COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Intraspecific variation in traits and tree growth along an elevational gradient in a subtropical forest

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Abstract

A conspicuous feature of natural communities is that individuals within species exhibit broad variation in their phenotype. While the phenotypic differences among species are prominent and have received considerable attention in earlier studies, recent findings suggest that about 40% of the trait variation is found within species. How this intraspecific variation is related to underlying environmental gradients and ultimately linked to performance is an outstanding question in ecology and evolution. Here, we study six broadly distributed species across an elevational gradient in a subtropical forest. We focused on five functional traits reflecting plant functional differentiation in stem transport, leaf architecture, and leaf resource acquisition. We found that leaf thickness, leaf toughness, and specific leaf area generally varied with elevation, while wood density and leaf area exhibited constrained variation. Results on multivariate trait axes also showed mixed evidence with the PC1 values (positively related to leaf toughness and negatively related to specific leaf area) shifting with elevation, while PC2 values (negatively related to wood density) did not change with elevation. We also found that, despite the important variation in some traits along the gradient, growth performance did not follow this same trend. This suggests that strong directional changes in traits along the gradient may result in similar levels of demographic performance. The results, therefore, challenge the simple expectation that a trait will correlate with a demographic rate. More nuanced approaches and additional mechanisms must be considered to advance understanding of the performance–trait relationships.

Introduction

A great diversity in form and function is conspicuous in nature, yet explaining the underlying factors promoting this great variation has been a long-lasting task in ecology. In

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particular, variation within species may account for up to 40% (Kattge et al. 2011) and empirical evidence has shown that intraspecific trait variation is remarkable for species widely distributed across environmental gradients (Jung et al. 2010; Messier et al. 2010; Fajardo and Siefert 2016). However, most previous ecological studies have focused on examining trait variation across species while intraspecific variation has remained frequently unstudied (reviewed by Violle et al. 2012; Roches et al. 2018), especially in species-rich ecosystems (Kraft et al. 2008; Swenson and Enquist 2009).

Species that exhibit wide spatial distributions generally encompass many different environments. As such, individuals often exhibit widespread variability in their characteristics that has been usually interpreted as the reflection of variation in environmental conditions and/or local adaptation (Cornwell and Ackerly 2009; Albert et al. 2011; Fajardo and Piper 2011). For example, trees occupying low elevations often have big and thin leaves, while individuals at high

elevations have smaller and thicker leaves (Vitousek et al. 1989; Hulshof et al. 2013). This high variation in leaf traits results as a response to environmental constraints in amount of radiation, CO_2 concentration, temperature, etc. that affect plant functioning (Körner 2007). These environmental constraints may operate on individual traits or simultaneously on sets of highly related traits that describe trade-offs in responses to the environment (Grime 1979; Shipley et al. 2006). Indeed, empirical evidence has shown that relationships between environment and multivariate trait axes can be stronger than with individual traits, suggesting that environmental filters select for ecological strategies that result from a combination of multiple traits (Kraft et al. 2015; Muscarella and Uriarte 2016).

Intraspecific responses to environmental gradients should also contribute to the fact that traits are not equally variable (Conover and Schultz 1995; Ackerly and Cornwell 2007; Albert et al. 2010; Jung et al. 2010; Messier et al. 2010; Siefert et al. 2015; Umaña et al. 2018a). For example, SLA and leaf thickness often show high intraspecific variation in response to environmental factors (Rozendaal et al. 2006; Vasseur et al. 2012) that results in changes that track the environment, while other leaf traits such as wood density show lower intraspecific variation (Siefert et al. 2015). This lack of variation across gradients may be due to constraints or due to counter-gradients that maintain phenotypes across the environment (Conover and Schultz 1995; Grether 2005). Thus, we may expect traits to shift across environments, but the magnitude of these shifts would vary depending on traits and the mechanisms governing this can be difficult to disentangle.

If traits vary across environments within species, then intraspecific variation in traits may be related to individual performance in one of two ways. First, traits and performance strongly covary within species along the gradient such that there is an optimal habitat for a species along the gradient that results in high performance due to an optimal trait or trait combination. Alternatively, variation in traits along the environment does not directly translate with clear variation in performance (Körner 1991) because organisms adjust their traits in order to maximize performance that remains relatively constant across the gradient of conditions. Similar ideas have been examined for communities at local scales showing that different species can achieve similar demographic performance through a different combination of traits (Hirose and Werger 1995; Alfaro et al. 2005; Marks and Lechowicz 2006; Pál et al. 2006). However, studies examining these ideas at the within-species level have received less attention with most of the literature focused on community-level responses (Jung et al. 2010; Liu et al. 2016; Umaña et al. 2018b).

To explore how traits and performance vary across environmental gradients, we focused on five leaf and wood density traits that represent major ecological strategies of plants related to resource acquisition strategies (Wright et al. 2004; Chave et al. 2009; Díaz et al. 2015; Messier et al. 2017). Specific leaf area describes the range of ecological strategies from "conservative" species characterized by low specific leaf area and long life span to "acquisitive" species with cheap leaves characterized by high specific leaf area and short life spans (Reich et al. 1997; Wright et al. 2004). Leaf area describes leaf structural support and organization to optimize light capture (Poorter and Rozendaal 2008; Messier et al. 2017). Leaf thickness and leaf toughness are structural traits positively related to leaf life span and negatively to herbivory rate (Kitajima and Poorter 2010). Wood density reflects trade-offs among three main aspects, mechanical stability, transport safety, and the efficiency in water transport (Chave et al. 2009). Individuals with higher wood density have greater mechanical support, higher conductive safety, but low conductive efficiency and slower volumetric growth rates (Stratton et al. 2000). In addition, we considered multivariate dimensions obtained from the combination of these five traits given that previous studies showed that environmental gradients also operate on multivariate trait dimensions (Kraft et al. 2015; Muscarella and Uriarte 2016).

