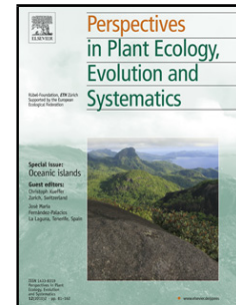# Accepted Manuscript

Title: VARIATION OF TROPICAL FOREST ASSEMBLY PROCESSES ACROSS REGIONAL ENVIRONMENTAL GRADIENTS

Author: Robert Muscarella María Uriarte David L. Erickson Nathan G. Swenson W. John Kress Jess K. Zimmerman

Please cite this article as: Muscarella, Robert, Uriarte, María, Erickson, David L., Swenson, Nathan G., Kress, W.John, Zimmerman, Jess K., VARIATION OF TROPICAL FOREST ASSEMBLY PROCESSES ACROSS REGIONAL ENVIRONMENTAL GRADIENTS.Perspectives in Plant Ecology, Evolution and Systematics http://dx.doi.org/10.1016/j.ppees.2016.09.007

VARIATION OF TROPICAL FOREST ASSEMBLY PROCESSES ACROSS REGIONAL ENVIRONMENTAL GRADIENTS

Robert Muscarella[1,2*], María Uriarte[1], David L. Erickson[3], Nathan G. Swenson[4], W. John Kress[3], Jess K. Zimmerman[5]

[1] Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York, USA

[2] Ecoinformatics and Biodiversity, Aarhus University, Aarhus, Denmark

[3] Department of Botany, National Museum of Natural History Smithsonian Institution, Washington, D.C., USA

[4] Department of Biology, University of Maryland, College Park, Maryland 20742, USA

[5] Department of Environmental Science, University of Puerto Rico, San Juan, Puerto Rico, USA

*Correspondence: bob.muscarella@gmail.com

Running head: Shifting assembly mechanisms across regional gradients

HIGHLIGHTS

- Our results suggest variation in assembly processes of forests in Puerto Rico.
- Shifts of mean traits link functional strategies with abiotic filtering processes.
- Diversity metrics suggest abiotic filtering and competition for light.
- We highlight the need to consider complex gradients at large spatial scales.

ABSTRACT

Determining how the relative strength of community assembly processes varies along resource

gradients is critical for understanding community responses to environmental change. A key

challenge for addressing this issue at regional scales is that environmental gradients typically

encompass multiple coupled resource gradients (*e.g.* water, light, soils), which can complicate

hypotheses about the drivers of community variation. We used data on functional traits and

phylogenetic relatedness to infer assembly processes of tree communities across regional

environmental gradients in Puerto Rico.

We censused trees in 24, 0.25-ha mature plots located along a precipitation gradient and

on soils derived from two parent materials (limestone and volcanic). In each plot, we quantified

abiotic conditions in terms of mean annual precipitation, canopy openness, and soil nutrients.

We used three functional traits with relevance for drought tolerance and resource acquisition

strategies (wood density [WD], leaf mass per area [LMA], and maximum height [H_{max}]), and a

molecular phylogeny, to characterize tree community composition in terms of (i) community-

weighted mean trait values (i.e., plot average trait values, weighted by relative basal area), (ii)

functional diversity, and (iii) phylogenetic diversity.

Mean annual precipitation was negatively correlated with understory light availability

(for plots on both soil types), and soil fertility (among plots on limestone soils). Soil fertility

varied substantially between plots on each parent material, and was generally higher among plots

on limestone-derived soils. Among the limestone soil plots, which occur on the drier half of the precipitation gradient, increasing mean annual precipitation was associated with lower community-weighted mean WD and LMA, and taller H_{max}. Additionally, functional diversity (of WD and H_{max}) and phylogenetic diversity increased with precipitation among limestone soil plots, suggesting an important role for abiotic filtering in driving functional and phylogenetic convergence in arid conditions. In contrast, we did not find significant relationships between environmental conditions and community-weighted mean traits or diversity metrics among plots on volcanic-derived soils, which occur along the wetter half of the precipitation gradient.

Together, our results suggest that drought tolerance is the dominant assembly mechanism controlling tree composition in dry forests. In wetter forests, functional diversity appears to be maintained by a combination of hierarchical competition for light and niche partitioning. Overall, our results exhibit geographic variation in the mechanisms governing composition of tropical forests across regional environmental gradients, and highlight the importance of considering complex environmental gradients at large spatial scales.

Abbreviations: *CWM = community-weighed mean, SES.MPD$_{FUN}$ = standardized effect size of mean pairwise functional distance, SES.MPD$_{PHY}$ = standardized effect size of mean pairwise phylogenetic distance, WD = wood density, LMA = leaf dry mass per area, H$_{max}$ = maximum height; PIC = phylogenetic independent contrasts*

Key-words: *Abiotic filtering; competition; wood density; LMA; maximum height; functional diversity*

INTRODUCTION

Determining how the relative strengths of community assembly processes vary along resource gradients is a central goal in ecology (Weiher et al., 2011; Whittaker, 1967). Addressing this issue across regional scales in natural systems is critical for understanding how environmental change will alter the composition of ecological communities. One major challenge, however, is that broad scale environmental gradients typically encompass multiple coupled resources (*e.g.* water, light, soils), which can complicate hypotheses about the drivers of community variation.

Plant functional traits can provide insight to the physiological mechanisms that link assembly processes with patterns of community composition (Bernard-Verdier et al., 2012; Mason et al., 2012; McGill et al., 2006). An important step for interpreting functional patterns as evidence for community assembly processes, however, is to identify the physiological mechanisms that link various functional traits to particular assembly processes. For instance, the concept of abiotic (or 'environmental') filtering implies a selective pressure for traits that confer conservative resource-use strategies under low resource conditions because species with acquisitive life history strategies are unable to persist (Reich, 2014; Weiher and Keddy, 1995). In drought-prone environments, high wood density (WD, g cm^{-3}) confers a survival advantage for trees because it is associated with greater resistance to drought-induced xylem cavitation (Chave et al., 2009; Hacke et al., 2001). Leaf traits associated with low water loss through transpiration (e.g., high leaf dry mass per area, LMA = 1/SLA, g m^{-2}) also reflect tolerance to limited water availability (Poorter et al., 2009; Wright et al., 2001). In wetter conditions, traits that confer 'acquisitive' strategies associated with rapid resource acquisition and exploitation may be favored via competitive dominance hierarchies (Kunstler et al., 2016). For instance, rapid growth and tall stature can confer competitive dominance for light capture that may become a

stronger determinant of community composition as water availability (and productivity) increases.

