Relating leaf traits to seedling performance in a tropical forest: building a hierarchical functional framework

María Natalia Umaña [ID],[1,6] Nathan G. Swenson,[2] Philippe Marchand [ID],[3] Min Cao,[4] Luxiang Lin [ID],[4] and Caicai Zhang[5]

[1]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48019 USA*
[2]*Department of Biological Sciences, University of Notre Dame, South Bend, Indiana 46556 USA*
[3]*Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Quebec J9X 5E4 Canada*
[4]*CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, Yunnan, China*
[5]*Institute of Eastern-Himalaya Biodiversity Research, Dali University, Dali, Yunnan, China*

Abstract. Trait-based approaches have been extensively used in community ecology to provide a mechanistic understanding of the drivers of community assembly. However, a foundational assumption of the trait framework, traits relate to performance, has been mainly examined through univariate relationships that simplify the complex phenotypic integration of organisms. We evaluate a conceptual framework in which traits are organized hierarchically combining trait information at the individual- and species-level from biomass allocation and organ-level traits. We focus on photosynthetic traits and predict that the positive effects of increasing plant leaf mass on growth depend on species-level leaf traits. We modeled growth data on more than 1,500 seedlings from 97 seedling species from a tropical forest in China. We found that seedling growth increases with allocation to leaves (high leaf area ratio and leaf mass fraction) and this effect is accentuated for species with high specific leaf area and leaf area. Also, we found that light has a significant effect on growth, and this effect is additive with leaf allocation traits. Our work offers an approach to gain further understanding of the effects of traits on the whole plant-level growth via a hierarchical framework including organ-level and biomass allocation traits at species and individual levels.

Key words: biomass allocation traits; canopy openness; China; leaf area; leaf thickness; relative growth rates; seedlings; specific leaf area.

Introduction

Tropical forests harbor the majority of Earth's tree diversity, yet ecologists still have a limited understanding of forest dynamics and factors determining community structure in these regions. A promising approach for predicting changes in community structure and dynamics is the use of functional traits: morphological and physiological features that have an impact on organisms' performance (growth, survival, reproduction; Arnold 1983, McGill et al. 2006, Violle et al. 2007). However, previous analytical approaches examining the trait–performance relationship have been largely focused on examining univariate relationships in which tree performance is predicted from individual traits (Poorter et al. 2008, Wright et al. 2010, Paine et al. 2015), but traits typically work in combination with other traits to achieve particular functions (Olson and Miller 1958). Thus, the univariate

approach is an inaccurate representation of organismal function (Berg 1960, Arnold 1983, Armbruster et al. 2014, Laughlin and Messier 2015). It is, therefore, important to develop models that integrate the effect of different traits to drive performance (Laughlin and Messier 2015, Yang et al. 2018).

Among all plant traits, leaf traits are the best studied (Reich et al. 1999, Bonser 2006, Poorter 2009); however, surprisingly, their ability to predict plant demographic rates has been generally modest (Sterck et al. 2006, Poorter et al. 2008, Adler et al. 2014, Paine et al. 2015). Leaf traits are mostly responsible for carrying out photosynthesis that results in carbon gain for the plant and, therefore, should contribute to increasing plant size (i.e., plant growth). While this prediction has been corroborated by previous studies showing that leaf traits such as specific leaf area relate positively to maximum photosynthetic rates (Reich et al. 1999, Wright et al. 2004) and tree growth (Sterck et al. 2006), the effects of these organ-level leaf traits on carbon gain and plant demography have been rarely scaled-up at the whole organism level (Sterck

et al. 2011). The total carbon gain of a given tree does not only depend on the photosynthetic capacity of individual leaves, but also on the total biomass/area allocated to photosynthetic tissues (foliage; Poorter and Remkes 1990, Garnier 1991, Niklas and Enquist 2001, Niinemets et al. 2002). For instance, species with high specific leaf area (SLA, leaf area divided by dry mass) that allocate high biomass to photosynthetic tissues should obtain higher total carbon than a species with the same SLA, but that allocate less biomass to photosynthetic tissues. The combined effect of different traits (biomass allocation and organ-level leaf traits) could lead to important variations in total carbon gain and tree demography that should be considered when studying trait–performance relationships (Yang et al. 2018).

The integrated effects of different traits on tree performance have been often represented through a hierarchical framework in which traits at low levels of organization have effects on traits at higher levels of organization that in turn have effects on performance (Arnold 1983, Marks and Lechowicz 2006, Marks 2007). This framework could be applied to build a hierarchical arrangement of trait interactions in which the effect of traits at lower organizational levels (i.e., organ-level traits, such as SLA) is scaled up at the whole organism level via another set of traits (i.e., biomass allocation traits) and, ultimately, to performance. In other words, theory on carbon economy states that relative growth rate depends on the biomass allocated to tissues for capturing carbon (Evans 1972, Poorter 1989, Garnier 1991). As biomass allocation traits tend to be quite plastic in response to environmental variation and show a high variation within species (Umaña et al. 2018), the growth–allocation trait relationships should be defined at the individual level. These growth–allocation trait relationships may, in turn, vary by species depending on whether species have conservative or acquisitive traits for resource acquisition (Lambers and Poorter 1992, Poorter and van der Werf 1998). This species-level variation along the acquisitive-conservative spectrum for carbon processing is defined by organ-level leaf economics traits (Reich et al. 1999, Wright et al. 2004) that tend to be more variable across species than within species (Messier et al. 2010, 2017b, Umaña et al. 2018). This multilevel organization depicting the trait effects on performance not only represents a more realistic approach to understand the trait relationships in which a distinction in different organization levels (species and individuals) and trait types is explicitly considered, but also could explain the existence of the diverse range of phenotypes found in tropical regions and that seem to represent alternative ecological strategies (i.e., combinations of different traits such as biomass allocation and organ-level traits, that lead to equivalent performance; Laughlin et al. 2018, Umaña et al. 2020a, Worthy et al. 2020).

