

On the modelling of tropical tree growth: the importance of intra-specific trait variation, non-linear functions and phenotypic integration

Jie Yang¹, Xiaoyang Song¹, Min Cao¹, Xiaobao Deng¹, Wenfu Zhang¹, Xiaofei Yang¹ and Nathan G. Swenson^{2,*}

¹CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, 666303, China and ²Department of Biology, University of Maryland, College Park, MD 20742, USA

*For correspondence. E-mail swenson@umd.edu

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- **Background and Aims** The composition and dynamics of plant communities arise from individual-level demographic outcomes, which are driven by interactions between phenotypes and the environment. Functional traits that can be measured across plants are frequently used to model plant growth and survival. Perhaps surprisingly, species average trait values are often used in these studies and, in some cases, these trait values come from other regions or averages calculated from global databases. This data aggregation potentially results in a large loss of valuable information that probably results in models of plant performance that are weak or even misleading.
- **Methods** We present individual-level trait and fine-scale growth data from >500 co-occurring individual trees from 20 species in a Chinese tropical rain forest. We construct Bayesian models of growth informed by theory and construct hierarchical Bayesian models that utilize both individual- and species-level trait data, and compare these models with models only using individual-level data.
- **Key Results** We show that trait–growth relationships measured at the individual level vary across species, are often weak using commonly measured traits and do not align with the results of analyses conducted at the species level. However, when we construct individual-level models of growth using leaf area ratio approximations and integrated phenotypes, we generated strong predictive models of tree growth.
- **Conclusions** Here, we have shown that individual-level models of tree growth that are built using integrative traits always outperform individual-level models of tree growth that use commonly measured traits. Furthermore, individual-level models, generally, do not support the findings of trait–growth relationships quantified at the species level. This indicates that aggregating trait and growth data to the species level results in poorer and probably misleading models of how traits are related to tree performance.

Key words: Tree growth, intra-specific trait variation, tropical forest, rain forest.

INTRODUCTION

The structure and dynamics of communities ultimately emerge from differential individual-level performance. Tropical forests play a major role in the global carbon cycle, thereby making our understanding of forest dynamics critical for models of our future (e.g. Malhi and Phillips, 2004; Fyllas *et al.*, 2014). Models of individual- or population-level tree performance often utilize trait information (e.g. Uriarte *et al.*, 2010; Fyllas *et al.*, 2014; Liu *et al.*, 2016; Katabuchi *et al.*, 2017). The traits utilized are chosen because they represent a common currency that can be measured and compared across systems (Westoby, 1998; Westoby *et al.*, 2002; Reich, 2014) and because they are believed to represent fundamental life history trade-offs that should be related to performance (e.g. McGill *et al.*, 2006).

In practice, trait data are often collected on a handful of individuals in a population and averaged. These population- or species-level average data are then used for downstream analyses ranging from models of individual-level tree performance to correlations of average trait values with average demographic rate values (e.g. Hérault *et al.*, 2011; Kraft *et al.*, 2015;

Paine *et al.*, 2015). While collecting trait data from a small number of individuals may be a pragmatic approach, particularly in diverse systems (Swenson, 2013), the analysis of population- or species-mean trait data is conceptually misaligned with the vast evolutionary ecology literature relating traits to individual performance (Swenson *et al.*, 2020) and it may lead to weak or misleading models and inferences (e.g. Liu *et al.*, 2016; Yang *et al.*, 2018).

Relating traits to performance outcomes is foundational to ecology and evolutionary biology (Arnold, 1983; McGill *et al.*, 2006). In evolutionary ecology, the trait distribution in a population through time is shaped by the relationship between individual-level trait values and fitness (Conner and Hartl, 2004). Specifically, the relative fitness values of individuals are commonly regressed against the standardized trait data to derive fitness functions (Fig. 1). Positive or negative relationships implicate directional selection, whereas concave-down and concave-up relationships implicate stabilizing and diversifying selection, respectively. Ecologists using traits to predict performance outcomes of an entire population certainly do not measure the lifetime fitness of individuals, but the fitness

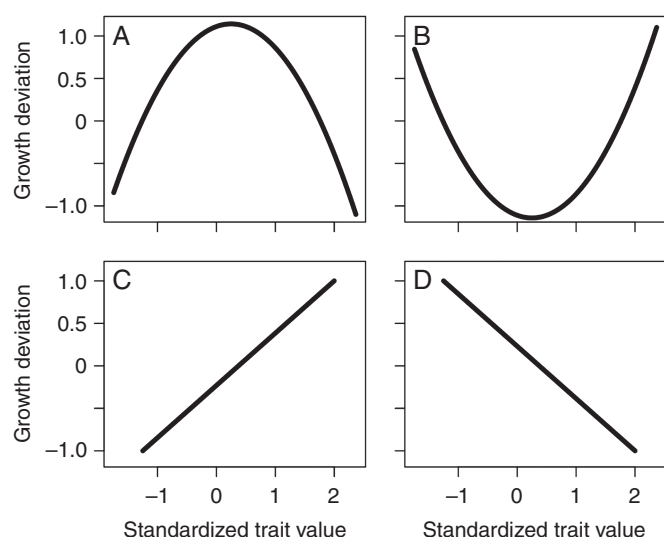


FIG. 1. A conceptual figure of how traits should be related to growth that is similar to analysing fitness functions in evolutionary ecology (Conner and Hartl, 2004). Here, we propose that one should regress a growth deviation against a standardized trait value. Each data point should be an individual tree (not species), and linear and second-order polynomial fits to the relationship should be compared. The growth deviation is the difference in the individual-level growth from the mean growth of the population. Thus, positive values are higher than average growth, and negative values are lower than expected. The standardized trait value is the z -scaled trait value for the individual. The graphs are analogous to fitness functions where relative fitness is regressed onto standardized trait values. Under that framework, (A) concave-down relationships indicate stabilizing selection, (B) concave-up relationships indicate diversifying selection and (C, D) linear relationships indicate directional selection. Here, we stress that growth is not a clear or reliable metric of fitness, but we do propose plotting growth and trait data in this way, and explicitly considering polynomial relationships between traits and growth should help trait-based ecology grow conceptually and empirically while allowing for a clearer integration with the evolutionary ecology literature.