Interactions among resource gradients can, however, complicate these relatively straightforward predictions (Fig. 1). For example, higher annual precipitation is generally associated with higher net primary productivity (NPP; Chapin et al., 2002; Zhao and Running, 2010) and a concomitant reduction of understory light availability (Bazzaz, 1979; Bazzaz and Pickett, 1980). Because plants' water and carbon economies are inextricably linked, a negative relationship between water and understory light availability may lead to different hypotheses about functional strategies that should be favored at opposite ends of the gradient (i.e., drought tolerance vs. shade tolerance). Meanwhile, precipitation can also influence soil nutrient availability: higher precipitation is related to higher rates of soil leaching (Austin and Vitousek, 1998; Radulovich and Sollins, 1991; Schuur and Matson, 2001) but higher NPP can also be related to greater nutrient inputs via rapid litter recycling. Moreover, soil nutrient availability has been shown to interact with light availability to mediate plant performance (Russo et al., 2005). Disentangling the joint influences of such coupled gradients is essential for understanding the drivers of community composition at large spatial scales.

To date, the most prominent hypothesis in functional (and phylogenetic) community ecology is that relatively strong competitive interactions in areas of high resource availability should lead to high local diversity as a result of niche partitioning (Kraft and Ackerly, 2010; Mason et al., 2013; Muscarella et al., 2014; Swenson et al., 2006). In terms of coexistence theory (Chesson, 2000), this hypothesis emphasizes the role of interspecific niche differences in maintaining local diversity. In contrast, however, competitive dominance hierarchies can also constrain the local diversity of traits that mediate fitness differences among species (Grime,

2006; Kunstler et al., 2016; Kunstler et al., 2012; Lasky et al., 2014; Mayfield and Levine, 2010; Navas and Violle, 2009). This scenario can result in the opposite pattern whereby functional (and potentially phylogenetic) diversity declines with increasing resource availability. In fact, Navas and Violle (2009) proposed that local functional diversity should be highest in sites where the importance of resource competition for structuring communities is intermediate because traits that convey both stress tolerance and competitive dominance would represent viable life history strategies. According to this hypothesis, communities that are very strongly influenced by either abiotic stress or competitive interactions are expected to display relatively low functional diversity (Grime, 2006; Mayfield and Levine, 2010).

Contemporary patterns of functional community composition reflect the combined effects of the assembly processes described above (i.e., abiotic filtering and niche partitioning) as well as biogeographic history. Analysis of the phylogenetic diversity in local communities can help clarify the degree to which functional patterns observed today result from shared ancestry versus convergent evolution to similar environmental conditions (Cavender-Bares et al., 2009; Muscarella et al., 2016). Combining metrics of functional and phylogenetic community composition can offer under-exploited insight to the links between resource availability and (contemporary and historical) assembly process across environmental gradients (Fig. 1a; Bernard-Verdier et al., 2012; Cornwell and Ackerly, 2009; Mason et al., 2012; Muscarella et al., 2016; Spasojevic and Suding, 2012; Weeks et al., 2016).

We quantified functional and phylogenetic aspects of forest composition across regional environmental gradients on the island of Puerto Rico defined by precipitation, soil fertility, and understory light availability. To disentangle the processes structuring tree community composition, we focused on community-level patterns of three traits (WD, LMA, and maximum

6

height [H_{max}]) that are relevant to drought tolerance, light acquisition, and soil resource-use. We used an island-wide molecular phylogeny of trees to quantify phylogenetic community composition. We addressed the following questions:

1) **How do light and soil conditions vary along the precipitation gradient?** We expected mean annual precipitation to be negatively correlated with understory light availability irrespective of soil type. We also expected a negative correlation between mean annual precipitation and soil fertility because of higher rates of soil leaching in wetter forests.

2) **How do dominant trait values shift along the regional environmental gradients?** Based on their relevance to drought-tolerance, light acquisition, and soil resource-use strategies, we predicted that community-mean values of WD and LMA would (i) decline with increasing precipitation and (ii) be lower in plots with volcanically-derived versus limestone-derived soils with similar levels of precipitation because of they generally have lower water holding capacity (Camacho, 2005; Soil Survey Staff, 2015). Additionally, if hierarchical competition for light becomes a stronger determinant of community composition with increasing water availability, we expected (i) community-mean H_{max} to increase with precipitation and (ii) to be higher in plots with volcanically-derived versus limestone-derived soils.

3) **How do functional and phylogenetic diversity patterns vary along these environmental gradients?** If tolerance to drought is the strongest determinant of community composition in arid sites, we expected that species in dry plots on limestone-derived soils would exhibit a relatively clustered subset of traits related to drought-tolerance and conservative water balance (high WD, LMA, and low H_{max}). If competitive dominance for light capture becomes a stronger determinant of local composition as water availability increases, we expected functional clustering of traits related to rapid and pre-emptive light acquisition

7

strategies (low WD and LMA, high H_{max}). Alternatively, a strong role of niche partitioning for light resources in more productive sites could lead to high functional diversity of traits that mediate light acquisition and growth strategies. If biogeographic history is a strong determinant of local community composition, we expected local communities to be phylogenetically clustered regardless of functional patterns. Alternatively, we expected random patterns of phylogenetic composition if the most relevant traits are not phylogenetically conserved and biogeographic history plays a relatively minor role in structuring community patterns at the island scale.

MATERIALS AND METHODS

Study system

Puerto Rico covers a land area of 8,740 km^2 and encompasses six Holdridge life zones ranging from subtropical dry forests that receive ca. 800 mm of rainfall per year to subtropical rainforests that receive upwards of 4,000 mm yr^{-1} (Daly et al., 2003; Ewel and Whitmore, 1973). Across the island, the majority of rainfall occurs from May – November but precipitation seasonality is spatially variable with the driest forests exhibiting the strongest degree of intra-annual rainfall variation. The island's complex geologic history is reflected in its rugged topography (0 – 1,338 m a.s.l.) and diverse soil parent materials that include volcanic, limestone, alluvial, and ultramafic materials (Bawiec, 1998; Beinroth et al., 2003). Limestone and volcanic materials are the two most extensive geologic substrates, which differ in water-holding capacity and nutrient availability (Camacho, 2005; Miller and Lugo, 2009; Sanchez et al., 2015). The distribution of these soils in Puerto Rico co-vary with elevation and precipitation; limestone-derived soils are generally found at lower (drier) elevations (range of mean annual precipitation = 698 – 2,326

8

mm yr^{-1}) whereas volcanic soils tend to occur at higher (wetter) elevations (718 – 4,608 mm yr^{-1})
(Bawiec, 1998; Daly et al., 2003).