An additional factor that needs to be considered when modeling growth as a function of traits is the role of the environmental conditions (Grime 1979, Violle et al. 2007). Micro-environmental variation in abiotic factors has shown to have significant effects on plant demography (Blonder et al. 2018). In particular, for aboveground strategies, light availability is one of the most important resources determining plant strategies and functional diversity (Poorter and van der Werf 1998, Poorter and Rozendaal 2008, Umaña et al. 2020a). Further, for tropical forests, light in the understory is highly limiting and key for determining the successful recruitment and establishment of seedlings (Chazdon and Fetcher 1984, Denslow 1987, Umaña et al. 2020b). Therefore, predictions of plant demography should consider light heterogeneity in the understory when modeling plant growth rates as a function of functional traits.

Here, we study trait-growth relationships in a plant-level integrated framework, using a combination of organ-level and biomass allocation traits. Our model also accounts for potential effects of light heterogeneity in the understory on plant performance. To do this, we use growth data on over 1,500 seedlings from tree seedling species distributed across >200 1-m^2 plots in a tropical forest in China. All seedlings in these plots were monitored for growth for one year and collected for trait measurements at the end of the study. We paired these measurements with information on canopy openness (a proxy for light availability in the understory) that was assessed for all plots.

We hypothesize that biomass allocation to leaves will result in increased growth rates, but this effect will be magnified when species have acquisitive traits: high specific leaf area, high leaf area, or low leaf thickness (Poorter and Nagel 2000). Biomass allocation traits, unlike organ-level traits, exhibit higher variability across individuals of the same species than across species that is attributed to the ability of species to adjust their ecological strategies to maximize resource acquisition (Poorter et al. 2012, Umaña et al. 2018). Organ-level traits, on the other hand, exhibit higher variation across, than within species (Umaña et al. 2018). The heterogeneity in the degrees of trait variation between trait types is likely the result of different ecological and evolutionary constraints operating on these two types of traits (Armbruster 1991, Armbruster and Schwaegerle 1996). We propose a multi-level approach to account for this differential variation in traits by implementing a hierarchical framework. We modify a recent approach that modeled adult tree growth as a function of individual-level tree crown and leaf area index (LAI) data (LAI is a measure of the total area of leaves per unit of ground area) and species-level leaf mass per area (LMA; Yang et al. 2020). Here, we implement community-level analyses for seedlings that include individual-level biomass allocation and species-level organ-level traits. We also compare the performance of our hierarchical models with models that evaluate the interaction between species-level organ-level traits and biomass allocation (Poorter 1990, Garnier 1991). These (interaction) models, do not consider the

differential degree of variation between both types of traits and assume that biomass allocation traits are species-specific fixed values.

MATERIAL AND METHODS

Study site

The study was conducted in a seasonal tropical rainforest in Xishuangbanna, Yunnan province in China (101.340° E, 21.360° N), where we established 218 1-m² seedling plots. The site is characterized by a monsoonal climate, with distinct seasons, the dry season (November to April), and the wet season (May to October). The annual average temperature is 21°C and the annual mean rainfall is 1,493 mm, which mainly occurs in the wet season (a total of 1,256 mm, 84% of the annual average rainfall; Cao et al. 2008). Seedling plots were spaced every 10 m covering an approximate area of 2 ha. In each plot, we identified and tagged all free-standing woody seedlings with a maximum height lower than 50 cm and we monitored all individuals for growth and survival during 1 yr between April 2013 and April 2014 (Umaña et al. 2015).

Relative growth rates and trait measurements

We calculated the relative growth rate of each individual by computing the change in log-transformed height over one year. For functional traits, we collected trait data from all individuals that were monitored in the seedling plots. All seedlings were harvested at the end of the study period by excavating the soil surrounding the seedlings with a shovel. Next, we put them in plastic bags with water and transported them to the lab. Once in the lab, the seedlings were carefully cleaned, dissected, and measured for traits (additional details can be found in [Umaña et al. 2015]). The traits included biomass allocation traits (leaf area ratio and leaf mass fraction) and organ-level leaf functional traits (specific leaf area, leaf area, and leaf thickness). Leaf area ratio (LAR, cm²/g) represents the amount of leaf area per unit of plant mass (Poorter et al. 2012). Leaf mass fraction (LMF, g/g) represents the biomass organ fraction. Specific leaf area (SLA, cm/g) is a leaf economics trait that describes carbon acquisition and processing strategies in which species with high SLA are more acquisitive than species with low SLA (Wright et al. 2004, Díaz et al. 2016). Leaf area (LA, cm²) reflects the photosynthetic area displayed to capture light (Poorter and Rozendaal 2008) and leaf thickness is a mechanical trait (Th, mm) (Onoda et al. 2011). For all organ-level traits, we calculated the species average trait values and this value was used in posterior analyses. We also checked for trait correlations for biomass allocation and organ-level traits (Appendix S1: Tables S1, S2).

Light availability in the understory

To measure light conditions in the understory we took hemispherical photographs at the center of each seedling plot. The photos were taken at 1 m above the ground using a Nikon FC-E8 lens attached to a Nikon Coolpix 4500 camera (Nikon, Tokyo, Japan). All photographs were taken with uniform light conditions before sunrise between March and April 2014 and posteriorly analyzed using Gap Light Analyzer software (Frazer et al. 2000; software *available online*).[7] The analysis consisted of classifying all pixels in the photograph into two categories: sky and vegetation. After the classification, the program calculated the percentage of light in each photograph.

Analyses

To evaluate the relationship between traits and performance we constructed hierarchical Bayesian models. At the first level, we modeled the expected individual-level relative growth rate of tree i of species j in a plot p as a power function of individual-level biomass allocation traits (BAT; i.e., LAR or LMF) and canopy openness (Light; Eq. 1). We also included seedling maximum height (MH; measured per seedling) in the first level since size can affect seedling demography (Comita and Hubbell 2009). At the second level, we specified species-specific intercepts (β_0) and slopes (β_1) as linear functions of species-level organ-level leaf traits (OLT, which are SLA, LA, or leaf thickness; Eq. 2). Our multispecies approach allows us to account for between-species variation in growth that is explained by organ-level leaf traits, as well as other unexplained factors shared by individuals of the same species (via the random effects). In total, we fitted six models that considered all possible combinations of individual-level biomass allocation and species-level leaf traits

$$\log(\mathrm{RGB}_{i,j,p}) = \beta_{0,j} + \beta_{1,j} \times \mathrm{BAT}_{i,j} + \beta_2 \times \mathrm{Light}_p \\ + \beta_3 \times \mathrm{MH}_{i,j,p} + \varphi_p + \varepsilon_{i,j} \quad (1)$$

$$\beta_{n,j} = \gamma_0 + \gamma_1 \times \mathrm{OLT}_j + v_{n,j} \, (n = 0, \ 1 \text{ in Eq. 1}). \quad (2)$$

