Functional Ecology

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

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Competing Interests Statement

The authors declare no competing interests.

Author Contributions

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

Data availability

Data and model code deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.mkkwh713s, (Browne et al., 2022)

Abstract

1. A fundamental assumption of functional ecology is that functional traits are related to interspecific variation in performance. However, the relationship between functional traits and performance is often weak or uncertain, especially for plants. A potential explanation for this 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-rate relationships across environmental gradients.

2. In this study, we examined trait-rate relationships for six functional traits (seed mass, wood density, maximum height, leaf mass per area, leaf area, and leaf dry matter content) using long-term data on seedling growth and survival of woody plant species from eight

forest sites spanning a pronounced precipitation and soil phosphorus gradient in central Panama.

3. For all traits considered except for leaf mass per area-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 relationships showed no overall trend but displayed wide site-to-site variation. In a small subset of cases, variation in trait-rate relationships were explained by soil phosphorus availability.

4. Our results demonstrate that environmental gradients have the potential to influence how functional traits are related to growth and mortality rates, though much variation remains to be explained. Accounting for site-to-site variation may help resolve a fundamental issue in trait-based ecology - that traits are often weakly related to performance - and improve the utility of functional traits for explaining key ecological and evolutionary processes.

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

Resumen

Una suposición fundamental de la ecología funcional es que los rasgos funcionales están relacionados con la variación interespecífica del rendimiento. Sin embargo, la relación entre los rasgos funcionales y el rendimiento es a menudo débil o incierta, especialmente para las plantas. Una posible explicación de esta inconsistencia es que la relación entre los rasgos funcionales y las tasas vitales (por ejemplo, el crecimiento y la mortalidad) depende de las condiciones ambientales locales, lo que llevaría a una variación en las relaciones entre rasgos y tasas a través de los gradientes ambientales. En este estudio, examinamos las relaciones rasgo-tasa para seis rasgos funcionales (masa de la semilla, densidad de madera, altura máxima, masa de hoja por área, área de hoja y contenido de materia seca de hoja) utilizando datos a largo plazo sobre el crecimiento y la supervivencia de las plántulas leñosas de ocho sitios que abarcan un pronunciado gradiente de precipitación y fósforo del suelo en el centro de Panamá. Para todos los rasgos considerados, excepto para las relaciones masa foliar por área-mortalidad, masa foliar por área-crecimiento, y área foliar-mortalidad, encontramos una amplia variación en la fuerza de las relaciones rasgo-tasa entre sitios. Para algunos rasgos, las relaciones rasgo-tasa no mostraron ninguna tendencia general, pero sí una amplia variación entre lugares. En unos casos, la variación en las relaciones entre rasgos y tasas se explicó por la disponibilidad de fósforo en el suelo. Nuestros resultados demuestran que los gradientes ambientales pueden influir la relación de los rasgos funcionales con las tasas de crecimiento y mortalidad, aunque queda mucha variación por explicar. Tener en cuenta la variación entre lugares puede ayudar a resolver un problema fundamental en la ecología basada en los rasgos -que los rasgos suelen estar débilmente relacionados con el rendimiento- y mejorar la utilidad de los rasgos funcionales para explicar procesos ecológicos y evolutivos clave.

Introduction

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

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

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

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

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

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

Materials and Methods

Study area and seedling censuses

This study was conducted in eight 1-ha plots in seasonally moist tropical forests across the Isthmus of Panama (Fig. 2). These plots span a relatively short 65-km gradient, where mean annual precipitation ranges from ~3,200 mm to ~1,600 mm. Plant-available soil phosphorus 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 established from September-December 2013, where within each 1-m^2 plot, all woody seedlings ≥ 200 mm in height and < 1 cm DBH (diameter at 1.3m above ground) were tagged, identified, and measured following Comita *et al.* (2007). Seedling plots were re-censused annually near the beginning of the annual dry season (November–February). The maximum stem height of all marked seedlings was measured, and all seedlings were evaluated whether they were alive or dead. Any new seedlings that recruited into the size criterion (≥ 200 mm height) were entered into the census. Seedlings without a definitive species identification (n = 519 individuals) and lianas were excluded from analyses. Due to limited access, one site, Oleoducto, in 2019 or 2020, and another site, Panamá Pacifico, in 2018, were not censused. The last census included in this study occurred in 2021, for a total of 7 annual census intervals. The overall dataset, before filtering based on trait availability, included 28,303 observations of 9,267 individuals belonging to 358 tree species. The research was conducted in Panama under permits from the Ministry of Environment (MiAmbiente) and the Agencia Panama Pacífico (APP).