Here, we studied six species distributed along an elevational gradient in a subtropical forest located in El Yunque, Puerto Rico. The variation in elevation encompasses shifts in several biotic and abiotic factors that affect species and functional composition of communities (Körner 2007; Swenson et al. 2011; Tello et al. 2015; Arellano et al. 2017). In particular for tropical systems, communities in high elevations experience increases in radiation, rainfall, humidity, and wind velocity as well as decreases in CO_2 concentration compared to low elevations (Brown et al. 1983; Körner 2007). Based on these environmental shifts, we asked whether the within-species traits varied along elevations and whether shifts in traits were reflected in shifts in performance. For the first question, we predict that leaf traits will become increasingly conservative at higher elevations in response to the high radiation, lower CO_2 concentration, and colder temperatures (Billings and Mooney 1968; Körner and Diemer 1987; Körner 2007). In addition, we expect to find declines in wood density along elevation suggesting more hydraulic efficiency and less structural support for individuals located at higher elevations given the high precipitation and short canopy height. The magnitude of these trait variations, however, will be trait dependent. Given that wood density has shown more constrained variation in previous studies (Siefert et al. 2015), we expect limited variation for this trait compared to the other leaf traits studied. Moreover, if environment operates strongly on multivariate axes than on single traits (Kraft et al. 2015; Muscarella and Uriarte 2016), we expect to find stronger effects of elevation on

multivariate axes than on individual traits. For the question on whether shifts in traits are reflected in shifts in performance, we expect two alternative outcomes, growth rates, like the traits, may vary with the environment, emphasizing the strong link between function and performance (Arnold 1983). If true, individuals with conservative traits (i.e., lower SLA and LA, and higher leaf thickness and toughness and wood density) should exhibit slower growth than individuals with more acquisitive traits. Alternatively, growth may not be correlated with trait variation and remain invariant along the gradient. This scenario would indicate that variation in traits is adjustments that individuals do to keep similar growth rates along the gradient or that traits are related to other unmeasured aspects of performance (i.e., reproduction).

Determining how within-species traits and growth vary along an environmental gradient for species that have wide distributions will provide further insights into population dynamics and has implications for predicting community structure in response of environmental changes (Hillebrand and Matthiessen 2009; Roches et al. 2018).

Materials and methods

Study area

The study was conducted near the El Verde Field Station (18º20′N, 65º49′W), which is located in the LTER site in the Luquillo Experimental Forest, Puerto Rico. The elevation in the study site ranges from 250 to 1075 m above the sea level (a.s.l). The lowest elevation is a pre-montane rainforest with a mean annual temperature of 24.5 °C and a mean annual rainfall of 2300 mm. The highest elevation (above 1000 m.a.s.l.) is a cloud forest with a mean temperature of 20 °C and a mean annual rainfall of 3600 mm. This study used information on the distribution of species along the Sonadora River based on 16 0.1-ha tree inventory plots that were established in 2001–2002. These plots were installed every 50 m in elevation from 250 to 1000 m.a.s.l. and all the trees with a diameter at breast height (DBH) > = 1 cm were identified to species and tagged (Swenson et al. 2011).

Species selection

Based upon the abundance of species in the 16 plots of 0.1-ha in area, we selected six distantly related focal species: *Cecropia schreberiana* Miq. subsp. *schreberiana* (Urticaceae), *Cordia borinquensis* Urb. (Boraginaceae), *Dacryodes excelsa* Vahl (Burseraceae), *Micropholis garciniifolia* Pierre (Sapotaceae), *Sloanea berteroana* Choisy ex DC. (Elaeocarpaceae), and *Henriettea squamulosa* (Cogn.) Judd (Melastomataceae). Specifically, we used the following

criteria for species selection: (1) distribution across at least eight out of 16 plots along the elevational gradient; (2) abundance higher than ten individuals per plot; and (3) stems at least 7 cm in diameter at breast height, thereby facilitating the installation of the dendrometers for measurements of growth. Among all the species recorded along the elevation plots, these were all the species that met the criteria. *C. schreberiana* Miq. subsp. *schreberiana* (CECSCH) is a pioneer species broadly distributed from 100 to 1300 m.a.s.l. *C. borinquensis* Urb. (CORBOR) is a mid-to-late-successional endemic species distributed from 300 to 1100 m.a.s.l. *D. excelsa* Vahl (DACEXC) is a late-successional tree distributed from 100 to 650 m.a.s.l and is one of the most common trees at low elevations. *H. squamulosa* (Cogn.) Judd (HENSQU) is an endemic species from Puerto Rico distributed from 600 to 1000 m.a.s.l and common in the Luquillo Sierra. *M. garciniifolia* Pierre (MICGAR) is an endemic late-successional species distributed from 500 to 1000 m.a.s.l. *S. berteroana* Choisy ex DC. (SLOBER) is a pioneer species distributed from 250 to 850 m and abundant between 300 and 350 m.a.s.l. DACEXC and SLOBER are shade-tolerant species.