The intercept, $\beta_{0,j}$, represents the log-transformed seedling relative growth rate of species j for the community average values of BAT, Light, and MH. The slope of BAT ($\beta_{1,j}$) represents the effects of biomass allocation traits on seedling growth (RGR). The slope γ_1 between OLT and species-specific slope of BAT ($\beta_{1,j}$) represents the relationship between species-specific OLT and the slope of the RGR–BAT relationship. The slope γ_1 between OLT and species-specific intercept ($\beta_{0,j}$) represents the species-specific OLT effect on RGR at community average BAT, Light, and MH. The parameter φ_p

represents plot random effects, $v_{n,j}$ represents species random effects and $\epsilon_{i,j}$ represents individual residuals; random effects and residuals are normally distributed.

We compared the performance of our hierarchical models with models that included an interaction effect between species-level BAT and OLT (hereafter referred as to species-level interaction models) using Leave-One-Out Information Criterion (LOOIC; function loo_compare from package loo in R; Vehtari et al. 2017a). LOO uses log-likelihoods from posterior simulations of the parameter values to estimate point-wise out-of-sample prediction accuracy and determine the relative predictive performance of the model to the data. The lower LOOIC, the higher the predictive accuracy (Vehtari et al. 2017b).

We also considered another set of models that included an interacting term between biomass allocation trait (BAT) and light in the first level, instead of considering these terms as separate (additive) factors. However, these (interacting) models performed worse than the first set of models and were no longer considered for discussion (Appendix S1: Table S3).

Before the analyses, we log-transformed SLA, LA, and Th in order to reduce skewness and centered all the traits, MH, and Light (mean = 0 and standard deviation = 1) for easy interpretation and comparison. All analyses were performed using Stan via the R package rstan (R Development Core Team 2017, Stan Development Team 2020). Each model was fitted using uninformative priors (all details can be found in Data S1), four chains with 3,000 iterations, and a warm-up of 1,500 iterations. To assess parameter convergence, we used the Gelman and Rubin's convergence diagnostics (cutoff = 1.01). The code used to run the model and diagnostics are included as supporting information (Data S1 and Appendix S2).

Results

Overview

In total, we analyzed growth rates of 1,574 seedlings from 97 species. The mean seedling relative growth rate was around 0.19 cm·cm^{-1}·yr^{-1} but there was a high variation across species (Appendix S1: Fig. S1). Our data set consists of many species that were rare with less than 15 individuals per species and few common species (Appendix S1: Table S4 includes the abundances for the species used in the analyses). Also, the percentage of canopy openness in our study site ranged between 0.66 and 10.10 (coefficient of variation = 0.49, Appendix S1: Fig. S2), and this variable had a significant effect on seedling growth across all models (Table 1).

Comparing hierarchical and species-level interaction models

We compared two sets of models, the hierarchical models, which used a combination of individual-level

TABLE 1. Posterior mean of light and seedling height effects on seedling growth, 95% credible interval, and Gelman-Rubin diagnostic value (R hat).

Model and parameter	Mean	2.50%	97.50%	R hat
LAR and LA				
Height	−0.35	−0.43	−0.26	1.00
Light	0.20	0.12	0.29	1.00
LAR and SLA				
Height	−0.36	−0.45	−0.28	1.00
Light	0.21	0.12	0.29	1.00
LAR and Thickness				
Height	−0.36	−0.44	−0.27	1.00
Light	0.21	0.12	0.29	1.00
LMF and LA				
Height	−0.40	−0.49	−0.31	1.00
Light	0.19	0.11	0.27	1.00
LMF and SLA				
Height	−0.40	−0.48	−0.32	1.00
Light	0.20	0.11	0.28	1.00
LMF and Thickness				
Height	−0.41	−0.49	−0.32	1.00
Light	0.19	0.11	0.27	1.00

Notes: Light effect on seedling growth rates for all six models. Abbreviations: LA, leaf area; LAR, leaf area ratio; LMF, leaf mass fraction; SLA, specific leaf area; Thickness, leaf thickness.

and species-level trait information, and the interaction models, that used species-level trait information. Consistently, the hierarchical models outperformed the interaction models (Table 2). Below, we only describe the results of the hierarchical models.

Effects of biomass allocation on seedling growth

We found that increases in leaf mass per area (LMF) and leaf area ratio (LAR) result in higher seedling growth ($\mu\beta_1$; Fig. 1, Appendix S1: Table S5).

Effects of species-level leaf traits on seedling growth at mean biomass allocation trait

For models using leaf area (LA), we found nonsignificant effects on growth when LAR and LMF were at their mean community values (Fig. 2, Appendix S1: Table S5). For models using specific leaf area (SLA), instead, we found that species with low SLA grew slower than species with high SLA when LAR and LMF were at their mean community values (intercept; Fig. 2, Appendix S1: Table S5). For models using leaf thickness, we found nonsignificant effects on growth when LAR and LMF were at their mean community values (95% credible intervals overlapped zero).

Effects of species-level leaf traits on biomass allocation trait-growth effect

We found that the positive effect of LAR on seedling growth was significant and positively related to species-

TABLE 2. Pairwise comparisons between hierarchical models and species-level interaction models.