function framework, nonetheless, should be utilized in their work more frequently for multiple reasons (Swenson *et al.*, 2020). First, an evolutionary ecology framework is focused on individuals as the unit of study, whereas much of trait-based ecology focuses on trait and performance data aggregated to the population or species level. Secondly, this evolutionary ecology framework explicitly considers the possibility of concave trait–performance relationships, whereas most trait-based ecology searches for simple positive or negative relationships between traits and performance. It may be reasonable to expect that concave relationships between traits and performance should be common as natural selection is not only directional. Thirdly, an evolutionary ecology framework serves as a unifying conceptual and analytical language that could be used to encourage communication between ecology and evolutionary biology.

Individual-centric analysis of traits as they relate to plant performance not only permit a connection with evolutionary ecology, but they can also facilitate a second major challenge in trait-based ecology. This second challenge concerns the importance of phenotypic integration. Specifically, a trait may not be a strong predictor of plant performance by itself and its importance is only understood in the context of other trait values from the individual (Yang *et al.*, 2018). Such a context is critical for modelling the performance of large and long-lived individual organisms such as trees. Existing theory built upon first

principles can be leveraged to direct our analyses of growth as it relates to phenotypic integration. For example, the growth of photosynthetic organisms is expected to isometrically scale with photosynthetic mass (Niklas and Enquist, 2001). In a hypothetical tree where the leaves are the only photosynthetic tissue, we can deconstruct the photosynthetic mass into multiple trait axes an ecologist may measure. Specifically, the 2-D crown area of a tree combined with the average tree-level leaf area index (LAI; a measure of the amount of leaf area above an area of ground) provides an estimate of the leaf area for that tree. This value, combined with one of the most widely measured leaf traits, leaf mass per area (LMA; the inverse of specific leaf area), provides a rough estimate of the photosynthetic mass of a tree. This value standardized by the body size of the tree (i.e. an estimate of leaf mass divided by tree diameter) is expected to predict the relative growth rate (i.e. growth standardized by tree diameter) (Yang *et al.*, 2018). Measuring the traits discussed above (i.e. crown area and LAI) requires the measurement of traits on individuals as allocation traits are uninformative when averaged across a population or species. This is because individuals within and across species vary widely in their allocation due to differences in ontogeny and other factors (e.g. microenvironmental differences). Additionally, integrating phenotypes using data from multiple individuals or averaged data will result in an inadvertent and erroneous loss or gain of trait–trait relationships in the phenotype, resulting in poorer models of growth. In sum, individual-level concepts and analyses permit a clearer modelling of tree growth that is informed by theory derived from first principles.

In this work, we consider the relationship between traits and, for tropical trees, relative growth rates (RGRs). We focus on 20 species of trees in a Chinese rain forest where we have collected individual-level trait and growth data on hundreds of individuals. The analyses we present are designed to compare the outcomes of species- and individual-level analyses of growth. To do this, we constructed Bayesian models of growth informed by theory derived from first principles and we constructed hierarchical Bayesian models that utilize both individual- and species-level trait data, and compare these models with models only using individual-level data. The specific questions we ask are as follows. (1) Are the results of trait–RGR analyses conducted at the species level consistent with those obtained from individual-level analyses? (2) Is there evidence for non-linear trait–RGR relationships within species? (3) Do models that consider phenotypic integration outperform models that do not? (4) Do models that partially rely on species-level data perform as well as those that only use individual-level data?

MATERIALS AND METHODS

Study location

The study was conducted in the 20 ha Xishuangbanna forest dynamics plot (FDP) in a seasonal tropical rain forest of Southwest China (21°37′08″N, 101°35′07″E), characterized as a monsoonal climate, with a distinct dry season (November to April) and wet season (May to October). The annual average temperature is 21.0 °C and the annual mean rainfall is 1493 mm in the forest. A total of 1256 mm, 84 % of the annual average, of

rainfall occurs in the wet season (Cao et al., 2006). This forest is dominated by large individuals of *Parashorea chinensis* (Dipterocarpaceae). All freestanding woody stems ≥ 1 cm diameter at breast height (dbh), i.e. 130 cm from the ground, are measured, tagged, identified and mapped. A detailed description of the climate, geology and flora of this plot can be found in Cao et al. (2008).

Tree growth and trait measurements

This study used a sub-set of evergreen trees in the forest plot that have growth monitored by dendrometer bands. The stainless steel dendrometer bands were installed in the plot in January 2009 following a standardized protocol (Muller-Landau and Dong, 2008); since then the dendrometers have been re-measured every 3 months. The RGRs used in this study were calculated by $\ln(\text{dbh}_f/\text{dbh}_i)/(t_f - t_i)$ from August 2009 to August 2018, where t is year and the subscripts f and i are final and initial values of the dbh. To guarantee data accuracy, we discarded the cases where (1) the tree had damaged dendrometer bands; (2) the tree died during the study period; or (3) the tree had incomplete trait or growth data. In total, our study included 510 individual trees from 20 species varying in the number of individuals measured per species from nine to 104 (Supplementary data Table S1).