Trait data

We focused on six widely available, species-level traits from Wright *et al.* (2010) that are related 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, 184 species), maximum height (m, 186 species), seed mass (g, 180 species), and leaf area (cm^2, 184 species. A full description of the methods of trait data collection are available in Wright *et al.* (2010). Briefly, wood density data was collected from ~5 adult individuals per species within 15 km of the Barro Colorado Island (BCI) 50-ha forest dynamics plot, which is located near the center of the rainfall gradient. Leaf traits were collected from leaves receiving indirect sunlight from six of the smallest individuals of each species at the BCI 50-ha plot. Maximum height was estimated as the mean height of the six individuals with the largest DBH in the 50-ha plot on BCI and a nearby 38.4 ha plot (King et al., 2006; Wright et al., 2010). Seed mass is the mean dry mass that includes the endosperm and embryo only, measured from 1-11 individuals and 1-139 seeds per species. Pairwise correlations among traits ranged from Pearson's $r = 0.01$ to 0.57 (Fig. S1). It is also important to note that the trait data used in this study was obtained from a single 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 trait variation across individuals, life stages and populations (Dayrell et al., 2018; Havrilla et al., 2021; Palow et al., 2012; Umaña & Swenson, 2019).

Environmental data

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

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):

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

where t_2 = time two, t_1 = time one, $Height_2$ = height at time 2, $Height_1$ = height at time 1. We used a Box-Cox transformation (lambda = 0.15) to reduce skewness and normalize the distribution of growth rates (Condit et al., 2017). This reduced the number of model divergences as well. RGR values were back-transformed to the original scale for presentation in all figures. While our choice of growth metric (relative growth rate of stem height) provides valuable information on the vertical position of the stem in the understory, which influences access to light and competitive dynamics, it fails to account for other types of growth such radial growth, biomass increase, or below ground growth. To reduce noise in growth measurements, we focused only on positive growth rates in this study, though including negative growth rates (due to stem breakage or measurement error) produced qualitatively similar results (results not shown).

In growth models, the response variable (RGR) was assumed to be Normally distributed for each individual observation *i*:

$$RGR_i \sim Normal(\hat{y}_i, \sigma)$$

In mortality models, the response variable (1 = dead, 0 = alive) was assumed to be Bernoulli distributed and adjusted to account for varying census intervals (*time*):

$$Mortality_i \sim Bernoulli\left(logit(\hat{y}_i)^{time}\right)$$

We estimated overall (*i.e.,* across sites) trait-rate relationships using a model (Model 1) where trait-rate relationships were not allowed to vary across sites:

Model 1: Trait-rates fixed across sites

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

$$\alpha 1_{spp} \sim \mathrm{Normal}(0, \sigma^2)$$

$$\alpha 2_{c,s} \sim \mathrm{Normal}(0, \sigma^2)$$

$$\alpha 3_p \sim \mathrm{Normal}(0, \sigma^2)$$

where $\hat{y}_i$ is either Box-cox-transformed RGR or mortality status (1 = dead, 0 = alive) for 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 random effect for each 1x1 m seedling plot p, $\beta 1$ estimates the effect of height at the previous 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. We log-transformed and standardized initial seedling height within each species such that mean = 0 and standard deviation = 1 to account for differences in mean seedling height across species.