Traits and model type	looic	elpd_diff	se_diff
LAR-LA			
Hierarchical	6397.2	0	0
Interaction	6419.1	−11.1	4.9
LAR-SLA			
Hierarchical	6395.0	0	0
Interaction	6419.7	−13.2	4.7
LAR-Thickness			
Hierarchical	6395.8	0	0
Interaction	6420.2	−12.6	4.7
LMF-LA			
Hierarchical	6396.0	0	0
Interaction	6420.4	−11.7	4.9
LMF-SLA			
Hierarchical	6392.9	0	0
Interaction	6421.6	−14.2	4.7
LMF-Thickness			
Hierarchical	6397.9	0	0
Interaction	6420.3	−12.6	4.7

Notes: Trait codes are the same as in Table 1. The parameter looic (−2 × eldp [expected log predictive density]) is the leave-one-out cross-validation information criterion, eldp_diff is the difference in eldp for a pair of hierarchical and interaction models, se_diff is the standard error of component-wide differences of eldp between a pair of models. If elpd difference (elpd_diff) is small than 4, the difference between models is not significant. If the elpd_diff is larger than 4, then we compare the difference in standard error (se_diff). In all cases, elpd_diff for the interaction model was >2 times higher compared to se_diff.

level LA, with large-leaved species exhibiting the highest growth rates (Fig. 3, Appendix S1: Table S5). Similarly, we found that the positive effect of LMF on seedling growth was positively related to species LA and SLA with species having acquisitive traits (i.e., high LA and SLA) exhibiting the highest growth, but was only significant for SLA (Fig. 3, Appendix S1: Table S5). Species-level leaf thickness was not related to biomass allocation trait effect on seedling growth for any of the biomass allocation traits used (LAR and LMF; Fig. 3, Appendix S1: Table S5).

DISCUSSION

In this study, we implement an approach that moves beyond the univariate trait classical analytical methods to contribute to an integrated understanding of the effect of leaf traits on performance using a hierarchical framework for plant communities. We show that seedling growth results from the integrated effect of individual-level and species-level leaf traits in which increased biomass allocation to leaves and high values of SLA and LA result in high plant growth. Our findings represent a multi-level perspective on trait integration and highlight the importance of combining biomass allocation and organ-level trait information at the individual and species-level to gain further insights about

the whole plant-level strategies in species-rich tropical forests.

Increased allocation to leaves leads to high seedling growth

As predicted, we found that allocation to leaves results in high relative growth rates for tropical seedlings suggesting that the more the plants invest in photosynthetic tissues, the more the carbon gain that contributes to seedling growth. These results agree with previous findings that indicate that fast-growing plants are those that allocate more biomass to leaf tissues (Garnier 1991, Lambers and Poorter 1992). In particular, our results show that the strength of the LAR effect in growth was larger than the models with LMF and suggest that LAR is a predominant factor explaining variation in RGR. These results are concordant with the conclusions presented by Poorter (1989) who suggested that the amount of area allocated to leaves for a given dry mass is more relevant for determining plant growth than the allocation to dry weight into leaves (LMF).

Further, we found a positive and significant effect of light availability on seedling growth that agrees with previous findings on other tropical forests and highlights the importance of this resource for seedling performance (Augspurger 1984, Popma and Bongers 1988). Yet, the effect of light interacting with allocation traits did not improve the model fit, which suggests that variation in growth is better predicted by a consistent effect of leaf allocation traits that does not depend on the light conditions. Although previous studies have reported similar results in which light effects are independent of trait effects, other studies have reported an interactive effect of both factors (reviewed by Poorter and Nagel 2000). Combined, our results indicate that in our study site, light is one of the main resources limiting seedling growth, and those organisms that allocate more biomass to leaf tissues have a demographic advantage.

Species-level leaf traits relate to seedling growth

We observed that species-level leaf area and leaf thickness were not directly related to seedlings RGR (at mean community LAR and LMF), whereas species with high SLA (more acquisitive carbon processing strategies) grew faster than seedlings with low SLA. While the SLA result agrees with our predictions, the LA and thickness results do not, as we predicted that species displaying larger areas for light acquisition and lower leaf thickness should attain high seedling growth. One potential explanation for this is that LA and thickness are structural traits involved in several functions that may lead to conflicting responses to enhance growth. For example, having large leaves is beneficial for capturing light but may bring costs for mechanical support that impair performance (Niklas 1992, 1999), self-shading (Sterck and Bongers 2001), or costs in transpiration (McDonald
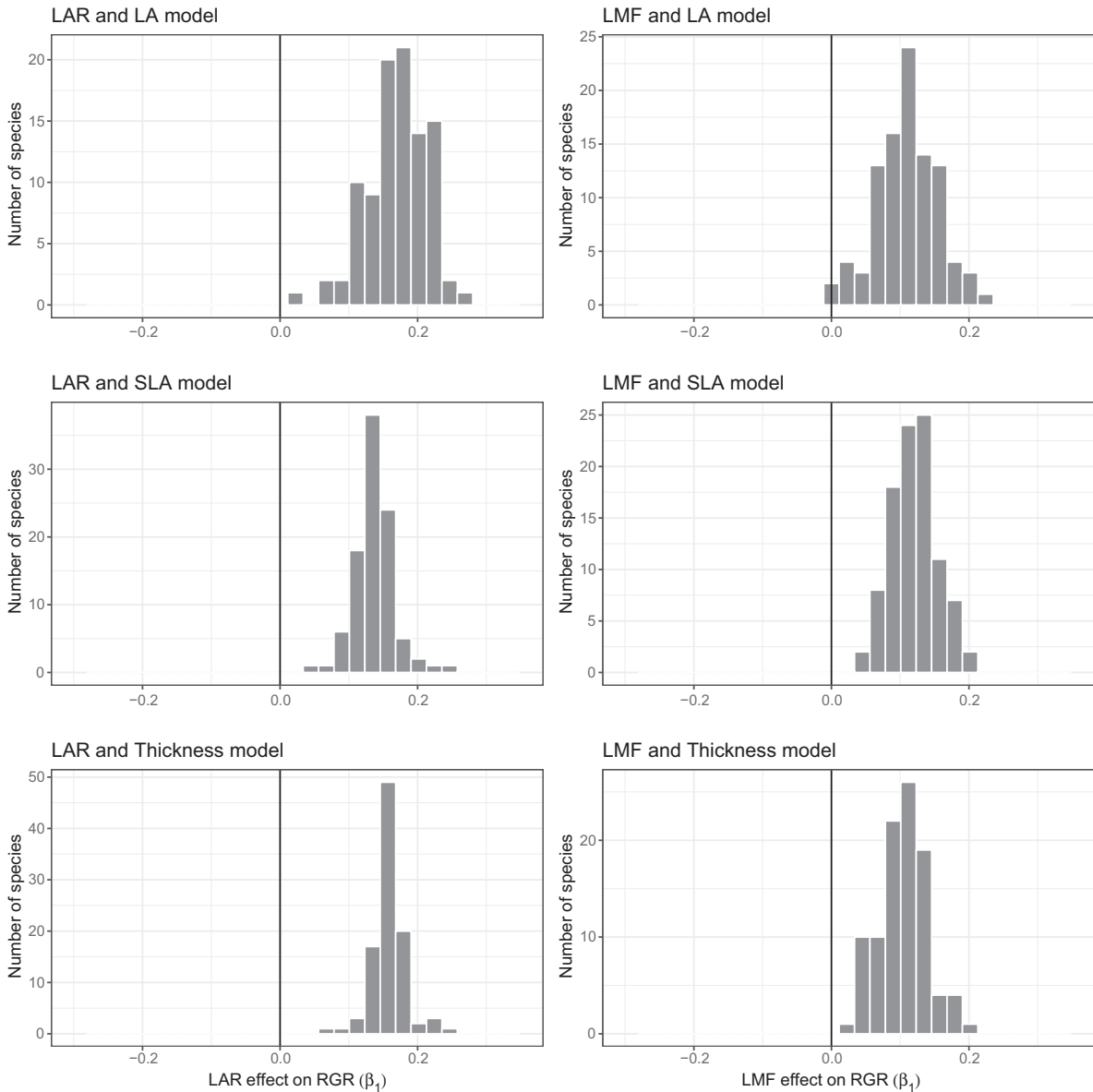
FIG. 1. Histograms of species-level posterior means of biomass allocation trait effects (β_1) on seedling relative growth rate (RGR, cm·cm^{-1}·yr^{-1}) for seedling communities in a tropical forest in China. The title in each plot corresponds to the biomass allocation trait used in the first level of the model and to the species-level organ-level trait used in the second level. Trait codes are the same as in Table 1.