Tree census plots and environmental conditions

We established 24, 50m × 50m (0.25 ha) plots in eight protected forests of Puerto Rico that span
four life zones: subtropical dry, moist, subtropical wet, and lower montane wet forests (Fig. 2,
Table S1). Three plots were established in each forest, and the forests are equally split across the
two most extensive soil parent materials. Plots were located randomly within mature stands
lacking signs of former land-use (*e.g.*, no plantation species and not dominated by species
associated with coffee plantations) or recent natural disturbance (*i.e.*, hurricanes). With the
exception of two plots in Guánica forest, plots were separated by > 1 km. In each plot, we
identified all woody stems (excluding lianas) ≥ 1 cm diameter at 1.3 m above the ground (DBH),
measured their DBH, and visually estimated their height to the nearest 0.5 m. Analyses
presented here are based on the largest stem only of multi-stemmed individuals.

We established our study plots along a gradient of mean annual precipitation based on
long-term climate data across the island (Daly et al., 2003; Table S1). To characterize
understory light availability, we used densiometers to measure canopy openness in a subset of 16
plots. Specifically, we took measurements in the four cardinal directions at each of 16 points
along a regular grid. We averaged the four measurements from each point and then took an
average across all 16 points per plot. To characterize variation in soil fertility, we collected soil
cores (0-20 cm depth) from 10 points along a grid in each of 18 study plots. We pooled samples
within plots to obtain a single soil sample for each plot. After sieving with a 2 mm mesh, we
dried samples at 25°C to constant mass and shipped 80g to the Agricultural Analytical Services

Lab at Penn State University (http://agsci.psu.edu/aasl/soil-testing). Lab analyses yielded total

N, total P, C:N ratio, cation exchange capacity (CEC), pH, P, K, Mg, Ca, Zn, Cu, S. We used

principal components analysis (PCA) to reduce the dimensionality of the soil variables. While

logistic constraints prevented us from collecting light and soil data from all 24 study plots, the

plots sampled for these variables span the studied precipitation gradient and provide a general

description of how these conditions vary across the study area.

Functional traits

We collected data on three functional traits from 1-67 individuals of each species (mean = 11)

with minor deviations from the standard methods of Cornelissen *et al.* (2003) noted below. First,

wood density (WD; g cm^{-3}) is related to a trade-off between relative growth rate and mortality

(Chave et al., 2009; Kraft et al., 2010). Species with low WD tend to be relatively fast-growing

compared to those with high WD because of the different levels of investment in structural

materials (Chave et al., 2006; Wright et al., 2003). High WD, however, conveys resistance to

drought-induced cavitation (Carlquist, 1977; Hacke et al., 2001). For trees 10-20 cm in

diameter, we measured WD on cores extracted with an increment borer. For species that do not

typically reach this size, we included branch WD measurements and used regressions of branch

and core samples from the same individuals to standardize across these different measurements

(Appendix 1). Second, *leaf dry mass per area* (LMA; g m^{-2}) is a key axis of the leaf economics

spectrum that is positively related to leaf lifespan and, more generally, to variation in life history

strategies that range from fast growth by rapid photosynthetic return on carbon investment and

high mortality (low LMA) to slow growth and low mortality by retaining nutrients for a longer

time (high LMA) (Reich et al., 2007; Wright et al., 2004). Some evidence suggests that species

10

with low LMA may have a fitness advantage in relatively resource-rich habitats (e.g., wet and fertile soils) while species with high LMA may have a fitness advantage in more harsh conditions, including water stress conditions (Markesteijn et al., 2011b; Poorter et al., 2009; Sterck et al., 2014). We used a flatbed scanner to measure leaf area on freshly collected entire leaves (including petiole) of fully expanded foliage from the outer crown (sun-exposed, when possible) of mature trees. We then dried and weighed the leaves to calculate LMA. Maximum height (H_{max}; m) is associated with competitive ability in light-limited environments (Givnish, 1995; Thomas and Bazzaz, 1999) and can be constrained by water and nutrient availability (Westoby et al., 2002). For each species, we calculated H_{max} as the maximum value between (i) the estimated height of tallest individual observed in our study and (ii) the maximum height reported by local experts (Little and Wadsworth, 1964; Little et al., 1974). Prior to analyses, we log-transformed LMA to correct for skewness. We examined pairwise correlations between traits using Pearson's r and phylogenetic independent contrasts (*see below*). Our trait database included measurements for ~96% of the total species recorded (N = 250), sampled from each forest where multiple individuals were available.

Phylogenetic analyses

We used a phylogeny inferred for 526 native and naturalized trees of Puerto Rico (Muscarella et al., 2014) to quantify phylogenetic diversity of our study plots and to evaluate functional aspects of community composition in light of evolutionary history. The phylogeny contains the majority (~89%) of the island's tree flora, including 92% of the species recorded in this study (which account for 95% of the observed individuals). For each trait, we used Pagel's λ (Pagel, 1999) to quantify the phylogenetic signal – the degree to which species trait values are explained by

11

evolutionary history. A trait has no phylogenetic signal (i.e., trait values are random with respect to phylogeny) if $\lambda = 0$; trait values correspond to a Brownian motion model of continuous trait evolution if $\lambda = 1$, and trait values are more strongly conserved than predicted by Brownian motion if $\lambda > 1$. We used maximum likelihood methods in the R package 'caper' (Orme et al., 2011) to estimate lambda with 95% confidence intervals. We also investigated pairwise trait correlations in light of evolutionary history using phylogenetic independent contrasts (PICs; Felsenstein, 1985).

Compositional metrics and statistical analyses

We used individual-based rarefaction (Heck et al., 1975) to compare species richness across plots while accounting for differences in the total number of individuals per plot. To characterize variation in the dominant trait values across environmental gradients (*Question 2*), we quantified the community-weighted mean trait (CWM) values for each plot based on the sum of species mean trait values weighted by their relative basal area.