We collected seven functional traits [leaf area, leaf chlorophyll content, leaf dry matter content (LDMC), leaf thickness, leaf toughness, leaf mass per area (LMA) and wood specific resistance (WSR)] for each tree with a dendrometer band using the standard protocols described in Cornelissen et al. (2003) or based upon the information below for leaf chlorophyll content and wood-specific resistance. Leaf chlorophyll content is directly related to the photosynthetic rate of plants (Vaieretti et al., 2007). Because SPAD readings and extractable chlorophyll content are highly correlated (Maderia et al., 2003), we measured relative leaf chlorophyll content using the Chlorophyll Meter SPAD-502Plus (Konica Minolta, Osaka, Japan). Wood density represents a trade-off between volumetric growth rate and mechanical strength (Cornelissen et al., 2003), but coring trees in the long-term forest dynamics plot is not allowed. Thus, we measured the WSR for each individual using a Resistograph (Rinntech Co., Germany), an electronically controlled drill that measures the relationship between drilling resistance and stem density (Isik and Li, 2003; Yang et al., 2014). The WSR of an individual is strongly correlated with the more commonly measured wood density, while being a less destructive measurement on individuals undergoing long-term monitoring (Isik and Li, 2003).

To examine crown allocation, we measured the dimensions of tree crowns to estimate the 2-D crown area and LAI values for each individual tree. In 2009, crown width and length were measured using a laser telemeter attached to an altimeter pole following the protocols described in Iida et al. (2012) to calculate the superficial area of an ellipsoid:

$$\text{Crown surface area} = \pi[(R_1 + R_2)/2]^2$$

where R_1 is the crown width and R_2 is the crown length. We used the crown surface area measures to estimate the leaf area

ratio (LAR) for each tree. Here, we define LAR as the crown surface area divided by the tree diameter at the time of the crown measurement. LAR is typically measured as total plant leaf area divided by total plant mass. Thus, we are presenting a rough estimate of the actual LAR. An LAI-2200 Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE, USA) was used to estimate the LAI under each focus tree, and measurements were taken following the LiCor protocols in the manual. The LAI in this study is the average number of leaves above any point on the ground below the tree and, therefore, is not equivalent to LAR and it does not have to be correlated with LAR.

Modelling growth: species- vs. individual-level data

The first goal of this study was to quantify the relationship between RGR and functional traits at the species level. The traits utilized for this set of analyses include LMA, LAR, leaf chlorophyll content, leaf thickness, leaf toughness, WSR, and LDMC. The trait and RGR data were collected on every individual tree in the study, but for this first analysis we calculated an average RGR and trait value for each species. The species-mean RGR values were then regressed onto the species-mean trait data. This approach was used to simulate the widely used practice of analysing RGR and trait data aggregated at the species level. For each RGR–trait relationship, we generated a linear regression model and a second-order polynomial regression model and recorded the r^2 and Akaike information criterion (AIC) for both models.

The second goal of this study was to conduct an analysis that models individual-level growth as a function of individual-level traits. These analyses were designed to be analogous to fitness function analyses in quantitative genetics (Conner and Hartl, 2004), with the recognition that we are not measuring fitness in this study. These analyses first quantified the deviation of the individual-level RGR from the mean value for the species, which we call the ‘growth deviation’. The growth deviation data were then regressed onto the individual-level trait data that were centred and scaled (i.e. z-transformed or standardized). This was repeated for each species. As with the previous analyses, we generated linear regression and second-order polynomial regression models and recorded the r^2 and AIC values for both models.

Modelling growth: building individual-level phenotypically integrated models

An alternative to blindly building models of trait–RGR relationships is to build and evaluate models of RGR that are informed by an understanding of phenotypic integration and functional ecology (Garnier 1991; Enquist et al., 2007; Yang et al., 2018). Thus, the third goal of this study was to build models of individual-level RGR that build from simple, and theoretically supported, expectations of how traits should impact RGR. Specifically, it is expected that the overall photosynthetic biomass of a plant relative to body mass should predict RGR (Niklas and Enquist 2001). For this portion of the study, we utilized hierarchical Bayesian models of RGR.

We began with a simple model regressing individual-level LAR onto individual-level RGR data with species-level random slopes and intercepts. This base model had the form of:

$$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij}$$

where μ_{ij} is the expected RGR of individual i in species j , α_j and β_{1j} are the intercept and slope for species j , and LAR_{ij} is the LAR of individual i in species j .

As the LAR is a measure of the canopy surface area relative to biomass on a 2-D plane, we built additional models that modified the above base model by including one piece of the individual-level LAI and LMA data at a time and in unison with and without an interaction between LAI and LMA. The form of these models, full model descriptions (including priors), directed acyclic graphs of the models and R code for running the models are provided in Supplementary data Appendices 1–4. The models were evaluated using STAN via the R package *rstan* (Stan Development Team, 2019). Each model was run with uninformative priors, run using four chains with 10 000 iterations and a warm up of 5000 iterations. A WAIC (Watanabe–Akaike information criterion; Watanabe, 2010) was calculated for each model, as was the posterior distribution of the pseudo- R^2 (Gelman et al., 2019).