et al. 2003). For leaf thickness, although leaves with thick mesophyll layers may display low photosynthetic capacity, these leaves might be more resistant to drought and herbivore damage that ultimately is advantageous for growth (Onoda et al. 2011). We suggest that different trade-offs involved in the variation of these traits may obscure their direct effect on RGR. However, as discussed below, the effects of LA were better captured via the integrated effect on biomass allocation traits. On the other hand, results for SLA were consistent with our predictions. SLA is more strongly linked to physiological functions as maximum photosynthetic rate and carbon

processing strategies than LA and Th (Wright et al. 2004) and, as such, it is expected that SLA will show stronger effects on carbon gain that is ultimately translated into seedling growth than of compared to LA or leaf thickness.

Species-level leaf traits mediate the effect of leaf allocation on growth

Consistent with our predictions we found that the positive effects of LAR and LMF on growth were magnified for species with more acquisitive traits, high LA, and
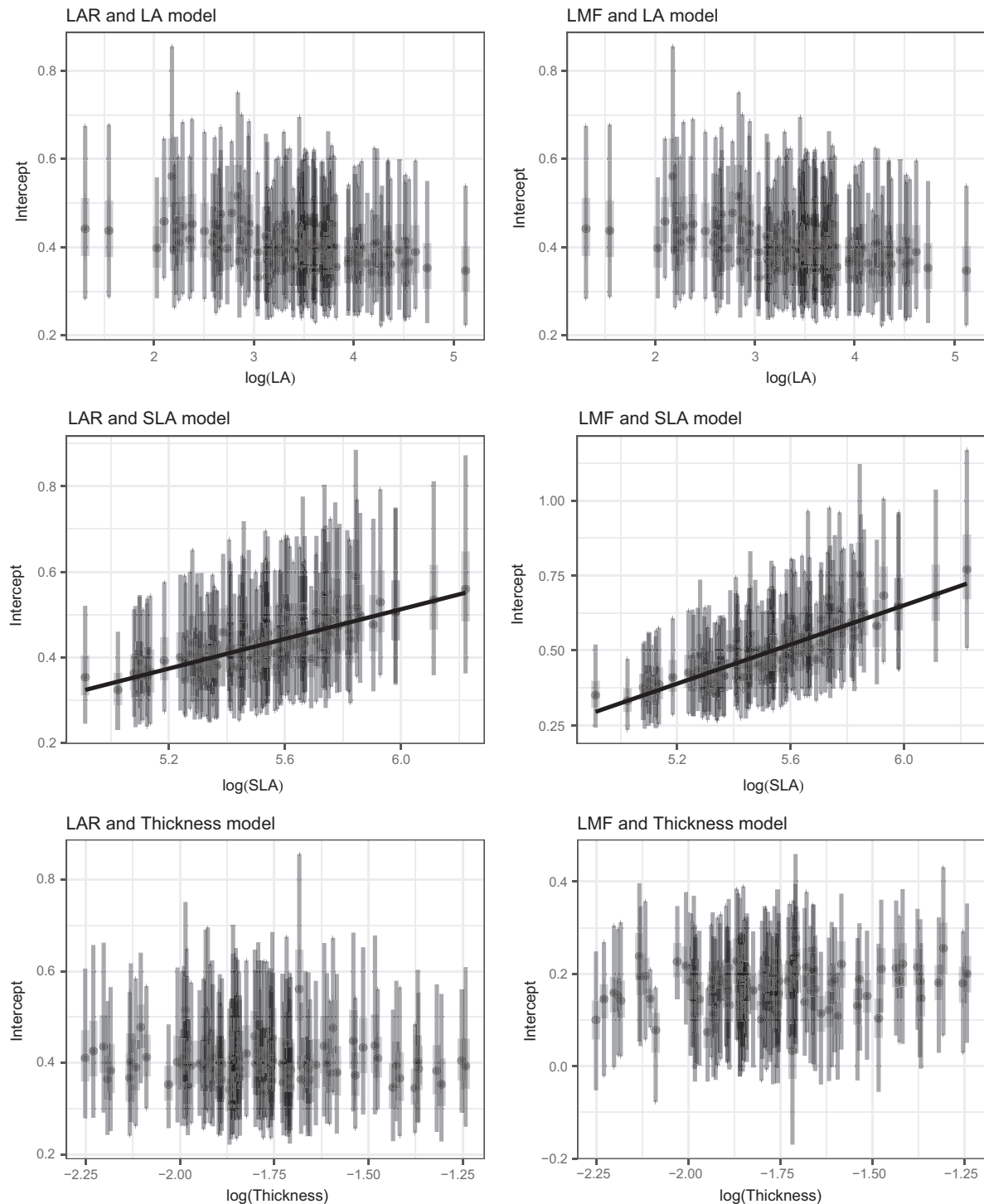
FIG. 2. Species-level leaf trait effects on seedling relative growth rate (RGR, cm·cm^{-1}·yr^{-1}) at community-mean biomass allocation trait (intercept, β_0). BAT refers to biomass allocation trait: LAR, or LMF. Black circles and gray lines indicate the means and the 95% credible intervals of the species-specific coefficients respectively. Black lines represent fitted significant relationships (95% credible intervals did not cross zero, see Appendix S1: Table S5). Trait codes are the same as in Table 1. LA was measured in cm^2, SLA in cm^2/g, and thickness in mm.