Annual growth rate

Dendrometers were installed between August 2013 and November 2013 in 410 individuals for all six species. Between four and 13 individuals per species were selected from each elevation belt (except for 950 and 1000 m where individuals of HENSQU and MICGAR were extremely rare and only one to three individuals were monitored) (Table S1). The individuals were selected from the 0.1-ha inventory plots or the surroundings in cases when no more trees were found within the plots. When individuals were selected from outside of the plots, we checked the elevation with a GPS to assure that all individuals were within the same elevation belt. After installation, the dendrometers were allowed to settle and the first stable measurement was recorded in July 2014. Annual diameter increment rate was estimated for each individual tree as a function of diameter growth (in millimeters) from summer 2014 to summer 2015 (the inter-census interval was estimated using exact census dates) following Condit (http://ctfs.si.edu/Public/CTFSRPackage/). Trees with annual diameter increment rate > 75 mm were not considered in the analyses (only one tree) (Rüger et al. 2011). Elevations with less than two individuals per species were removed from the analyses.

Functional traits

The 410 individuals monitored for growth were sampled to take measurements of specific leaf area (SLA in $cm^2\ g^{-1}$), leaf area (LA cm^2), leaf toughness (Newton), leaf thickness

(μm), and wood density (WD, g cm^{-3}). For HENSQU 62, individuals were collected, for CECSCH 56, for CORBOR 70, for DACEXC 66, for MICGAR 77, and for SLOBER 79. We selected these traits because they represent main trait dimensions of phenotypic variation not related to reproductive strategies. The SLA is correlated with mass-based photosynthetic rates (Wright et al. 2004) and has shown important intraspecific variation across environmental gradients (Jung et al. 2010; Messier et al. 2010). Leaf toughness and leaf thickness are correlated with SLA and are related to the leaf mechanical properties important in protecting against herbivore damage and leaf life span (Kitajima and Poorter 2010; Onoda et al. 2011; Westbrook et al. 2011; Messier et al. 2017). Leaf area is an architectural trait independent from the LES associated with strategies of light capture and is known to vary with elevation (Dolph and Dilcher 1980; Westoby et al. 2002; Poorter and Rozendaal 2008). Wood density is highly correlated with stem wood density and represents the wood economic spectrum representing trade-offs between mechanical support and transport efficiency and safety (Swenson and Enquist 2008; Chave et al. 2009).

We collected branches from the top-half of the crown using a telescopic pole and selected the most sun-exposed leaves. The leaf traits were measured for each individual of each species by selecting 1–3 fully expanded leaves. Leaf thickness was measured on fresh material with a digital micrometer (Mitutoyo, 0.001 mm), and leaf toughness was also measured on fresh material using a penetrometer (IMADA, DS2-11). For leaf area and specific leaf area, we scanned fresh leaves and then measured the dry mass after putting the leaves in the oven at 72 °C for 72 h. Our methods followed the methodology described by Cornelissen et al. (2003). For wood density, we selected branches between 5 and 10 cm in length from each of the individuals. These branches were all from the peripheral crown exposed to the full sun. Each branch cylinder was carefully peeled to remove the most external cortex, measured for total length and diameter at the midsection, and then dried for 4–5 days at 72 °C to assess the dry biomass. Wood density for CECSCH was assessed in a different way, given that this species has hollow stems. We removed the internal tissue carefully and measured the internal diameter in addition to the external diameter and total length. We subtracted the internal from the external cylinder.

All traits, except wood density, were log-transformed to reduce skewness and all traits were posteriorly standardized to mean 0 and standard deviation of 1 before conducting the analyses for easy comparison. In addition, we performed a principal component analysis using all traits for multivariate analyses; these traits were reduced to two orthogonal axes that explained the 91% of the variance in the total traits by performing a principal component analysis (Table S2, Fig. S1). The first PC axis (PC1) explained the 69% of the

trait variation and was strongly and positively related to leaf toughness and negatively related to specific leaf area. The second PC axis (PC2) explained the 17% of the trait variation and was strongly and negatively related to wood density.

Analyses

Variation in traits along the elevational gradient

The first part of analyses consisted of evaluating the change in traits within species along the elevational gradient. Separately for each species, each trait was analyzed independently to evaluate its relationship with elevation. For these models, we modeled the elevation and DBH as fixed effects. Log-transformed DBH was included in the model to control for any effect that size might have on functional traits (Spasojevic et al. 2014). We used a different set of linear models (LM) to analyze our data using the function lm in R (R Core Team 2018). In addition, to compare the amount of trait variation explained by elevation, species, and within-species levels, we compared the variance in traits across different organization levels: across elevation, species, populations (individuals within a given elevation belt), and individuals. To do this, we performed variance-partitioning analyses by fitting general linear models to the variance across the four nested organization levels. Then, we performed a variance component analysis using the function "varcomp" in R.