Modelling growth: building models that mix individual- and species-level data

The final portion of this study aimed to determine whether models of RGR that applied a mixture of individual-level and species-level trait data were comparable with models of RGR that utilized only individual-level data. This was meant to simulate a situation where a researcher has individual-level data on tree structure (i.e. LAR and LAI), but species-level data for a leaf trait (i.e. LMA). Such a situation would occur if one had remotely sensed data (e.g. LiDAR) regarding tree structure, but could only measure LMA on a few individuals per species. To accomplish this, we began by modelling individual-level RGR as a function of individual-level LAR data with species-specific intercepts and slopes. These species-specific slopes and intercepts were modelled as a function of species-level LMA data. This hierarchical model had the form of:

$$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij}$$

$$\alpha_j = \gamma_\alpha + \gamma_\beta \times \text{LMA}_j$$

$$\beta_{1j} = \delta_\alpha + \delta_\beta \times \text{LMA}_j$$

where μ_{ij} is the expected RGR of individual i in species j , α_j and β_{1j} are the intercept and slope for species j , LAR_{ij} is the LAR of individual i in species j , γ_α and γ_β are the intercept and slope of the model of α_j as a function of the species-mean LMA values, LMA_j , and δ_α and δ_β are the intercept and slope of the model of β_{1j} as a function of LMA_j . Building from this model, we added individual-level LAI data in a second model as shown in Table 1. The full model descriptions (including priors), directed acyclic graphs of the models and R code for running these models are also provided in Supplementary data Appendices 1–4. As in the previous analyses, the models were evaluated using STAN via the R package *rstan* (Stan Development Team, 2019). We recorded the WAIC and the posterior distribution of the pseudo- R^2 values for each model. Each model was run with uninformative priors, run using four chains with 10 000 iterations and a warm up of 5000 iterations.

RESULTS

Species-level growth–trait correlations

The RGR was significantly correlated with LMA, leaf toughness, wood resistance and LDMC at the species level (Fig. 2). We compared linear and second-order polynomial model fits using AIC. If a model had an AIC two or more units smaller than another, it was selected. The best RGR–leaf toughness, RGR–wood resistance and RGR–LDMC models were all linear. On the other hand, the best RGR–LMA model was concave up (Fig. 2, $r^2 = 0.58$). The leaf toughness and wood resistance decreased linearly with increasing RGR (Fig. 2, $r^2 = 0.2$, $r^2 = 0.17$); however, the LDMC increased linearly with increasing RGR (Fig. 2, $r^2 = 0.22$). Thus, species with low leaf toughness, low wood resistance and higher LDMC tended to grow faster.

TABLE 1. Form of growth models at the individual level and hierarchical models using a mixture of species- and individual-level data

Type of Data	Model	WAIC	Pseudo- R^2 (95 % CI)
All individual-level data	$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij}$	–1889.4	0.292 (0.231 – 0.350)
	$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij} \times \text{LAI}_{ij}$	–1890.9	0.297 (0.234 – 0.356)
	$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij} + \beta_{2j} \times \text{LAI}_{ij}$	–1893.5	0.307 (0.245 – 0.363)
	$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij} + \beta_{2j} \times \text{LAI}_{ij} \times \text{LMA}_{ij}$	–1910.2	0.329 (0.266 – 0.387)
	$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij} + \beta_{2j} \times \text{LAI}_{ij} + \beta_{3j} \times \text{LMA}_{ij}$	–1912.6	0.339 (0.277 – 0.397)
	$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij} \times \beta_{2j} \times \text{LAI}_{ij}$	–1912.6	0.339 (0.277 – 0.397)
Species average LMA and individual-level data	$\alpha_j = \gamma_\alpha + \gamma_\beta \times \text{LMA}_j$ $\beta_{1j} = \delta_\alpha + \delta_\beta \times \text{LMA}_j$	–1888.9	0.312 (0.255 – 0.363)
	$\mu_{ij} = \alpha_j + \beta_{1j} \times \text{LAR}_{ij}$ $\alpha_j = \gamma_\alpha + \gamma_\beta \times \text{LMA}_j$ $\beta_{1j} = \delta_\alpha + \delta_\beta \times \text{LMA}_j$	–1887.9	0.295 (0.232 – 0.350)

The WAIC and pseudo- R^2 values are provided for each model.

Individual-level growth–trait correlations

Next, we generated linear and second-order polynomial regression models of RGR regressed onto LMA, leaf chlorophyll content, leaf thickness, leaf toughness, wood resistance and LDMC at the individual level. Again, we used AIC to select the best model for each trait. In most cases, we did not find a relationship between RGR and a trait value at the individual level (Table 2; Supplementary data Table S2). We found evidence for three concave-down RGR–trait relationships (Fig. 3). Specifically, LMA for the species *Archidendron kerrii*, *Colona thorelii* and *Nephelium chryseum* had a concave-down relationship. Thus, extreme trait values had negative growth deviations (i.e. lower RGR than the population mean) and intermediate trait values had the highest growth deviations (i.e. higher RGR than the population mean) (Fig. 3; Supplementary data Table S2).

We found two concave-up relationships in our analyses. Specifically, chlorophyll content and LDMC had concave-up relationships with r^2 values of 0.45 and 0.06, respectively (Supplementary data Table S2). This indicates that species with extreme values for these traits had higher than average growth in the population.