To characterize the functional and phylogenetic diversity of each plot (*Question 3*), we calculated the abundance-weighted mean pairwise distance in functional trait space (MPD_{FUN}; calculated separately for each trait) and phylogenetic branch length (MPD_{PHY}) among co-occurring individuals. We used a null model to scale the observed values of MPD in terms of expectations based on random assemblages drawn from the full island species pool and observed patterns of species richness. We focus here on the full island species pool (as opposed to alternative species pool delineations) because our primary interest was to identify processes mediating community composition at the regional scale. Our null model consisted of first generating 9999 random assemblages from the list of species in our data set by randomizing

species names across the trait matrix (or phylogeny tips) and calculating a value of MPD for each iteration (MPD_{rand}). We then used these assemblages to convert the observed MPD metrics to standardized effect sizes (i.e., $SES.MPD_{FUN}$ and $SES.MPD_{PHY}$) calculated as: (MPD_{obs} – mean(MPD_{rand}))/sd(MPD_{rand}), where MPD_{obs} is the observed mean pairwise distance in trait space (for $SES.MPD_{FUN}$) or phylogenetic branch length (for $SES.MPD_{PHY}$) among all co-occurring individuals in a plot (Webb et al., 2002). This procedure maintains the observed plot-level species richness, species occupancy rates, and stem density while randomizing traits (or position on the phylogeny) and is appropriate when species abundances do not exhibit phylogenetic signal (Hardy, 2008), as was the case in our dataset (95% CI's for λ of abundance and basal area, respectively, were: $0.00 - 0.06$ and $0.00 - 0.48$). Positive values of SES.MPD indicate overdispersion (or 'evenness', i.e., co-occurring individuals are less functionally or phylogenetically similar than expected by chance); negative values indicate clustering (i.e., co-occurring individuals more similar than expected by chance). Individual values of SES.MPD < -1.96 or > 1.96 are considered to differ significantly from the null expectation ($\alpha = 0.05$). In this study, we focus mainly on significant trends of SES.MPD values across environmental gradients as opposed to statistical significance of individual values.

We used linear mixed models to characterize the bivariate relationships of plot environmental conditions (*Question* 1), the relationships between mean annual precipitation and CWM trait values (*Question* 2), as well as the relationships between mean annual precipitation and functional and phylogenetic diversity (*Question* 3). We conducted these analyses separately for plots on each of the two soil parent materials because of the strong covariation between precipitation and soil parent material (*e.g.,* Fig. 4). Due to the covariance between soil type and precipitation, we also used linear mixed models to compare CWM, $SES.MPD_{FUN}$, and

13

$SES.MPD_{PHY}$ between a subset of six plots on each soil type that receive similar amounts of precipitation (i.e., Guajataca, Río Abajo, Carite, and Toro Negro; Table S1). In all cases, we included a random effect for forest reserve to account for potential autocorrelation among plots in the same forest reserve.

We used the package 'arm' (Gelman et al., 2006) to sample posterior distributions of model parameters, and we assigned statistical significance when 95% quantiles of parameter estimates did not overlap zero. We report marginal and conditional R^2_{GLMM} (R^2_m, the proportion of variance explained by fixed factors alone; and R^2_c, the proportion of variance explained by fixed and random factors combined) following Nakagawa & Schielzeth (2012). We used Phylocom (Webb et al., 2008) and 'picante' (Kembel et al., 2010) , 'MuMIn' (Bartoń, 2013), and 'lme4' (Bates et al., 2013) in R version 3.1.3 (R Development Core Team, 2013).

RESULTS

Question 1: How do light and soil conditions co-vary with precipitation?

Modeled mean annual precipitation (Daly et al., 2003) ranged from 934 – 2,147 mm yr^{-1} on the limestone soil plots and from 2,025 – 3,896 mm yr^{-1} on volcanic soil plots (Table S1). Canopy openness (i.e., understory light availability) ranged from 4 – 29% and was negatively related to mean annual precipitation among plots on both soil types ($R^2_m = 0.72$ and 0.87 on limestone and volcanic soils, respectively; Fig 4a, Table S3). The first two axes of the PCA of soil variables explained 59% and 17% of the total variance, respectively. The first axis reflected increasing soil fertility and separated plots on the two parent materials (limestone and volcanic) and across the precipitation gradient based primarily on pH, CEC, total P, total N, CEC with limestone soils having higher values for these metrics. The second axis was most strongly related to variation in

14

several micronutrients (especially Zn, S, and Cu) and the CN ratio. Soil parameters varied

significantly between plots on the two different parent materials and also with respect to mean

annual precipitation (Figs 3-4, Table S2). Specifically, PCA1 (i.e., the fertility axis) decreased

with respect to precipitation among limestone plots ($R^2_m = 0.44$) but was not significantly related

to precipitation among volcanic soil plots (Fig 4b, Table S3).

Question 2: How do dominant trait values shift along regional environmental gradients?

Across all plots, we recorded a total of 34,301 individual trees representing 292 species. Based

on existing knowledge (Acevedo-Rodríguez and Strong, 2011; Axelrod, 2011; USFS, 2006), this

sample represents ~50% of the total tree species known to occur in Puerto Rico. We recorded

209 species in plots on limestone-derived soils and 138 species in plots on volcanic-derived

soils. Fifty-five species (19% of the total observed) occurred in plots on both parent materials.

Stem density declined with precipitation and ranged from 3,224 – 16,408 stems ha^{-1} in plots on

limestone-derived soils and from 1,728 – 5,836 stems ha^{-1} in plots on volcanic-derived soils.

Rarefied species richness was positively associated with precipitation among plots within soil

types, and was lower for plots on volcanic soils compared to plots on limestone soils that have

similar levels of precipitation (Tables S4-5).

All three functional traits exhibited a wide range of variation in our dataset: WD ranged

from 0.29 – 1.04 g cm^{-3}, LMA ranged from 15.8 – 388.6 g m^{-2}, and H_{max} ranged from 2 – 35 m.

As expected, correlations for all three pairwise comparisons of traits were significant ($p < 0.001$)

based on both species-mean values and PICs. Specifically, WD and LMA were positively

correlated (species-mean Pearson's $r = 0.53$, PIC Pearson's $r = 0.41$), whereas H_{max} was

15

negatively correlated with both WD (species-mean Pearson's r = -0.23, PIC Pearson's r = -0.27)

and LMA (species-mean Pearson's r = -0.15, PIC Pearson's r = -0.38).