Relationships between traits and tree growth

To address the second question, we modeled log-transformed annual diameter increment as a function of traits or trait-based PC axes. We included tree size (log-transformed DBH) as a fixed effect as tree size can significantly influence growth rates (Laurance et al. 2006). We also included elevation as a fixed effect to account for the potential variation in growth along elevation. For this part, we tested a total of nine models for each species that included individual and multivariate traits as fixed effects. The list of models includes: a model that only included DBH and elevation as fixed effects with no trait data included; five models testing for univariate relationships for each trait; two models using the first two PC axes as fixed factors separately; an additional model that included both orthogonal PC axes as fixed effects. The models were compared using the Akaike's information criterion (AIC), and the model with the lowest AIC value was chosen as the best fit. Models with AIC differences in less than two units were considered not different (Burnham and Anderson 2002). The residual plots for each of the models were checked for linearity, homoscedasticity, and normality. In addition, we evaluated model fits using adjusted R^2. The models were implemented using linear

effect models using the function "lm" in R (R Core Team 2018).

Results

Variation in traits along the elevational gradient

Individual and multivariate traits varied significantly along the range of elevations, but the magnitude of variation was highly dependent on the trait and species (Table 1). Specifically, LA decreased along elevation but the effect was only significant in one out of six species and the adjusted R^2 value for this model was 0.17 (Table 1). SLA decreased along elevation (four species) and the adjusted R^2 values ranged between 0.04 and 0.56. Wood density increased with elevation for one species, and the adjusted R^2 value for this model was 0.34. Leaf thickness increased along the gradient (five species), and the adjusted R^2 values ranged between 0.16 and 0.37. Leaf toughness increased along the gradient (three species), and the adjusted R^2 values ranged between 0.14 and 0.19. Results for multivariate axes showed that that PC1 (strongly and negatively associated with SLA and positively associated with leaf thickness and toughness) increased along the elevation (five species) and the adjusted R^2 values ranged between 0.18 and 0.47 (Table 1, Fig. 1). PC2 (negatively associated with wood density and positively associated with leaf area) was positively related to elevation, but the effect was only significant in one species and the adjusted R^2 was 0.32 (Table 1, Fig. 2). Combined, these results show that for all six species, leaves at higher elevations tend to be thicker and display a more conservative strategy on carbon assimilation rates than at lower elevations.

In addition, we performed variance-partitioning analyses in traits to compare the amount of variation explained across and within species. The results showed that trait variation across species ranged between 46.8% and 31.2%, the variation across populations (individuals within the same elevation belt) ranged between 46.5% and 31.2%, and the variation across individuals in the same elevation ranged between 6.7% and 19.1% (Table 2).

Relationships between traits and tree growth

Results from the models evaluating the relationship between annual diameter increment and traits showed that traits were not good predictors of tree growth (Tables 3 and S3, Fig. 3). We found that several models per species performed equally well and were all selected as best models (AIC values = < 2) (Tables 3). Although the set of best models varied depending on species, in all cases, the model that did not include any trait information was selected as one of the best models. This indicates that including trait information does not improve
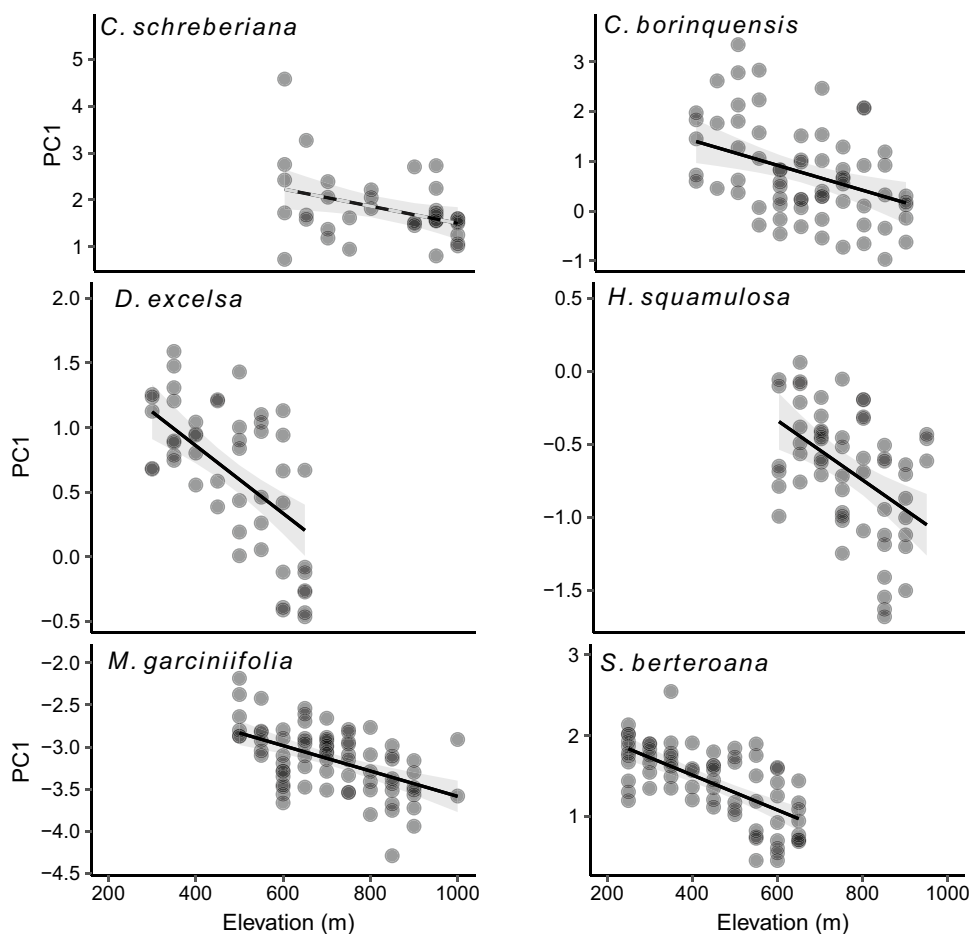
Table 1 Coefficient estimates of elevation and adjusted coefficients of determination for linear models predicting trait variation within species