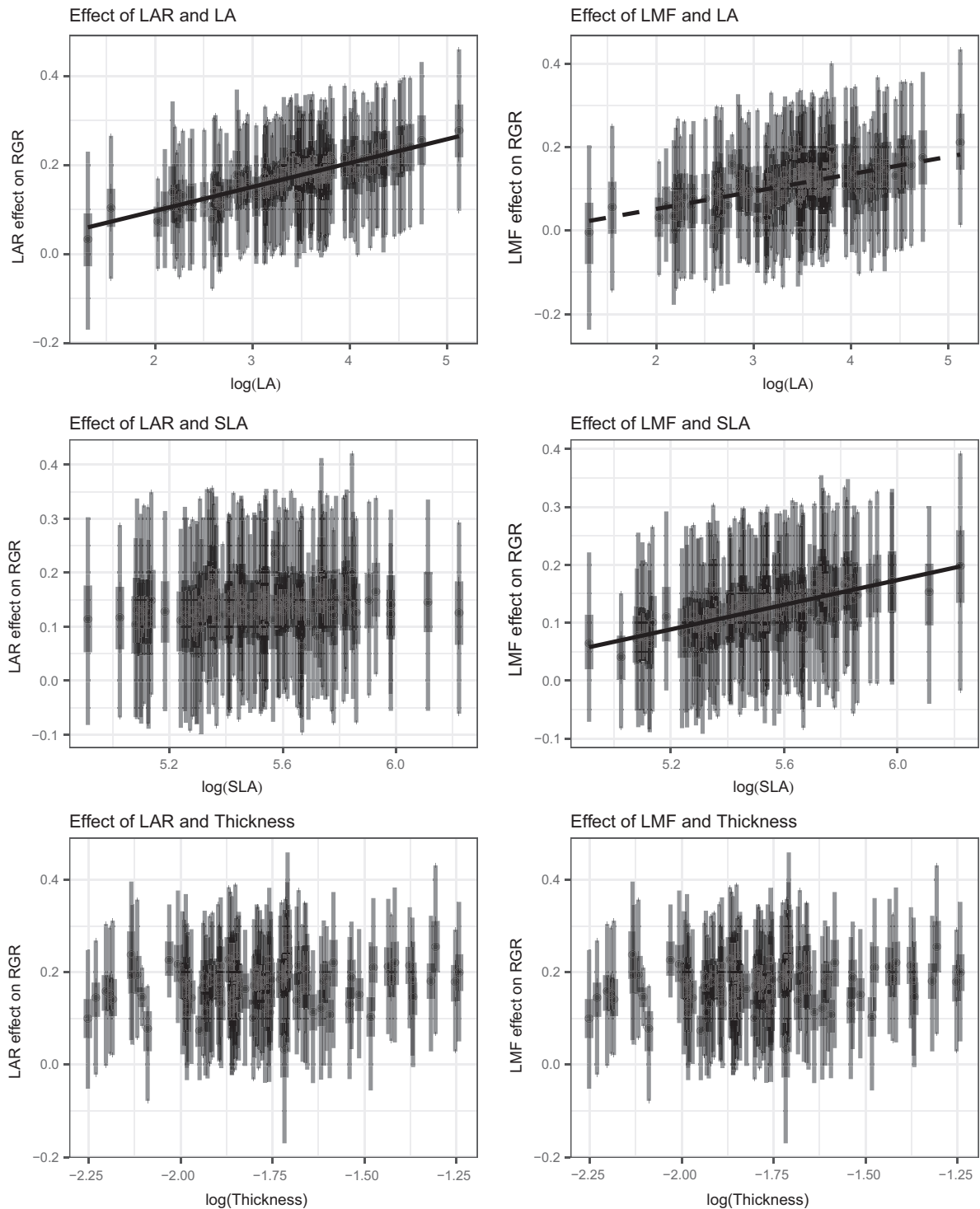
FIG. 3. Species-level leaf trait effects on the relationship between biomass allocation trait (LAR or LMF) and relative growth rate (RGR, cm·cm^{-1}·yr^{-1}). Black circles and gray lines indicate the means and the 95% credible intervals of the species-specific coefficients, respectively. The solid black line represents fitted significant relationships (95% credible intervals crossed zero, see Appendix S1: Table S5). Dashed line represents fitted significant relationships (90% credible intervals did not cross zero). Trait codes are the same as in Table 1.

SLA (Fig. 3). Our results agree with previous studies showing that higher values of SLA and LA may lead to higher plant growth (Sterck et al. 2006, Poorter et al. 2008). Yet, our analyses go one step further by indicating that the positive effects of acquisitive species-level leaf traits on plant demography depend and can be modified by individual-level leaf allocation traits. Our approach allows us to model the integrated effect of different traits via a hierarchical arrangement to predict variation in plant growth across distinct organizational levels (within and across species). This approach has important implications in terms of defining functional trade-offs for species, given that if we only focus on examining one trait, SLA, for classifying species as acquisitive and conservative for resource uptake we will be ignoring important information regarding how these strategies are modified by foliage allocation. The combined effect of SLA and leaf allocation traits could result in alternative phenotypes with equivalent carbon gains and, therefore, equivalent performance (Hirose and Werger 1995, Marks 2007, Worthy et al. 2020).