Among plots on limestone-derived soils, CWM values for all three traits varied

significantly with respect to mean annual precipitation in ways consistent to our hypotheses (Fig.

5, Table S6). Specifically, WD and LMA declined while H_{max} increased with increasing

precipitation. In contrast, none of the CWM values were significantly associated with mean

annual precipitation among the plots on volcanic-derived soils. Additionally, we found no

difference between CWM values of plots that receive similar levels of precipitation but occur on

different soil parent materials (Fig. 5, Table S7).

Question 3: How do functional and phylogenetic diversity patterns vary along regional

environmental gradients?

As we predicted, local functional diversity (SES.MPD$_{FUN}$) of both WD and H_{max} significantly

increased with precipitation among plots on limestone-derived soils (Fig. 6; Table S6). The

driest plots (in Guánica forest) comprise a significantly clustered subset of Puerto Rican trees

with high WD and short stature. In contrast, the wetter plots on limestone soils tended to be

overdispersed with respect to H_{max} (although only one of these values differed significantly from

the null expectation). Functional diversity of LMA did not vary systematically with precipitation

for plots on either soil type. Although values of SES.MPD$_{FUN}$ for both LMA and WD were

almost consistently negative across the gradient (suggesting a tendency towards clustering), these

values did not differ significantly from the null expectation. When comparing the subset of plots

on different parent materials that receive similar levels of precipitation, only H_{max} showed

16

significant differences; plots on limestone-derived soils had higher diversity of H_{max} than plots on volcanic-derived soils (Fig. 6; Table S7).

Two traits (WD and LMA) showed significant phylogenetic signal that was weaker than predicted by Brownian motion (i.e., Pagel's λ was significantly different from both 0 and 1). Of these, phylogenetic signal of WD was stronger (λ [95% CI's] = 0.79 [0.63 – 0.89]) than LMA (0.56 [0.34 – 0.72]). In this dataset, H_{max} values were not statistically associated with phylogenetic relatedness (0.00 [0.00 – 0.56]). Partly mirroring the functional diversity results for WD and H_{max}, phylogenetic diversity (SES.MPD$_{PHY}$) increased with precipitation among plots on limestone-derived soils but was not associated with precipitation among plots on volcanic-derived soils (Fig. 6d). Nearly all plots (including all volcanic soil plots) had positive (but nonsignificant) values of SES.MPD$_{PHY}$, suggesting a tendency towards phylogenetic overdispersion with respect to the full island species pool. We did not find a significant difference in phylogenetic diversity when comparing the subset of plots on different soil parent materials that receive similar levels of precipitation (Fig. 6d).

DISCUSSION

We found correlations between environmental conditions that imply a shift from drought stress to understory light and nutrient limitation as mean annual precipitation increases. Patterns of functional and phylogenetic composition both suggested a shift in the relative importance of assembly mechanisms along these regional environmental gradients. Specifically, we inferred a strong role of abiotic filtering on traits conferring drought tolerance and conservative resource-use strategies in dry forests. In wetter forests, our results support an increasing role for light niche partitioning and competitive dominance of acquisitive resource-use strategies. Moreover,

17

low phylogenetic diversity in the driest plots suggests that abiotic filtering acts on phylogenetically conserved traits to determine broad scale patterns of forest tree composition in Puerto Rico. We discuss these results in the context of how different aspects of resource use and competition may drive community composition along resource gradients.

Environmental drivers of forest functional composition

As predicted, the strong negative correlation between mean annual precipitation and canopy openness suggests an increased importance for shade-tolerant regeneration and competition for light in wetter forests. While many of the complex interactions between climate and soil nutrient availability are beyond the scope of this research (Matías et al., 2011), we did identify strong variation in soil characteristics that was largely captured by differences in the soil parent material. For instance, CEC (perhaps the strongest single indicator of soil fertility) was relatively high among limestone soil plots (compared to volcanic soil plots) and was negatively associated with mean annual precipitation. This result suggests at least a partial decoupling of hydraulic and nutrient stress at the regional scale. At the same time, total soil N increased and the soil CN ratio decreased with mean annual precipitation among plots on limestone-derived soils, potentially resulting from slow decomposition of organic matter and high nutrient retention by live plants in the driest areas. It is also possible that higher N fixation under less water-limited conditions may help explain both higher total N and lower CN ratio with increasing precipitation (Gei and Powers, 2015).

Community-weighted mean values for all three traits exhibited strong directional shifts with respect to the precipitation, which, in turn was related to canopy openness and soil conditions for plots on limestone-derived soils. These shifts were consistent with our hypothesis

18

that selection for drought-tolerant strategies in dry forests gave way to competitive dominance hierarchies for light capture in wet forests. In contrast, community-weighted mean trait values for plots on volcanic-derived soils, which occur on the wetter half of the precipitation gradient, were not significantly associated with mean annual precipitation. Although the absolute range of mean annual precipitation received by plots on limestone-derived soils was smaller than for the plots on volcanic-derived soils (122 cm yr^{-1} vs. 187 cm yr^{-1}), overall water availability appears to be a stronger driver of tree composition at the lower end of the precipitation gradient. In forests on the typically wetter, volcanic-derived soils, it is possible that the effect of water availability on tree composition may be more strongly related to short-term and severe droughts. Ongoing monitoring in our study plots will eventually provide critical dynamic data regarding the shorter-term demographic responses of tree species to rainfall variability.

Given the strong correlation between the soil fertility axis and mean annual precipitation among limestone soil plots, we cannot rule out at least a partial role of soil conditions in driving the observed shifts in community-weighted mean trait values. Nonetheless, (i) the directions of the shifts are consistent with our physiological hypotheses based on drought-tolerance, (ii) we did not find significant differences in community-weighted mean trait values between plots on different soil types that had similar levels of precipitation, and (iii) previous work from our system has shown limestone soils to have a lower water-holding capacity than volcanic soils (Camacho, 2005; Soil Survey Staff, 2015), which compounds the potential effects of drought. Together, these findings support a strong role for water availability in driving the observed patterns.