Species	LA		SLA		WD		Leaf thickness		Leaf toughness		PC 1		PC 2	
	Effect	Adj. R^2	Effect	Adj. R^2	Effect	Adj. R^2	Effect	Adj. R^2	Effect	Adj. R^2	Effect	Adj. R^2	Effect	Adj. R^2
CECSCH	0.001	0.08	<−0.001	0.04	**0.002**	**0.34**	<0.001	0.07	−0.001	0.18	−0.001	0.02	**−0.003**	**0.32**
CORBOR	−0.001	0.05	<−0.001	0.15	<0.001	0.09	**<0.001**	**0.3**	**<0.001**	**0.11**	**−0.002**	**0.22**	<0.001	−0.03
DACEXC	−0.001	−0.01	**−0.001**	**0.56**	<0.001	0.06	**<0.001**	**0.35**	<0.001	0.16	**−0.003**	**0.47**	<0.001	−0.05
HENSQU	<−0.001	−0.03	**<−0.001**	**0.04**	<0.001	0.02	**<0.001**	**0.16**	**<0.001**	**0.19**	**−0.002**	**0.18**	<0.001	−0.02
MICGAR	**−0.001**	**0.17**	**−0.001**	**0.25**	<−0.001	−0.02	**<0.001**	**0.37**	<0.001	−0.01	**−0.002**	**0.25**	<0.001	0.06
SLOBER	−0.001	0.06	**−0.001**	**0.45**	<0.001	0.13	**<0.001**	**0.25**	**<0.001**	**0.14**	**−0.002**	**0.41**	<0.001	−0.01

Adjusted coefficients of determination with negative values can be interpreted as zero. Numbers in bold represent significant values with $P < 0.05$

LA leaf area, *SLA* specific leaf area, *WD* wood density, *PC1* and *PC2* axis 1 and 2 from principal component analysis for trait values. CECSCH *Cecropia schreberiana* Miq. subsp. *schreberiana*, CORBOR *Cordia borinquensis* Urb., DACEXC *Dacryodes excelsa* Vahl, HENSQU *Henriettea squamulosa* (Cogn.) Judd, MICGAR *Micropholis garciniifolia* Pierre, SLOBER *Sloanea berteroana* Choisy ex DC

Fig. 1 Variation in multivariate trait axis PC1 along the elevational gradient for six tropical tree species. Continuous lines indicate significant relationships (95% confidence intervals do not cross zero), and the dashed line shows a nonsignificant relationship (*C. schreberiana* is the only nonsignificant relationship)

the predictive power of the models. The R^2 values for the best models ranged from 0 to 0.08 (Table 3). In addition, the trait coefficient estimates for the best models were not significant (Fig. 3, Table S3).

Discussion

Species distributions often encompass different environments that influence their phenotype and performance. In this study, we examined the intraspecific variation in traits for six species distributed along an elevational gradient and its relationship with annual diameter growth rates. We found that SLA, leaf thickness, and toughness varied along elevation for most of the species, a pattern that was also consistent with results in multivariate space, with PC1 showing a significant positive relationship with elevation. However, this variation in traits did not translate to variation in tree growth. We infer from these results that trait changes along environmental gradients might not relate to growth due to a variety of factors including the balance between cost and benefits of different functions that combined result in a similar diameter growth performance. We discussed in more detail our

results below and their implications for the assumption in trait-based ecology that trait values can be directly related to performance.

Intraspecific trait variation along elevation

In terms of the intraspecific trait variation along elevation, we found that leaf variation reflects a similar trend to the changes observed at the community-level across species in this forest (Swenson et al. 2011). Leaves at higher elevations tend to be thicker, tougher, and with lower light capturing area per unit of biomass investment (low SLA), characteristics that are necessary for the high radiation and the lower CO_2 concentrations occurring at high elevations (Billings and Mooney 1968; Körner and Diemer 1987; Körner 2007). This result is congruent with the high trait variance found at the intraspecific level (Table 2) and emphasizes the great ability of these broadly distributed tree species to adjust leaf traits to the local environmental conditions. Our findings are also consistent with results from other tropical and temperate forests that have shown remarkable intraspecific variation in SLA along environmental gradients and suggest that SLA tends to be, in general, more variable than other traits at the