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:

Model 2: Trait-rates variable across sites

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

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

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

RGR_i or $Mortality_i$, depending on whether it was a growth or mortality model. If the LOOIC score was lower for any model where β_{trait} was allowed to vary across sites compared to the model where $\beta 2$ was fixed across sites, we considered this as evidence that trait-rate relationships varied across sites.

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

Model 3: DSS as predictor

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

Model 4: Soil Phosphorus as predictor

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

All models were fit using Stan (Carpenter et al., 2017) using the ‘rstan’ package vs. 2.21.2 (Stan Development Team, 2020). Following the Stan prior choice recommendations (Stan

Development Team, 2017), we used weakly-informative priors of $\text{Half-Normal}(0,1)$ for variance parameters, $\text{Student}_t(5, 0, 2.5)$ for coefficients in mortality models, and $\text{Normal}(0,1)$ 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 $\text{Half-Normal}(0.04, 0.05)$ for the variance parameter in the second level regression of growth models linking dry season severity or soil phosphorus to growth-trait variation across sites. Using a weakly-informative prior produced qualitatively similar results. For each model, we ran four independent chains for 3,000 iterations, with 1,500 iterations of burn in. We checked chain convergence visually and by ensuring the potential scale reduction factor statistic ('rhat') was < 1.10 (Kéry, 2010). We calculated LOOIC scores using the 'loo' R package v. 2.4.1 (Vehtari et al., 2020).

Results

(1) Overall trait-rate relationships across sites

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

(2) Variation in trait-rate relationships across sites

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

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

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

Variation in trait-growth relationships for wood density, leaf dry matter content, LMA, maximum height, seed mass, and leaf area was not explained by variation in either dry season 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).

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).

Discussion

The relationships between functional traits and vital rates in plants are often weak or inconsistent, and the underlying drivers of this pattern are currently unresolved (Paine et al., 2015). In this study, we found widespread evidence that trait-rate relationships varied for seedlings across eight sites along the Isthmus of Panama for a set of common functional traits related to major axes of life history variation. We found limited support for the hypothesis that local resource availability drives variation in trait-rate relationships. Environmental variables related to water and soil nutrient availability failed to explain site-to-site variation in trait-rate relationships for the majority of cases. In a small subset of cases, soil phosphorus levels explained variation in trait-mortality relationships. These results demonstrate that site-level 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 when these factors are not considered.

(1) Overall trait-rate relationships across sites

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

(2) Variation in trait-rate relationships across sites

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

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

(3) Dry season severity and soil phosphorus predicting variation in trait-rate relationships 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).

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

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

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Supporting Information

Table S1 - Mean and standard deviations of functional traits

Table S2 - Slope estimates of trait-rate relationships and dry season severity and soil phosphorus

Figure S1 – Pairwise correlations of functional traits

Tables and Figures

Table 1

Expected predictions of directionality of growth and mortality rates in seedlings and six functional traits. Shown are both the overall relationship (*i.e.*, averaged across sites) and how the strength of the relationship is expected to change going form low to high resource environments. '–' indicates an expected negative relationship and '+' indicates an expected positive relationship. A representative graphical depiction of these relationships is shown in Figure 1.

	Growth		**Mortality**	
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	–	–	+	–

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. ΔLOOIC 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 ΔLOOIC values < -2, where the model with variable trait-rate relationships was the better fit.

Vital rate	**Trait**	**Not variable across sites LOOIC (Model 1)**	**Variable across sites LOOIC (Model 2)**	**ΔLOOIC**
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

Table 3

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. 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). LOOIC is the leave-one-out information criterion, and lower values indicate better model fit. ΔLOOIC is the difference in LOOIC values between each model and the intercept only model. Values in bold indicate ΔLOOIC values < -2 where using dry season severity or soil phosphorus as a covariate improved model fit compared to the intercept only model.

Vital rate	**Trait**	**Intercept only LOOIC**	**Dry season severity LOOIC**	**Dry season severity ΔLOOIC**	**Soil phosphorus LOOIC**	**Soil phosphorus 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 dry 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 dry 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

Figure 1

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

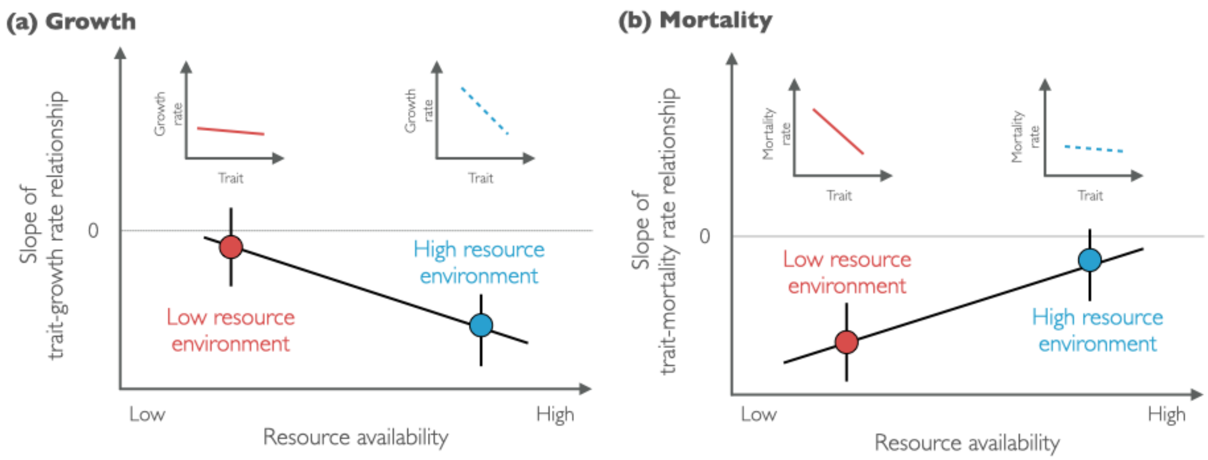


Figure 2

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.

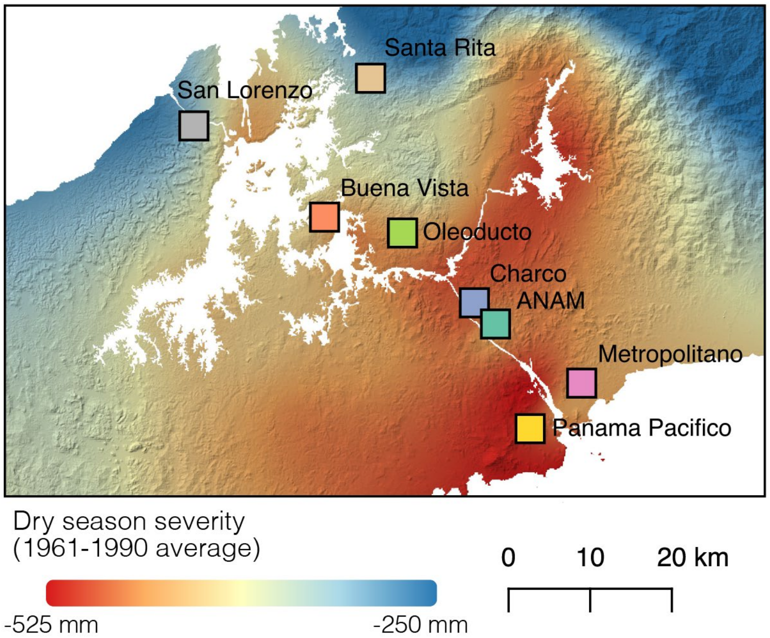
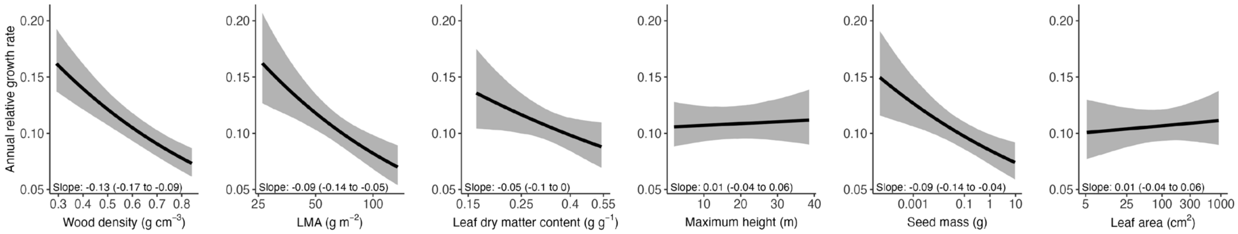


Figure 3

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.

(a) Growth



(b) Mortality

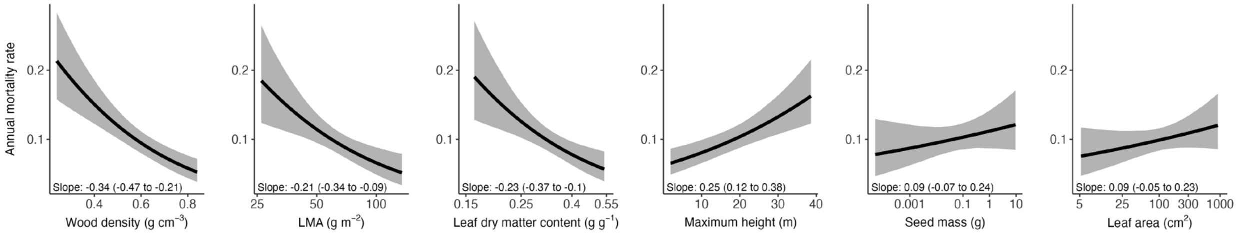


Figure 4

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

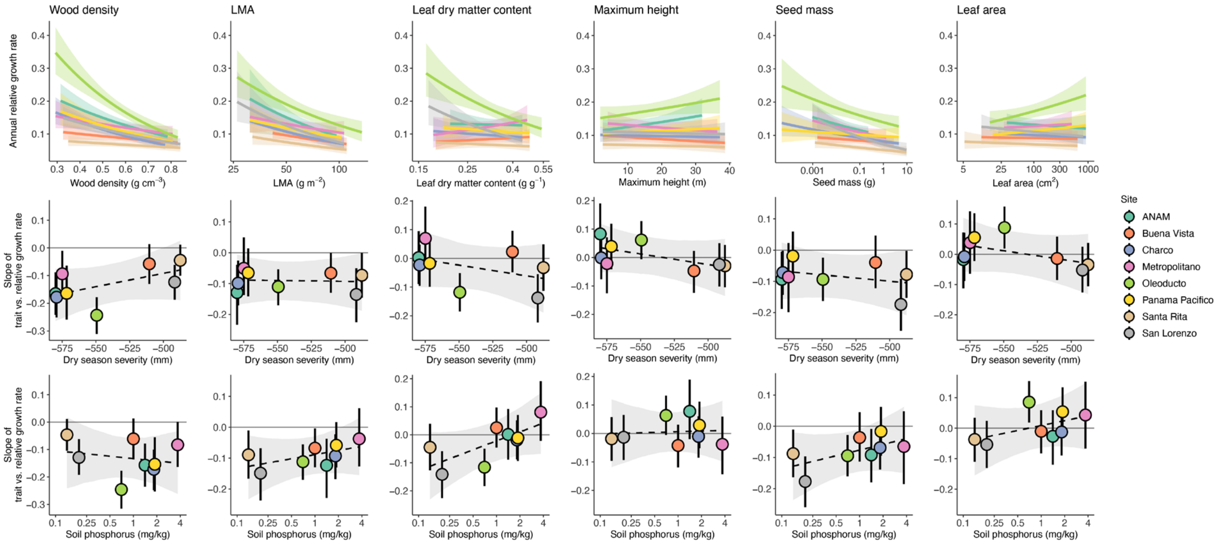


Figure 5

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