The concordant declines in both community-weighted mean WD and LMA among plots on limestone-derived soils appear to reflect coordination between stem and leaf functional

strategies to cope with water limitation (Markesteijn et al., 2011a; Méndez-Alonzo et al., 2012; Muscarella and Uriarte, 2016; Patiño et al., 2012). While studies across regional environmental gradients are few, several have found similar trends in community mean WD and LMA with respect to mean annual precipitation (Chave et al., 2006; Cornwell and Ackerly, 2009; Swenson and Enquist, 2007). Although we did not examine below-ground traits in this study, previous work from Puerto Rico has shown that the root component of live-plant biomass is much higher in dry sites (particularly Guánica dry forest) than wet sites, further emphasizing the role of limited water availability in driving forest composition for these sites (Murphy and Lugo, 1986; Roa-Fuentes et al., 2012).

We also observed an increase of community-weighted mean H_{max} among plots on limestone-derived soils that appeared to level off in the wetter half of the gradient. At the dry end of the gradient, the hydraulic limitation hypothesis (Ryan et al., 2006; Ryan and Yoder, 1997) offers a likely explanation for constraint to maximum tree height to avoid embolism. As water availability increases, hydraulic limitation is relaxed and the benefits of reaching tall heights in terms of maximizing carbon gain increase (Falster and Westoby, 2003; Givnish, 1995). However, in systems regularly exposed to wind disturbances (such as Puerto Rico), tall trees have a high probability of damage during storms and most forests have a relatively low canopy height compared to forests that do not receive wind disturbance (Brokaw et al., 2004; Mitchell, 2012; Zimmerman et al., 1994). This effect may be particularly acute in wet forests where hurricane return intervals are relatively short (Boose et al., 2004).

Functional and phylogenetic diversity patterns

Contrary to the idea that competitive exclusion and niche partitioning maintain high diversity of co-existing species in tropical forests, we found only limited evidence for functional overdispersion in this study (i.e., positive values of SES.MPD$_{FUN}$ for H_{max} in the wetter limestone plots). Instead, we detected significant functional clustering of both WD and H_{max} in the driest sites, suggesting strong abiotic filtering. These results further reinforce our conclusion that water availability is a primary driver of tree community composition for many forests of Puerto Rico.

While wetter, volcanic-derived soils do appear to be relatively poor in nutrients in this system, our results do not offer strong support for abiotic filtering from low nutrient availability. First, although SES.MPD$_{FUN}$ values for all traits were generally negative (suggesting clustering), functional diversity of plots on wetter, volcanic-derived soils did not generally depart significantly from null expectations. Additionally, values of community-weighted mean H_{max} were consistently high across all of the volcanic soil plots, suggesting that these communities are dominated by species of tall stature that are more commonly associated with fast growth rates and competitive dominance for light capture as opposed to tolerant of low nutrients. We did observe higher diversity of H_{max} in plots on limestone versus volcanic soils with similar levels of precipitation. This finding could indicate a stronger degree of abiotic filtering in volcanic soil plots. We suspect, however, that a more likely explanation is the relatively high degree of topographic heterogeneity at fine spatial scales in the moist limestone plots, which occur in areas of rugged karst topography (Lugo et al., 2001; Miller and Lugo, 2009). Finally, we note that here we focused on comparing local assemblages with the full island species pool. Future work addressing the influence of species pool delineation (e.g., de Bello et al., 2013; Eiserhardt et al.,

2013; Lessard et al., 2012) could provide additional insight to variation in the more fine-scale processes that govern forest composition in Puerto Rico.

Our study provides only limited support for the hypothesis proposed by Navas and Violle (2009) that functional diversity should be highest at intermediate levels of resource competition because both stress tolerance and competitive dominance traits could represent viable life history strategies. Although the highest values of functional and phylogenetic diversity were recorded in the middle of the precipitation gradient (Fig. 6), there was not a significant decline in diversity with precipitation among the volcanic soil plots. Additionally, the observed shifts in community-weighted mean WD and LMA indicate selection for opposing strategies at different ends of the water availability gradient. Gaining clear support for the hypothesis of Navas and Violle (2009) is challenging, however, because of the multidimensional nature of regional environmental variation in natural systems. For example, we considered high WD a stress tolerance trait under arid conditions because of its role in preventing drought-induced cavitation (Hacke et al., 2001; Kallarackal et al., 2013). In wetter sites, however, WD is involved in a growth/mortality tradeoff whereby some species capitalize on light acquisition via rapid growth (low WD) while others specialize on shade tolerant regeneration (high WD). Few existing studies have examined functional and phylogenetic variation along these types of complex resource gradients, which are inherent features of natural systems, particularly at broad spatial scales. Future work will benefit by explicitly considering how certain traits reflect different aspects of resource acquisition strategies in the context of multidimensional resource and stress gradients.

Similar to the functional patterns of WD and H_{max}, phylogenetic diversity increased with precipitation among plots on limestone-derived soils. The relatively low phylogenetic diversity

of trees co-occurring in the driest plots might offer some support to the assertion by Pennington *et al*. (2009) that association with the subtropical dry tropical forest biome represents a phylogenetically conserved niche. In particular, nitrogen-fixing leguminous trees (Fabaceae) are prominent components of subtropical dry forests, including those in Puerto Rico (Rivera, 2009). In contrast, wetter sites (particularly on volcanic soils) tended to have relatively high phylogenetic diversity, a pattern that was influenced by a high abundance of palms (especially *Prestoea montana* (R. Graham) G. Nicholson).

Three main caveats of our study require consideration. First is our dependence on species-mean trait values as opposed to incorporating intraspecific variation. Some recent work has demonstrated that intraspecific trait variation can be a substantial component of overall functional variation and can provide additional insight to the factors generating spatial variation in functional community composition (Bolnick et al., 2011; Laughlin and Messier, 2015; Violle et al., 2012). We do not expect that incorporating intraspecific trait variation would change the overall conclusions of this study, however, because the majority of species occurred only within one or two protected areas. Here, as in some other studies (e.g., Pérez-Ramos et al., 2012), variation in the functional composition of communities appears to be largely generated by turnover of species with contrasting resource-use strategies. A second limitation is that we relied on traits that integrate a variety of physiological processes. Wood density, for instance, has been related to hydraulic safety and efficiency, mechanical strength, resistance to herbivory, and shade tolerance (Fortunel et al., 2014; Poorter et al., 2010). The composite nature of such traits may obscure the particular physiological mechanisms driving the observed patterns. Nonetheless, the functional patterns we observed matched our *a priori* expectations and will help refine hypotheses about community diversity patterns that could be tested with more detailed

23

physiological data. Finally, although our sites are located in large protected areas (~950 to > 11,000 ha) and did not have any immediate signs of human activity, we cannot completely rule out a role for long-term legacies of human land-use in shaping the composition of these communities (Levis et al., 2012; Uriarte et al., 2009). Synthesizing research on natural resource and successional gradients represents an important and promising area for future work (Chazdon et al., 2016; Letcher et al., 2015; Lohbeck et al., 2013; Poorter et al., 2016).