We found two positive relationships between RGR and LMA, two negative and one positive RGR–leaf chlorophyll relationship, two positive RGR–leaf thickness relationships, one positive RGR–leaf toughness relationship, one negative and one positive RGR–wood resistance relationship, and one negative and two positive RGR–LDMC relationships. The r^2 values for these linear regressions ranged from 0.04 to 0.56 with a mean of 0.32. In sum, there were few relationships detected even when using individual-level data for these traits; the slopes

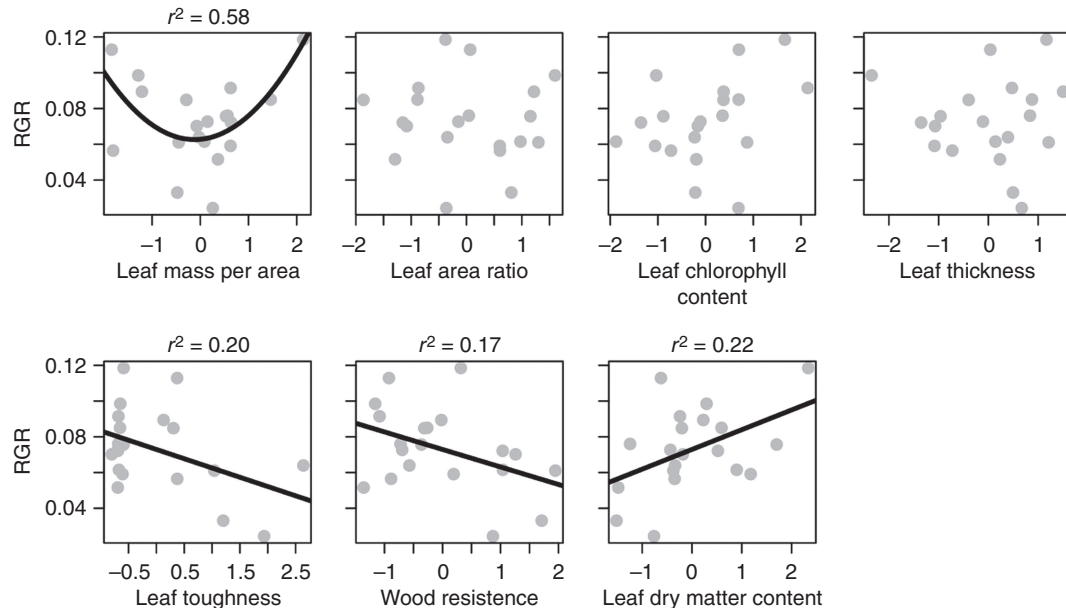


FIG. 2. The relationship between relative growth rate (RGR) and functional trait values. Each data point is a species in the data set. Three models had no relationship using a linear or second-order polynomial regression. Three models had significant linear relationships and one had a significant concave-up second-order polynomial relationship. Regression lines are only shown for significant relationships. The values on the x-axis are z-scaled (i.e. centred and scaled) transformations and are, therefore, unitless.

TABLE 2. Linear regression results for trait–RGR relationships at the individual level

Species	LMA		CHOL		THICK		TOUGH		WOOD		LDMC	
	M	r^2	m	r^2	m	r^2	m	r^2	m	r^2	m	r^2
ALSEPE			–	0.28			+	0.44	–	0.32		
CASTEC	+	0.10			+	0.05					–	0.04
CASTHY											+	0.14
DIOSHA			–	0.51								
FICULA					+	0.37						
KNEMTE	+	0.56										
MACRDI											+	0.48
MALLGA			+	0.28								
MANGFO									+	0.53		

m, sign of the slope; LMA, leaf mass per area; CHOL, leaf chlorophyll content; THICK, leaf thickness; TOUGH, leaf toughness; WOOD, wood specific resistance; LDMC, leaf dry matter content.

Blank cells indicate a relationship no different from zero ($P > 0.05$).

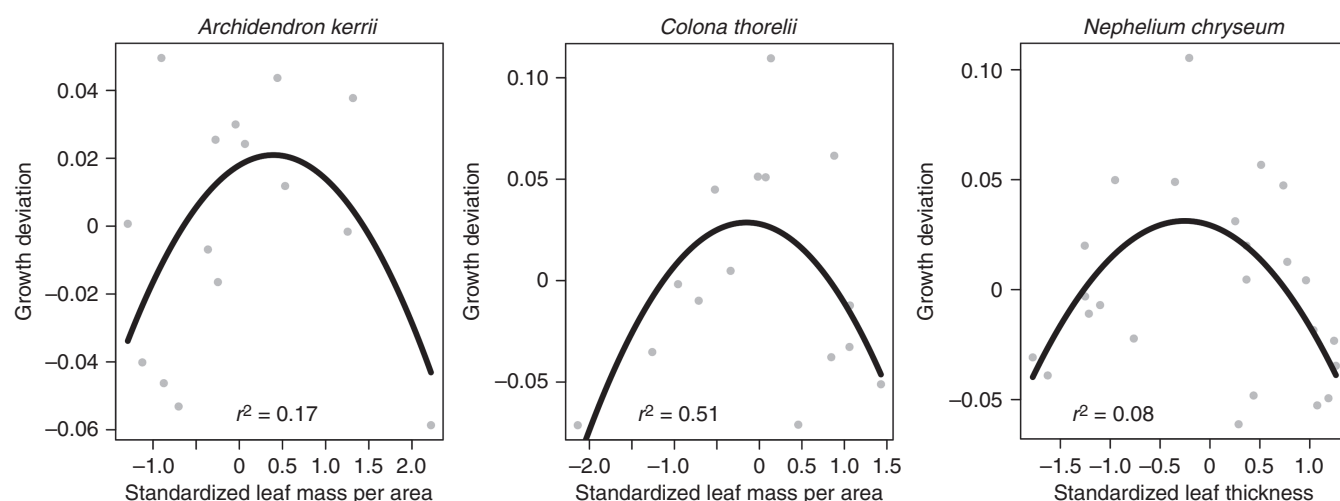


FIG. 3. The relationship between growth deviations and standardized (i.e. z-scaled) leaf mass per area and leaf thickness trait values for three species. The growth deviation is the difference between the individual tree RGR and the mean of all individuals in the data set for that species. Thus, positive values indicate trees growing faster than average and negative values indicate trees growing slower than average.

for significant models did vary for a few traits and the amount of variation explained was highly variable.

Individual-level growth–LAR correlations

Next, we regressed individual-level RGR onto our measures of individual-level LAR. There were 17 species that had a significant RGR–LAR relationship out of the 20 in total. Fourteen of these models were positive linear relationships. An additional two were concave-up second-order polynomial relationships and one was a negative linear relationship (Table 3). The positive linear relationships had r^2 values ranging from 0.04 to 0.93 with an average of 0.42 (Table 3; Fig. 4).

Individual-level phenotypically integrated models

We used a Bayesian model evaluation approach to model individual-level RGR. We began with a model using only LAR with species-specific slopes and intercepts (Table 1). This model had a pseudo- R^2 value of 0.292 [confidence interval (CI) 0.231–0.350]. We then added individual-level LAI and LMA data to this base model additively or using an interaction between LAR and LAI. We compared models using their WAIC values because model fit will improve simply by adding more parameters. The WAIC, like the AIC, penalizes for this, and lower WAIC values are preferred. We defined the superior models as those models that had a WAIC value that was two or more times lower than the model with which it was being compared. The best model identified in our individual-level analyses was an additive model including LAR, LAI and LMA [WAIC = −1912.6; pseudo- R^2 = 0.339 (CI 0.277–0.397)]. The additive model of $\mu_{i,j} = \alpha_j + \beta_{1,j} \times \text{LAR}_{i,j} + \beta_{2,j} \times \text{LMA}_{i,j}$ was the second ranked model and nearly as good as the model including all three independent variables (i.e. $\mu_{i,j} = \alpha_j + \beta_{1,j} \times \text{LAR}_{i,j} + \beta_{2,j} \times \text{LAI}_{i,j} + \beta_{3,j} \times \text{LMA}_{i,j}$; Table 1).

TABLE 3. Regression results for trait–RGR relationships at the individual level using linear and second-order polynomial models

Species	LAR			
	Linear		Poly	
	m	r^2	m	r^2
ALSEPE	+	0.48		
ARCHKE	+	0.42		
BACCRA			u	0.43
CASTEC			u	0.01
CASTHY	+	0.04		
CASTIN	+	0.14		
CINNBE	–	0.34		
COLOTH	+	0.23		
DIOSHA	+	0.74		
ELAEGGL				
FICULA	+	0.27		
GARCCO	+	0.49		
KNEMTE	+	0.56		
MACRDI	+	0.56		
MALLGA				
MANGFO	+	0.41		
NEPHCH				
OROPLA	+	0.18		
PHOELA	+	0.93		
PITTKE	+	0.32		

m, sign of the slope for linear regressions; u, concave up for polynomial models.

Blank cells indicate a relationship no different from zero ($P > 0.05$).

Mixed individual- and species-level trait models

We used a Bayesian approach to evaluate hierarchical models of individual-level RGR with individual-level LAR or LAR and LAI data as independent variables. In these models, we modelled the species-specific intercept and slope of LAR as a function of the species-level LMA value (Table 1). Using both

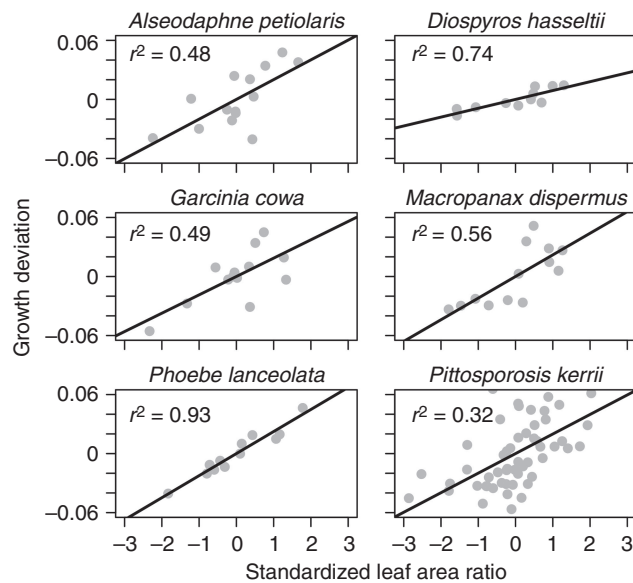


FIG. 4. The relationship between growth deviations and standardized (i.e. z-scaled) leaf area ratios. The growth deviation is the difference between the individual tree RGR and the mean of all individuals in the data set for that species. Thus, positive values indicate trees growing faster than average and negative values indicate trees growing slower than average.

WAIC and pseudo- R^2 as guides, we found that these models were not superior to the individual-level models. They were indistinguishable in quality from one another and from the most simple LAR-based individual-level model (Table 1). These hierarchical models were inferior to all other non-LAR-based individual-level models, indicating that adding species-level trait data to an individual-level base model did not improve it and in some cases it noticeably reduced the quality of the model (Table 1).

DISCUSSION

Trait-based ecology is built upon the premise that differential performance can be attributed to variation in traits, and that differential performance (McGill *et al.*, 2006) should scale up to explain emergent patterns such as community and ecosystem structure and dynamics (Reich, 2014). In many – but not all – cases, researchers aggregate trait data to generate species-level means that are used in downstream analyses (e.g. Kraft *et al.*, 2010; Uriarte *et al.*, 2010; Paine *et al.*, 2015; Katabuchi *et al.*, 2017), but relying on only inter-specific variation and ignoring intra-specific variation may have critical conceptual and empirical consequences (Yang *et al.*, 2018; Swenson *et al.*, 2020). The results provided herein show that models of individual-level tree growth in a tropical rain forest were greatly improved when using individual-level trait data and when growth models are built upon first principles. These results not only inform us on how we should model tree growth upon the basis of traits in future work, but they also indicate that trait-based ecology should rethink how it conceptually and analytically aligns with evolutionary ecology. In the following, we discuss the results and their implications in more detail.

The shape and strength of trait–growth relationships

Our first series of analyses focused on simple trait-based regression models of tree RGR. We generated models where species-mean RGR was modelled as a function of species-mean trait values and models where individual-level RGR and trait data were used. The species-level analyses found negative relationships between RGR and leaf toughness and wood resistance (Fig. 2). Tougher leaves and wood are considered conservative traits that are expected to lead to lower growth rates, making these results consistent with expectations from the previous literature (e.g. Coley, 1988; Chave *et al.*, 2009; Kitajima and Poorter, 2010; Kitajima *et al.*, 2012). We found a positive relationship between LDMC and RGR, which was not consistent with our expectation as higher LDMC is a conservative trait strategy. The positive relationship between RGR and LDMC may be explained by reduced herbivory levels in high LDMC species. However, the negative relationship between RGR and leaf toughness would suggest otherwise. These three relationships each explained about 20 % of the variation in RGR. Interestingly, we found a concave-up relationship between RGR and LMA that explained 58 % of the variation in RGR (Fig. 2). This may indicate that species with intermediate LMA values perform less well in this forest as compared with those with very acquisitive (i.e. low) or conservative (i.e. high) LMA values. This may be due to inter-specific partitioning of light gradients within the forest. The other three traits considered, LAR, leaf chlorophyll content and leaf thickness, had no relationship to RGR at the species level (Fig. 2).

The individual-level analyses regressed the growth deviation of an individual tree against the centred and scaled trait data from that tree. Recall, the growth deviation is the deviation in RGR of the individual tree from the mean RGR for the species. Thus, positive values indicate a tree with a faster RGR than average in the population. For all traits, except LAR, there were a few species with a linear or polynomial relationship with RGR. For example, two species had positive LMA–RGR relationships and two species had positive leaf thickness–RGR relationships (Table 2). Additionally, species varied in the sign of their trait–RGR relationship for three traits – leaf chlorophyll content, wood resistance and LDMC. These linear relationships indicate that traits on one extreme of the population-level trait distribution conferred a growth advantage during the study period. This contrasts with a handful of polynomial relationships we uncovered. Specifically, two species had concave-down LMA–RGR relationships, one species had a concave-up leaf chlorophyll content–RGR relationship, one species had a very weak concave-down leaf thickness–RGR relationship and one species had a very weak concave-up LDMC–RGR relationship (Supplementary data Table S2). The concave-down relationships indicate that extreme trait values in the population conferred a growth disadvantage, whereas concave-up relationships indicated that trait values on both extremes of the population-level trait distribution were advantageous. While we underscore, again, that our measurement of RGR over the study period is not a reliable predictor of individual fitness, we do argue that ecologists conducting trait-based analyses of plant performance should more routinely analyse their data on the individual level and place them into the present analytical context as it allows a clearer pathway for the integration of concepts

and empiricism between trait-based population and community ecology and evolutionary ecology.

Our results from the individual-level LAR–RGR analyses differed dramatically from those using other traits. Specifically, 17 out of 20 species had significant linear ($n = 15$) or polynomial models ($n = 2$). Both polynomial models were concave up, with one being quite weak. All but one of the linear relationships were positive (Table 3). The variance explained by the linear models was frequently higher than 30 % and in two cases exceptionally high (>70 %). Out of the 17 species with significant LAR models, 12 had r^2 values higher than any r^2 from a model using any other trait (Tables 2 and 3). From these results, we draw a few conclusions. First, we found trait–RGR relationships that varied in their shape, strength and sign across species. This, as with the other results, indicates that expecting consistent relationships between a single trait and RGR across species is unrealistic. It also may support the work of others indicating that interactions between traits or alternative traits should be considered (Iida et al., 2016; Swenson et al., 2017, 2020; Zambrano et al., 2017; Worthy et al. 2020). Secondly, LAR, while not totally consistent across species in its relationship with RGR, was clearly the best and most reliable predictor of tree RGR in this study. Importantly, when this trait is aggregated to a mean at the species level, it did not predict species-mean RGR (Fig. 2), which indicates that this trait can only be logically used at the individual level. Thirdly, while there is good reason to believe that the important trade-offs that occur at the organ or tissue scale such as leaf or wood economics traits (Reich et al., 1997; Chave et al., 2009) should be related to growth, the importance of allocation information and trade-offs at the organismal scale are underappreciated in most current trait-based studies of plant performance despite their importance being underscored in the plant growth literature (e.g. Poorter, 1989; Garnier, 1991; Enquist et al., 2007). Thus, models of tree growth that incorporate individual-level allocation information and integrate this information with organ-level, leaf-level in particular, traits representing key trade-offs should be a major focus going forward.