Fig. 2 Variation in multivariate trait axis PC2 along the elevational gradient for six tropical tree species. The continuous line indicates a significant relationship (95% confidence intervals do not cross zero), and dashed lines show nonsignificant relationships
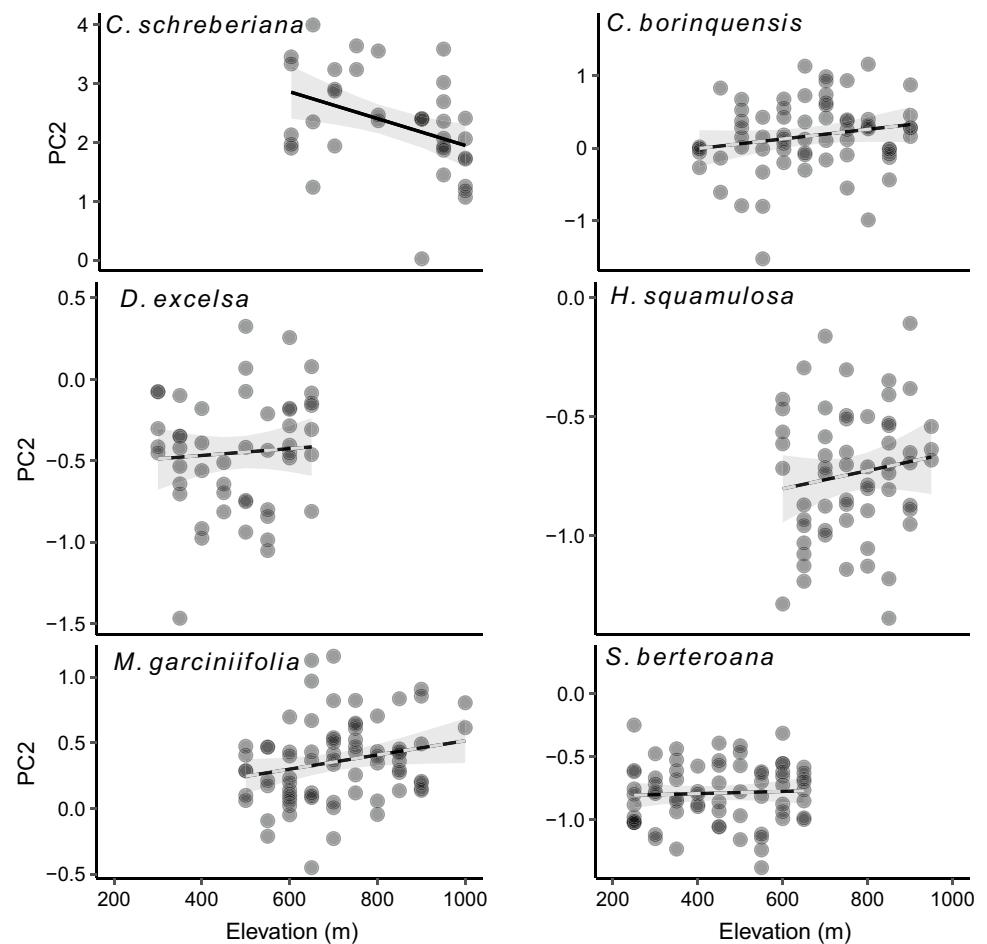

Table 2 Percentage of variance explained across elevation, species, populations (individuals of a given species within a particular elevation belt), and individual trees (and error variance component) for leaf and wood traits

	Elevation (%)	Species (%)	Population (%)	Individual + error (%)
Log leaf area	0.0	46.8	46.5	6.7
Log specific leaf area	0.0	40.5	40.5	19.1
Log leaf thickness	29.2	31.2	31.2	8.4
Log leaf toughness	0.0	44.3	44.2	11.5
Wood density	0.0	42.5	42.7	14.7

within-species level (Albert et al. 2010; Messier et al. 2010; Fajardo and Piper 2011).

Among the leaf traits analyzed, leaf area showed a distinctive pattern of intraspecific variation characterized by weak variation along elevation (only one species showed significant trend along elevation). Leaf area (LA) has been described as an independent axis of the leaf economic traits (i.e., SLA) (Westoby et al. 2002); therefore, it is not surprising to observe discrepancies in trait variation patterns between SLA and LA at the within-species level. This result suggests that environmental gradients operate with different strengths on distinct functional dimensions and species.

Similarly, as with leaf area, the patterns of variation along elevation for wood density were nonsignificant for five out of the six species studied. Although previous studies have also found low variation in wood density at the intraspecific level, within and across different communities (Fajardo and Piper 2011; Siefert et al. 2015; Fajardo 2016), we expected to find some signal of trait adjustment to this gradient. The elevational gradient in Puerto Rico exhibits a pronounced variation in precipitation and canopy height with high elevations being wetter and shorter in maximum tree stature. Thus, we expected these two factors to impact the distribution of wood density along elevation. The observed lack of signal

Table 3 Differences in AIC values (Δ), weight of AIC values (W), and adjusted coefficients of determination (R^2) for the different models evaluating the impact of traits on diameter growth

Model	CECSCH			CORBOR			DACEXC			HENSQU			MICGAR			SLOBER		
	Δ	W	R^2	Δ	W	R^2	Δ	W	R^2	Δ	W	R^2	Δ	W	R^2	Δ	W	R^2
AGR ~	**0.04**	**0.22**	**−0.02**	**1.16**	**0.16**	**−0.01**	**0**	**0.29**	**0.08**	**0**	**0.41**	**0.05**	**0.79**	**0.09**	**−0.01**	**0**	**0.32**	**−0.01**
AGR ~ log(LA)	**0**	**0.22**	**0.03**	3.35	0.05	−0.02	2.75	0.07	0.06	2.82	0.1	0.04	**0.54**	**0.11**	**0.02**	3.99	0.04	−0.05
AGR ~ log(SLA)	**1.91**	**0.09**	**−0.02**	2.94	0.07	−0.01	2.73	0.07	0.06	3.91	0.06	0.02	**0.45**	**0.11**	**0.02**	2.22	0.11	−0.02
AGR ~ log(WD)	**1.24**	**0.12**	**−0.002**	**0**	**0.28**	**0.03**	3	0.06	0.06	3.92	0.06	0.02	**0.04**	**0.14**	**0.03**	3.11	0.07	−0.03
AGR ~ log(thickness)	2.11	0.08	−0.03	2.29	0.09	−0.003	**1.84**	**0.12**	**0.08**	2.05	0.15	0.05	**0.45**	**0.11**	**0.02**	2.4	0.1	−0.02
AGR ~ log(toughness)	**1.99**	**0.08**	**−0.02**	2.95	0.07	−0.01	**1.48**	**0.14**	**0.09**	3.71	0.06	0.02	**0.07**	**0.13**	**0.03**	**1.04**	**0.19**	**−0.002**
AGR ~ PC1	2.11	0.08	−0.03	**1.81**	**0.11**	**0.004**	**1.69**	**0.13**	**0.08**	3.94	0.06	0.02	**0.46**	**0.11**	**0.02**	3.45	0.06	−0.04
AGR ~ PC2	2.1	0.08	−0.03	3.06	0.06	−0.01	3.06	0.06	0.06	3.36	0.08	0.03	**0**	**0.14**	**0.03**	3.82	0.05	−0.04
AGR ~ PC1 + PC2	4.09	0.03	−0.06	2.06	0.1	0.01	3.57	0.05	0.07	5.34	0.03	0.01	**1.95**	**0.05**	**0.01**	5.39	0.02	−0.05

Columns represent the different species and rows represent the different models that were tested. Bold numbers highlight the best models for each species. All models include log(DBH) and elevation as additional fixed effects. AGR refers to log-transformed annual diameter growth. Species and trait codes are the same than in Table 1
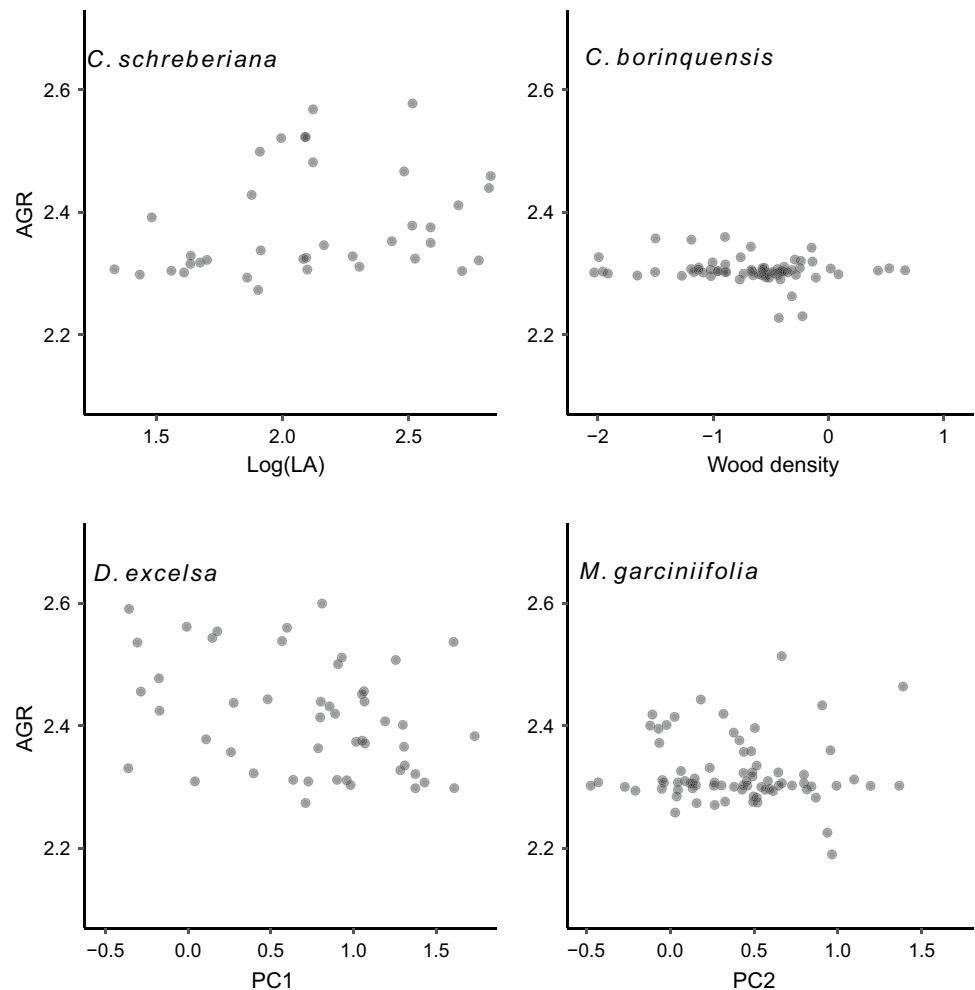
for wood density might be related to the fact that this trait is related to distinct functions. (i.e., support and hydraulic functions) that may conflict when multiple abiotic factors change along elevation. In fact, previous studies have found mixed evidence for the different trade-offs that are related to this trait (Preston et al. 1999; Pratt et al. 2007; Chave et al. 2009). Alternatively, the lack of shifts in trait values across the gradient may simply be the outcome of counter-gradients (genetic and environmental; Conover and Schultz 1995) and future investigations are needed to disentangle these possibilities.

In terms of multivariate trends, PC1 showed a higher number of significant relationships with elevation than for most of the individual traits and, in some cases, the relationships were stronger (Table 1). This result agrees with previous studies that show stronger relationships when using multivariate axes compared to individual traits (Kraft et al. 2015; Muscarella and Uriarte 2016) and supports the idea that environmental shifts in this forest exert a stronger constraint on the combination of SLA, leaf thickness, and leaf toughness traits than over single traits. On the other hand, the analyses of PC2 did not result in a larger number of significant or stronger relationships with elevation than the analyses based on individual traits (Table 1). The PC2 explained only 17% of the trait variation and the two traits that were more strongly related to this axis (LA and wood density) did not show strong individual responses to shifts in elevation. Only in the case of CECSCH, wood density and PC2 showed significant relationships with elevation suggesting that environmental selecting forces depend on species and traits considered. Combined, our results suggest that, while environmental constraints may operate strongly on some multivariate axes, we should consider that organismal traits are multidimensional and that the environment may operate differentially on distinct dimensions. Thus, our results support the use of a combination of multivariate and individual traits to gain insights into the variation of functional strategies along environmental gradients.

Variation in traits across species

We found that the strength of the relationships between elevation and intraspecific traits depends on species. This result is expected given that different taxa may have different plasticity and genetic variability (Rozendaal et al. 2006). In addition, the species in this study vary widely in life history strategies, which might also explain some of the observed differences in trait and growth trends across taxa. For example, CECSCH is a pioneer species characterized by fast growth rates and acquisitive traits (i.e., low wood density), while MICGAR is a more late-successional species that grows more slowly and exhibits more conservative traits (i.e., small and thick leaves and high wood density).

Fig. 3 Relationships between traits (individual traits or multivariate trait axes) and tree annual growth rates for models with the lowest AIC values. Wood density and log-transformed leaf area values were standardized to mean 0 and standard deviation of 1. For HENSQU and SLOBER, the lowest AIC models did not include trait information and are not shown in this figure. All trait effects were nonsignificant (Table S3)

Growth responses to trait variations along elevation

Despite the important variation in leaf traits tracking environmental changes along elevation, the patterns for annual diameter growth rates showed nonsignificant relationships with the traits measured. Even when considering the combined effects of multivariate axes, trait variation did not reflect changes in growth. These results disagree with previous studies showing that the integration of trait information on individual-level improves the strength of the relationships between traits and growth (Liu et al. 2016; Umaña et al. 2018b).

One potential explanation for the lack of trait effect on growth is that species might adjust their traits to different conditions in order to maintain similar performance along the elevational gradient. This is congruent with our second hypothesis for question two. For example, individuals at lower elevations have thin and "cheap" leaves that may also have bigger crowns (high architectural costs), while at higher elevations species tend to exhibit thick and low SLA leaves that often involve high construction cost and small crowns

(low construction cost) (personal observation). We know of one previous study that found evidence for compensatory strategies among tree species that balanced light-use efficiency and light capturing (Hirose and Werger 1995). Additional work has shown that integrating leaf traits with crown architecture can lead to strong models of tree performance (Enquist et al. 2007; Yang et al. 2018). Therefore, the balance in costs and benefits could be similar between individuals at high and low elevations, which results in flat slopes for performance across the gradient. This further suggests that the pathways relating functional traits and performance are not dependent on single traits, or few multivariate axes (Clark et al. 2007). Instead, tree performance may result from the aggregated impact of multiple and highly dimensional traits (Arnold 1983; Marks and Lechowicz 2006; Armbruster et al. 2014). Although in this study we focused on only five traits, there are additional unmeasured traits that potentially have direct or indirect effects on performance. Indeed, previous studies have described the relationship between traits and performance as a hierarchical network of interactions where the performance currency is at the top

underlying traits of different levels of integration (e.g., low levels in the hierarchy would represent traits of a low level of integration) (Arnold 1983; Marks 2007). A further step for future studies would require the integration of organ-level traits at higher organizational orders that are likely playing a stronger role in determining individual performance and would provide a better explanation of how individuals are distributing different costs to different traits (Arnold 1983; Marks 2007).

An additional non-mutually exclusive explanation for the lack of predictive power of traits could be that there are additional fitness components such as survival and reproduction that were not explicitly evaluated in this study and that could have been more strongly affected by the variation in traits (Arnold 1983). Furthermore, the local abiotic environment and biotic interactions at the neighborhood scale might have an important effect on trees' annual growth rates (Uriarte et al. 2010; Paine et al. 2011; Lasky et al. 2014) and these effects were not explicitly considered in this study. Ideally, future work will be able to consider the genetic structure within and across populations, perform common garden experiments, and measure the impacts of all possible biotic interactors.

Conclusions

In summary, our results indicate that at intraspecific level, species are able to adjust their traits in response to the environment. Further, using multivariate axes may improve the strength of the relationships with environment. However, the traits responses to elevation did not translate into variation in tree growth rates. These results indicate that the adjustments in traits may bring cost and benefits that are balanced across individuals in different environments resulting in similar performance along environmental gradients. We suggest that a deeper understanding of the linkage between traits and growth requires an additional step of linking traits at higher organization levels and adding traits that represent additional functional dimensions. Our results have implications for predicting population and community structure by suggesting that forest responses to environmental shifts cannot be assessed without accounting for intraspecific trait information. It is important to use multiple traits that reflect the multidimensional functionality of organisms and the diversity of responses across species. Ultimately, integrating intraspecific information will refine our understanding of biodiversity and ecosystem functioning.

Compliance with ethical standards

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