Although trait integration has long been studied in ecological and evolutionary studies (Olson and Miller 1958, Berg 1960, Cheverud and Cheverud 1982, Schlichting 1989), there are still a limited number of studies that examine the integrated effects of traits on performance for communities with high species diversity species (but see Freschet et al. 2015, Messier et al. 2017, Yang et al. 2020). Some key results from previous studies show that trait effects on plant performance can be contingent to the effects of other traits (Wildová et al. 2007, Blonder et al. 2018, Pistón et al. 2019, Worthy et al. 2020) and suggest that variations in plant performance are highly sensitive to the interactive effect of functional traits. Our results suggest that we can gain additional insights about the role of traits predicting variation in growth not only by accounting for trait interactions but by considering the different patterns of trait variation (individual and species level) across trait types (Armbruster 1991) using hierarchical approaches (Marks 2007; Table 2). The individual-level traits would represent the adjustability to local conditions showing high intraspecific variation (biomass allocation; Umaña et al. 2020b), while the species-level traits are likely subject to different types of constraints that makes them less variable within species than across species (i.e., SLA; Umaña et al. 2018). We suggest, therefore, that traits should be modeled by recognizing differences in constraints across trait types such that biomass allocation traits display high within species variation, have a more direct effect on performance, and interact with organ-level traits.

Among all species-level leaf traits studied here, leaf thickness showed the weakest effects on growth. We expected that higher leaf thickness would result in lower seedling growth given that high leaf thickness implies higher construction cost (high carbon investments; Chabot et al. 1979, Poorter et al. 2006). However, none of the relationships examined in this study were significant or close to being significant for any of the models tested. We infer from this that leaf thickness might not strongly and directly affect carbon processing strategies and this would explain the weak relationships we found. Instead, leaf thickness, as a mechanical trait, might relate to structural resistance but less directly to photosynthetic functions that can translate into carbon gain (Onoda et al. 2011).

Conclusion

The integration of functional traits to understand variations in plant demography is central for building a robust predictive functional framework. Here, we propose a hierarchical framework that combines two trait types measured at two organization levels, individual-level biomass allocation and species-level leaf traits, to predict seedling growth. Our results indicate that the effects of species-level leaf traits on demography depend on the individual variation in biomass allocation traits. This study represents an effort for describing the complex relationships between traits that underly organisms' function. We suggest that recognizing and explicitly accounting for the differences in trait variation across organization levels and trait types reveals functional interactions that improve our understanding of the link between plant functionality and variation in performance for species-rich communities.

Literature Cited

Adler, P. B., et al. 2014. Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences USA 111:10019.

Armbruster, W. S. 1991. Multilevel analysis of morphometric data from natural plant populations: insights into ontoogenetic, genetic and selective correlations in *Dalechampia scandens*. Evolution 45:1229–1244.

Armbruster, W. S., C. Pelabon, G. H. Bolstad, and T. F. Hansen. 2014. Integrated phenotypes: understanding trait covariation in plants and animals. Philosophical Transactions of the Royal Society B 369:20130245.

Armbruster, W. S., and K. E. Schwaegerle. 1996. Causes of covariation of phenotypic traits among populations. Journal of Evolutionary Biology 9:261–276.

Arnold, S. J. 1983. Morphology, performance and fitness. American Zoology 361:347–361.

Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. Journal of Ecology 72:777–795.

Berg, R. L. 1960. The ecological significance of correlation pleiades. Evolution 14:171–180.

Blonder, B., R. E. Kapas, R. M. Dalton, B. J. Graae, J. M. Heiling, and Ä. H. Opedal. 2018. Microenvironment and functional-trait context dependence predict alpine plant community dynamics. Journal of Ecology 106:1323–1337.

Bonser, S. P. 2006. Form defining function: interpreting leaf functional variability in integrated plant phenotypes. Oikos 114:187–190.

Cao, M., H. Zhu, H. Wang, G. Lan, Y. Hu, S. Zhou, X. Deng, and J. Cui. 2008. Xishuangbanna tropical seasonal rainforest dynamics plot: tree distribution maps, diameter tables and species docunetation. Yunnan Science and Technology Press, Kunming, Yunnan, China.

Chabot, B. F., T. W. Jurik, and J. F. Chabot. 1979. Influence of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. American Journal of Botany 66:940–945.

Chazdon, R. L., and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72:553–564.

Cheverud, J. M., and Cheverud. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution 36:499–516.

Comita, L. S., and S. P. Hubbell. 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. Ecology 90:328–334.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18:431–451.

Díaz, S., et al. 2016. The global spectrum of plant form and function. Nature 529:1–17.

Evans, C. G. 1972. The quantitative analysis of plant growth. University of California Press, Berkeley, California, USA.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 2000. Gap Light Analyzer (GLA), version 2.0. Page Technological tools. http://rem-main.rem.sfu.ca/downloads/Forestry/GLAV2UsersManual.pdf

Freschet, G. T., E. M. Swart, and J. H. C. Cornelissen. 2015. Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction. New Phytologist 206:1247–1260.

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

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, UK.

Hirose, T., and M. J. A. Werger. 1995. Canopy structure and photon flux partitioning among species in a herbaceous plant community. Ecology 76:466–474.

Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research 23:187–261.

Laughlin, D. C., and J. Messier. 2015. Fitness of multidimensional phenotypes in dynamic adaptive landscapes. Trends in Ecology and Evolution 30:487–496.

Laughlin, D. C., R. T. Strahan, P. B. Adler, and M. M. Moore. 2018. Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. Ecology Letters 21:411–421.

Marks, C. O. 2007. The causes of variation in tree seedling traits: the roles of environmental selection versus chance. Evolution 61:455–469.

Marks, C. O., and M. J. Lechowicz. 2006. A holistic tree seedling model for the investigation of functional trait diversity. Ecological Modelling 193:141–181.

McDonald, P. G., C. R. Fonseca, J. M. C. Overton, and M. Westoby. 2003. Leaf-size divergence along rainfall and soil-nutrient gradients: Is the method of size reduction common among clades? Functional Ecology 17:50–57.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–185.

Messier, J., M. J. Lechowicz, B. J. Mcgill, C. Violle, B. J. Enquist, and P. Val. 2017a. Interspecific integration of trait dimensions at local scales: the plant phenotype as an integrated network. Journal of Ecology 105:1775–1790.

Messier, J., B. J. Mcgill, B. J. Enquist, and M. J. Lechowicz. 2017b. Trait variation and integration across scales: is the leaf economic spectrum present at local scales? Ecography 40:685–697.

Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters 13:838–848.

Niinemets, Ü., A. Portsmuth, and L. Truus. 2002. Leaf structural and photosynthetic characteristics, and biomass allocation to foliage in relation to foliar nitrogen content and tree size in three Betula species. Annals of Botany 89:191–204.

Niklas, K. J. 1992. Petiole mechanics, light Interception by lamina and "economy in design." Oecologia 90:518–526.

Niklas, K. J. 1999. A mechanical perspective on foliage leaf form and function. New Phytologist 143:19–31.

Niklas, K. J., and B. J. Enquist. 2001. Invariant scaling relationships for interspecific plant biomass production rates and body size. Proceedings of the National Academy of Sciences USA 98:2922–2927.

Olson, E. C., and R. L. Miller. 1958. Morphological integration. The University of Chicago Press, Chicago, Illinois, USA.

Onoda, Y., et al. 2011. Global patterns of leaf mechanical properties. Ecology Letters 14:301–312.

Paine, C. E. T., et al. 2015. Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. Journal of Ecology 103:978–989.

Pistón, N., F. de Bello, A. T. C. Dias, L. Götzenberger, B. H. P. Rosado, E. A. de Mattos, R. Salguero-Gómez, and C. P. Carmona. 2019. Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. Journal of Ecology 107:2317–2328.

Poorter, H. 1989. Plant growth analysis: towards a synthesis of the classical and the functional approach. Physiologia Plantarum 75:237–244.

Poorter, H. 1990. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. Pages 45–68 in H. Lambers, M. L. Cambridge, H. Konings, and T. L. Pons, editors. Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague, The Netherlands.

Poorter, H., and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: a quantitative review. Australian Journal of Plant Physiology 27:595–607.

Poorter, H., K. J. Niklas, P. B. Reich, J. Oleksyn, P. Poot, and L. Mommer. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist 193:30–50.

Poorter, H., S. Pepin, T. Rijkers, Y. De Jong, J. R. Evans, and C. Körner. 2006. Construction costs, chemical composition and payback time of high- and low-irradiance leaves. Journal of Experimental Botany 57:355–371.

Poorter, H., and C. Remkes. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83:553–559.

Poorter, H., and A. van der Werf. 1998. Is inherent variation in RGR determined by LAR at low light and by NAR at high light? Pages 309–336 in H. Lambers, H Poorter, and M. M. I. Vn Vuuren, editors. Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden, The Netherlands.

Poorter, L., et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89:1908–1920.

Poorter, L. 2009. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. New Phytologist 3:890–900.

Poorter, L., and D. M. A. Rozendaal. 2008. Leaf size and leaf display of thirty-eight tropical tree species. Oecologia 158:35–46.

Popma, J., and F. Bongers. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. Oecologia 75:625–632.

R Development Core Team. 2017. R: A language and environment for statistical computing R Development Core Team. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80:1955–1969.

Schlichting, C. D. 1989. Phenotypic integration and environmental change. BioScience 39:460–464.

stan Development Team. 2020. RStan: the R interface to Stan. R package version 2(21):2. http://mc-stan.org/

Sterck, F. J., and F. Bongers. 2001. Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. Plant Ecology 153:279–292.

Sterck, F., L. Markesteijn, F. Schieving, and L. Poorter. 2011. Functional traits determine trade-offs and niches in a tropical forest community. Proceedings of the National Academy of Sciences USA 108:20627–20632.

Sterck, F. J., L. Poorter, and F. Schieving. 2006. Leaf traits determine the growth-survival trade-off across rain forest tree species. American Naturalist 167:758–765.

Umaña, M. N., G. Arellano, N. G. Swenson, and J. Zambrano. 2020a. Tree seedling trait optimization and growth in response to local-scale soil and light variability. Ecology 102: e03252.

Umaña, M. N., M. Cao, L. Lin, N. G. Swenson, and C. Zhang. 2020b. Trade-offs in above- and below-ground biomass allocation influencing seedling growth in a tropical forest. Journal of Ecology 109:1184–1193.

Umaña, M. N., M. Cao, L. Lin, N. Swenson, and C. Zhang. 2020c. Trade-offs in above and belowground biomass allocation influencing seedling growth in a tropical forest. Dryad, data set. https://doi.org/10.5061/dryad.bk3j9kd93

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

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

Umaña, M. N., E. F. Zipkin, C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2019. Data from: Individual-level trait variation and negative density dependence affects growth in tropical tree seedlings. Dryad, data set. https://doi.org/10.5061/dryad.6d1qm1j

Vehtari, A., A. Gelman, and J. Gabry. 2017a. loo package: Efficient leave-one-out cross-validation and WAIC for Bayesian models. Statistics and Computing 27:1413–1432.

Vehtari, A., A. Gelman, and J. Gabry. 2017b. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27:1413–1432.

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

Wildová, R., L. Gough, C. Hershock, and D. E. Goldberg. 2007. Architectural and growth traits differ in effects on performance of clonal plants: an analysis using a field-parameterized simulation model. Oikos 116:836–852.

Worthy, S. J., D. C. Laughlin, J. Zambrano, M. N. Umaña, C. Zhang, L. Lin, M. Cao, and N. G. Swenson. 2020. Alternative designs and tropical tree seedling growth performance landscapes. Ecology 101:e03007.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Wright, S. J., et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees. Ecology 91:3664–3674.

Yang, J., M. Cao, and N. G. Swenson. 2018. Why functional traits do not predict tree demographic rates. Trends in Ecology and Evolution 33:326–336.

Yang, J., X. Song, M. Cao, X. Deng, W. Zhang, X. Yang, and N. G. Swenson. 2020. On the modeling of tropical tree growth: the importance of intraspecific trait variation, nonlinear functions and phenotypic integration. Annals of Botany 127:533–542.