Individual-level phenotypically integrated models of growth

The results of our individual-level models showed that LAR was a strong, if not the strongest, trait predictor of RGR. Indeed, the amount of variation in RGR explained by this single trait is higher than most of the traits in the literature (Yang et al., 2018). Theory indicates that plant growth should scale with total photosynthetic mass (Niklas and Enquist, 2001), which may explain why LAR would predict RGR. However, this estimate of LAR is an imperfect measurement both of total crown leaf area and of leaf mass. Rather, the total leaf area in a crown would be better estimated by integrating our measure of LAR with a measure of LAI, which is the average number of leaves in a canopy per unit ground area. Adding an average LMA for the individual tree to a model including LAR and LAI would provide an estimate of the photosynthetic mass weighted by body size, which should produce improved models of RGR.

The results showed that our model of RGR that included LAR, LAI and LMA was superior, in terms of both WAIC and pseudo- R^2 , to any of the other sub-models that included some combination of LAR and LAI or LMA, or just LAR (Table 1). Additive models of LAR with LAI or LMA were superior to a model of RGR that just included LAR, but a model that included only an interaction between LAR and LAI did not provide a notable improvement over a model only including LAR (Table 1). Thus, a model that was based on a first principles integration of how crown properties and a leaf-level trait should impact growth outperformed a univariate model only considering LAR. We do note that the pseudo- R^2 values for these Bayesian models with slopes and intercepts for species modelled as random effects were generally lower than the r^2 values found for many of the species-specific ordinary least squares regression models of LAR onto RGR.

Hierarchical models of growth mixing individual- and species-level trait data

The models discussed to this point clearly demonstrate the importance of individual-level measurements of crown dimensions (i.e. LAR and LAI). Such data are not commonly measured in functional trait inventories, but they are not particularly hard to measure as they do not require leaf collection. As remote sensing (e.g. LiDAR) becomes more commonly utilized, we anticipate that estimates of LAR and LAI at the individual level may become commonplace. Our work shows that models of RGR that include these two variables perform well, but are slightly inferior to models that include individual-level LMA data. LMA can be challenging to collect in forests due to the difficulty in obtaining leaves from tall individuals. Thus, the collection of LAR and LAI may be able to scale easily, but LMA may remain difficult to collect. We therefore wanted to determine whether models of RGR that utilized individual-level LAR and LAI data, but species-level LMA data, were comparable with models that utilized individual-level LMA data.

We built hierarchical Bayesian models of RGR where the species-specific intercept and the slope on the LAR term were, themselves, modelled as a function of species-level LMA values (Table 1; Supplementary data Appendices 1–4). We generated two models using this approach – one with only LAR and one with LAR and LAI. These models were indistinguishable from one another in their quality (Table 1). Furthermore, neither of these models was an improvement on any of the models that utilized individual-level LAR and LAI data (Table 1). In other words, including species-mean LMA data in models with individual-level LAR and LAI data did not provide an improvement over models that did not have this information (Table 1). Taken together, these results show that our attempts to improve individual-level models by adding in additional species-level trait data were unsuccessful. This further underscores the importance of individual-level data for modelling tree RGR. Thus, the challenge moving forward will be to determine which methods can obtain individual-level data beyond the shape of canopies and LAI. Recent work indicates that traits such as LMA may be robustly estimated using remote sensing data products (Marconi et al., 2019a, b) and this may allow for

a viable and scalable approach for modelling individual-level tree growth based upon individual-level traits of known importance on stand to regional scales.

Conclusions

The key advantages of functional trait-based ecology are that the traits measured are representative of fundamental trade-offs and they are relatively easy to measure across systems. However, these advantages would be weakened if the traits collected did not convey information regarding the performance of individuals and, therefore, populations. The trait literature frequently utilizes mean trait values to represent all individuals in a population or species. This approach greatly reduces the resources needed for trait inventories, but the negative consequences of such data aggregation are not well established. Here, we have shown, using detailed individual-level trait and growth data for >500 rain forest trees, that models of RGRs suffer when species-level mean trait data are used. When individual-level data are utilized and we integrate individual-level trait data, our models of tree growth perform very well. This indicates that trait-based approaches are particularly powerful for modelling tree growth when collected and analysed at the individual level. Data collection or analyses that aggregate data to the population or species level will provide some insights, but these insights will be limited in most cases when modelling plant performance and, in some cases, misleading. Thus, the next great challenges will be developing phenotypically integrative models of tree growth parameterized at the individual level that will be made possible by scalable data collection methods.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Table S1: the 20 focal species used in this study and the number of trees with dendrometers. Table S2: second-order polynomial regression results for trait–RGR relationships at the individual level. Appendices 1 and 2: model description and directed acyclic graph (DAG) for the base model regressing individual-level leaf area ratio onto relative growth rate. Appendices 3 and 4: the STAN code utilized via the rstan package in R to run the base model regressing individual-level leaf area ratio onto relative growth rate.

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