Conclusions

By examining functional and phylogenetic aspects of community composition across regional environmental gradients, we found evidence for variation in the key processes of tree community assembly in the forests of Puerto Rico. We found particularly strong patterns of nonrandom community composition in the driest sites, supporting the perspective that limited resource availability leads to strong abiotic filtering and convergence on trait values that convey tolerance to resource limitation. In contrast, we did not find conclusive evidence for a single driver of community variation in wetter sites with lower soil fertility. In these sites, tree composition appears to be controlled by both hierarchical competition for light and niche partitioning. Explicitly identifying the physiological mechanisms that link functional traits to particular assembly processes allowed us to interpret functional patterns as evidence for community assembly processes.

24

REFERENCES

Acevedo-Rodríguez, P., Strong, M.T., 2011. Flora of the West Indies: catalogue of the seed plants of the West Indies. Smithsonian Institution, National Museum of Natural History, Washington, D.C.

Austin, A.T., Vitousek, P.M., 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia 113, 519-529.

Axelrod, F.S., 2011. A systematic vademecum to the vascular plants of Puerto Rico. University of Puerto Rico, Río Piedras, PR.

Bartoń, K., 2013. MuMIn: Multi-model inference. R package version 1.9.13. http://cran.r-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B., 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2. http://cran.r-project.org/package=lme4.

Bawiec, W.J., 1998. Geology, geochemistry, geophysics, mineral occurrences, and mineral resource assessment for the commonwealth of Puerto Rico: Open-File Report 98-38, Geological Survey (U.S.).

Bazzaz, F.A., 1979. The physiological ecology of plant succession. Annual Review of Ecology & Systematics 10.

Bazzaz, F.A., Pickett, S.T.A., 1980. Physiological ecology of tropical succession: a comparative review. Annual Review of Ecology & Systematics 11, 287-310.

Beinroth, F.H., Engel, R.J., Lugo, J.L., Santiago, C.L., Ríos, S., Brannon, G.R., 2003. Updated taxonomic classificaiton of the soils of Puerto Rico, 2002. Bulletin 303, University of Puerto Rico, Agricultural Experiment Station, Río Piedras, PR., 1-73.

Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., Garnier, E., 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology 100, 1422-1433.

Bolnick, D.I., Amarasekare, P., Araújo, M.B., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26.

Boose, E.R., Serrano, M.I., Foster, D.R., 2004. Landscape and regional impacts of hurricanes in Puerto Rico. Ecol. Monogr. 74.

Brokaw, N., Fraver, S., Grear, J.S., Thompson, J., Zimmerman, J.K., Waide, R.B., Everham III, E.M., Hubbell, S.P., Condit, R., Foster, R.B., 2004. Disturbance and canopy structure in two tropical forests, in: Losos, E., Leigh, J.E.G. (Eds.), Tropical forest diversity and dynamism:

results from a long-term tropical forest network. The University of Chicago Press, Chicago, IL, pp. 177-194.

Camacho, J.L.L., 2005. The soil climate regimes of Puerto Rico - Reassessment and implications, Department of Agronomy and Soils. University of Puerto Rico, Mayagüez, Puerto Rico, p. 148.

Carlquist, S., 1977. Ecological factors in wood evolution: a floristic approach. American Journal of Botany 64, 887-896.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12, 693-715.

Chapin, F.S.I., Matson, P.A., Mooney, H.A., 2002. Principles of Terrestrial Ecosystem Ecology. Springer, New York.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12, 351-366.

Chave, J.m., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Steege, H.t., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecological Applications 16, 2356-2367.

Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Zambrano, A.M.A., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernández-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Lohbeck, M., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D.,

Powers, J.S., Rodríguez-Velazquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Poorter, L., 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Science Advances 2.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31, 343-366.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.t., Morgan, H.D., Heijden, M.G.A.v.d., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51, 335-380.

Cornwell, W.K., Ackerly, D.D., 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecol. Monogr. 79, 109-126.

Daly, C., Helmer, E.H., Quiñones, M., 2003. Mapping the climate of Puerto Rico, Vieques and Culebra. International Journal of Climatology 23, 1359-1381.

de Bello, F., Lavorel, S., Lavergne, S., Albert, C.H., Boulangeat, I., Mazel, F., Thuiller, W., 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. Ecography 36, 393-402.

Eiserhardt, W.L., Svenning, J.C., Borchsenius, F., Kristiansen, T., Balslev, H., 2013. Separating environmental and geographical determinants of phylogenetic community structure in Amazonian palms (Arecaceae). Botanical Journal of the Linnean Society 171, 244-259.

Ewel, J.J., Whitmore, J.L., 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service, Institute of Tropical Forestry.

Falster, D.S., Westoby, M., 2003. Plant height and evolutionary games. Trends in Ecology and Evolution 18, 337-343.

Felsenstein, J., 1985. Phylogenies and the Comparative Method. The American Naturalist 125, 1-15.

Fortunel, C., Ruelle, J., Beauchêne, J., Fine, P.V.A., Baraloto, C., 2014. Wood specific gravity and anatomy of branches and roots in 113 Amazonian rainforest tree species across environmental gradients. New Phytologist 202, 79-94.

Gei, M.G., Powers, J.S., 2015. The influence of seasonality and species effects on surface fine roots and nodulation in tropical legume tree plantations. Plant and Soil 388, 187-196.

Gelman, A., Su, Y.-S., Hill, J., Grazia Pittau, M., Kerman, J., Zheng, T., 2006. Package 'arm', version: 1.0-1. Data Analysis Using Regression and Multilevel/Hierarchical Models.

Givnish, T.J., 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions., in: Gartner, B.L. (Ed.), Plant stems: physiology and functional morphology. Academic Press, San Diego, pp. 3-49.

Gould, W.A., Alarcon, C., Fevold, B., Jimenez, M.E., Martinuzzi, S., Potts, G., Quinones, M., Solórzano, M., Ventosa, E., 2008. The Puerto Rico Gap Analysis Project volume 1: land cover, vertebrate species distributions, and land stewardship. Gen. Tech. Rep. IITF-39.

Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. Journal of Vegetation Science 17, 255-260.

Hacke, U.G., Sperry, J.S., Pockerman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126, 457-461.

Hardy, O.J., 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. Journal of Ecology 96, 914-926.

Heck, K.L., van Belle, G., Simberloff, D., 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56, 1459-1461.

Kallarackal, J., Otieno, D., Reineking, B.r., Jung, E.-Y., Schmidt, M.T., Granier, A., Tenhunen, J., 2013. Functional convergence in water use of trees from different geographical regions: a meta-analysis. Trees 27, 787-799.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463-1464.

Kraft, N.J.B., Ackerly, D.D., 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecol. Monogr. 80, 401-422.

Kraft, N.J.B., Metz, M.R., Condit, R.S., Chave, J., 2010. The relationship between wood density and mortality in a global tropical forest data set. New Phytologist 188, 1124-1136.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529, 204-207.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmerman, N.E., Kattge, J., Coomes, D.A., 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. Ecology Letters 15, 831-840.

Lasky, J.R., Uriarte, M., Boukili, V., Chazdon, R.L., 2014. Multiple effects of functional trait variation on successional forest dynamics. Proceedings of the National Academy of Sciences 111, 5616-5621.

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

Lessard, J.-P., Borregaard, M.K., Fordyce, J.A., Rahbek, C., Weiser, M.D., Dunn, R.R., Sanders, N.J., 2012. Strong influence of regional species pools on continent-wide structuring of local communities. Proceedings of Royal Society B 279, 266-274.

Letcher, S.G., Lasky, J.R., Chazdon, R.L., Norden, N., Wright, S.J., Meave, J.A., Pérez-García, E.A., Muñoz, R., Romero-Pérez, E., Andrade, A., Andrade, J.L., Balvanera, P., Becknell, J.M., Bentos, T.V., Bhaskar, R., Bongers, F., Boukili, V., Brancalion, P.H.S., César, R.G., Clark, D.A., Clark, D.B., Craven, D., DeFrancesco, A., Dupuy, J.M., Finegan, B., González-Jiménez, E., Hall, J.S., Harms, K.E., Hernández-Stefanoni, J.L., Hietz, P., Kennard, D., Killeen, T.J., Laurance, S.G., Lebrija-Trejos, E.E., Lohbeck, M., Martínez-Ramos, M., Massoca, P.E.S., Mesquita, R.C.G., Mora, F., Muscarella, R., Paz, H., Pineda-García, F., Powers, J.S., Quesada-Monge, R., Rodrigues, R.R., Sandor, M.E., Sanaphre-Villanueva, L., Schüller, E., Swenson, N.G., Tauro, A., Uriarte, M., van Breugel, M., Vargas-Ramírez, O., Viani, R.A.G., Wendt, A.L., Williamson, G.B., 2015. Environmental gradients and the evolution of successional habitat specialization: a test case with 14 Neotropical forest sites. Journal of Ecology 103, 1276-1290.

Levis, C., Souza, P.F.d., Schietti, J., Emilio, T., Pinto, J.L.P.d.V., Clement, C.R., Costa, F.R.C., 2012. Historical Human Footprint on Modern Tree Species Composition in the Purus-Madeira Interfluve, Central Amazonia. PLoS ONE 7, e48559.

Little, E.L., Wadsworth, F.H., 1964. Common trees of Puerto Rico and the Virgin Islands, Volume 1. USDA Forest Service, Washington, DC.

Little, E.L., Woodbury, R.O., Wadsworth, F.H., 1974. Trees of Puerto Rico and the Virgin Islands, Volume 2. USDA Forest Service, Washington, DC.

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H., Pérez-García, E.A., Romero-Pérez, I.E., Tauro, A., Bongers, F., 2013. Successional changes in functional composition contrast for dry and wet tropical forest. Ecology 94, 1211-1216.

Lugo, A.E., Castro, L.M., Vale, A., López, T.d.M., Prieto, E.H., Martinó, A.G., Rolón, A.R.P., Tossas, A.G., McFarlane, D.A., Miller, T., Rodríguez, A., Lundberg, J., Thomlinson, J., Colón, J., Schellekens, J.H., Ramos, O., Helmer, E., 2001. Puerto Rican karst – a vital resource. General Technical Report WO-65. August 2001. Available online: http://www.fs.fed.us/global/iitf/karst.pdf.

Markesteijn, L., Poorter, L., Bongers, F., Paz, H., Sack, L., 2011a. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. New Phytologist 191, 480-495.

Markesteijn, L., Poorter, L., Paz, H., Sack, L., Bongers, F., 2011b. Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. Plant, Cell and Environment 34, 137-148.

Mason, N.W.H., de Bello, F., Mouillot, D., Pavoine, S., Dray, S., 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. Journal of Vegetation Science 24, 794-806.

Mason, N.W.H., Richardson, S.J., Peltzer, D.A., de Bello, F., Wardle, D.A., Allen, R.B., 2012. Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. Journal of Ecology 100, 678-689.

Matías, L., Castro, J., Zamora, R., 2011. Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem. Global Change Biology 17, 1646-1657.

Mayfield, M.M., Levine, J.M., 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13, 1085-1093.

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

Méndez-Alonzo, R., Paz, H., Zuluaga, R.C., Rosell, J.A., Olson, M.E., 2012. Coordinated evolution of leaf and stem economics in tropical dry forest trees. Ecology 93, 2397-2406.

Miller, G.L., Lugo, A.E., 2009. Guide to the ecological systems of Puerto Rico. Gen. Tech. Rep. IITF-GTR-35, in: United States Department of Agriculture, Forest Service, International Institute of Tropical Forestry (Eds.), San Juan, PR, p. 437.

Mitchell, S.J., 2012. Wind as a natural disturbance agent in forests: a synthesis. Forestry.

Murphy, P.G., Lugo, A.E., 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18, 89-96.

Muscarella, R., Uriarte, M., 2016. Do community-weighted mean trait values reflect optimal strategies? Proceedings of Royal Society B 283: 20152434.

Muscarella, R., Uriarte, M., Aide, T.M., Erickson, D.L., Forero-Montaña, J., Kress, W.J., Swenson, N.G., Zimmerman, J.K., 2016. Functional convergence and phylogenetic divergence during secondary succession of subtropical wet forests in Puerto Rico. