intercept only model contains no environmental covariates (Model 2).

745 LOOIC is the leave-one-out information criterion, and lower values indicate better model fit.

746  $\Delta$ LOOIC is the difference in LOOIC values between each model and the intercept only model.

747 Values in bold indicate  $\Delta$ LOOIC values < -2 where using dry season severity or soil phosphorus

as a covariate improved model fit compared to the intercept only model.

749

Vital rate	Trait	Intercept	Dry season	Dry season	Soil	Soil
		only	severity	severity	phosphorus	phosphorus
		LOOIC	LOOIC	ΔLOOIC	LOOIC	ΔLOOIC
Growth	Wood density	-15.38	-15.85	-0.47	-13.23	2.15
	LMA	-23.30	-20.50	2.80	-21.35	1.95
Leaf di	ry matter content	-14.65	-13.47	1.18	-15.65	-1.00
	Max height	-19.22	-18.76	0.46	-16.90	2.32
	Seed mass	-18.86	-17.32	1.54	-18.48	0.38
	Leaf area	-19.62	-18.74	0.88	-18.14	1.48
Mortality	Wood density	-0.02	-1.05	-1.03	-6.80	-6.78
	LMA	-4.56	-1.07	3.49	0.69	5.25
Leaf di	ry matter content	4.76	7.46	2.70	8.00	3.24
	Max height	2.84	4.48	1.64	-0.02	-2.86
	Seed mass	8.01	10.58	2.57	10.81	2.80
	Leaf area	-1.76	0.74	2.5	-3.02	-1.26

750

753 Conceptual diagram showing how (a) growth rates and (b) mortality rates may vary based on 754 trait values and how these relationships may interact depending on resource availability. Both 755 panels show expected relationships for a trait assumed to be negatively related to growth and 756 mortality. For traits positively related to growth and mortality, we would expect opposite 757 relationships (not shown). Insets show the relationships between growth and mortality rates and a 758 hypothetical trait in both low resource (red solid line) and high resource (blue dashed line) 759 environments. The corresponding slopes of these lines are displayed on the larger plot, with 760 hypothetical 95% credible intervals. The solid black line shows the hypothetical relationship 761 between the slope of trait-rate relationships going from low to high resource environments. The 762 dashed line shows where the trait-rate relationship is 0.



764

- 766 Map of study area showing the eight sites across the Isthmus of Panama containing seedling
- plots, along with shading indicating dry season severity, with redder shades showing more
- intense dry seasons compared to bluer shades. Color coding of sites corresponds to legends in
- Figures 4 and 5.





772

- Across site trait-rate relationships for growth (a, top row) and mortality (b, bottom row). The
- black lines show the mean posterior slope estimate, and the shaded regions indicate the 95%
- credible interval (CI), with the slope estimates and 95% CI also provided as a text inset.



778 779

781 Variation of trait-growth rate relationships at eight sites with different environmental conditions. 782 The top row shows for each functional trait the relationship to growth rates for each site (colors 783 with the 95% credible interval shaded). The second and third rows show the mean trait-growth 784 slope for each site (circles, with 95% credible interval) plotted against site-level long-term dry 785 season severity (1961-1990 average) and soil phosphorus (log transformed). If the intercept only 786 model was the best fit model compared to models with either dry season severity or soil 787 phosphorus as covariates, the estimated slope is shown as a dashed line with the 95% credible 788 interval in light grey. The light grey horizontal line shows where the trait-growth relationship is 789 equal to 0.



791 792

794 Variation of trait-mortality rate relationships at eight individual sites with different 795 environmental conditions. The top row shows for each functional trait the relationship to 796 mortality rates for each site (colors with the 95% credible interval shaded). The second and third 797 rows show the mean trait-mortality slope for each site (circles, with 95% credible interval) 798 plotted against site-level long-term dry season severity (1961-1990 average) and soil phosphorus 799 (log transformed). If models with either dry season severity or soil phosphorus was the best fit 800 model, the estimated slope is shown as a filled black line and the corresponding 95% credible 801 interval is filled as dark grey. Otherwise, the estimated slope is shown as a dashed line with the 802 95% credible interval in light grey. The light grey horizontal line shows where the trait-mortality 803 relationship is equal to 0.



806

# 807 Supporting Information

# **Table S1**

- 810 Mean and standard deviations of six functional traits used in standardizing trait values in in
- 811 growth and mortality models.

Vital	Trait	Mean	Standard Deviation
rate			
Growth	Wood density	0.584	0.126
	LMA (log transformed)	4.152	0.249
	Leaf dry matter content (log		
	transformed)	-1.114	0.206
	Max height	16.9	8.5
	Seed mass (log transformed)	-2.761	2.130
	Leaf area (log transformed)	4.465	0.944
Mortality	Wood density	0.574	0.130
	LMA (log transformed)	4.139	0.246
	Leaf dry matter content (log		
	transformed)	-1.127	0.207
	Max height	17.5	9.0
	Seed mass (log transformed)	-2.657	2.174
	Leaf area (log transformed)	4.476	0.919

## 814 **Table S2**

815 Slope estimates of relationship between variation in the strength of trait-rate relationships and

816 dry season severity and soil phosphorus for growth and mortality models and for each trait. Mean

817 is the mean posterior estimate, and 2.5% and 97.5% show the 95% credible interval range. Trait

818 values were standardized to mean = 0 and SD = 1 prior to model fitting.

- 819
- 820

		Dry season severity				l Phosphor	us
Vital rate	Trait	Mean	2.5%	97.5%	Mean	2.5%	97.5%
Growth	Wood density	0.039	-0.027	0.102	-0.014	-0.081	0.054
	LMA	-0.002	-0.057	0.049	0.022	-0.030	0.077
	Leaf dry matter content	-0.030	-0.098	0.035	0.052	-0.010	0.116
	Max height	-0.030	-0.087	0.027	0.004	-0.060	0.064
	Seed mass	-0.016	-0.075	0.041	0.030	-0.028	0.086
	Leaf area	-0.027	-0.083	0.029	0.026	-0.032	0.089
Mortality	Wood density	0.092	-0.084	0.256	-0.141	-0.278	0.007
	LMA	0.015	-0.159	0.195	-0.025	-0.225	0.160
	Leaf dry matter content	0.008	-0.254	0.268	-0.047	-0.329	0.244
	Max height	-0.085	-0.320	0.146	0.151	-0.033	0.338
	Seed mass	0.044	-0.283	0.366	0.046	-0.276	0.377
	Leaf area	-0.019	-0.201	0.174	0.097	-0.066	0.257

#### 823 **Figure S1**

- 824 Correlation matrix for six functional traits included in this study. Traits include Wood density
- 825 ('wood dens',  $g / cm^3$ , 247 species), leaf mass per unit area ('lma',  $g / m^2$ , 184 species, log
- transformed), leaf dry matter content (leaf\_dmc, g / g, 184 species, log transformed), maximum
- height ('height\_max', m, 186 species), seed mass ('seed\_mass', g, 180 species, log transformed),
- 828 and leaf area ('leaf\_area', cm<sup>2</sup>, 184 species, log transformed). The upper triangle shows
- 829 estimated Pearson's correlation coefficients with asterisks indicating P < 0.05. The diagonal
- 830 shows a frequency histogram of the trait values in blue. The lower diagonal shows a scatter plot
- 831 of each trait plotted against each other, with a linear line of best fit shown in red.

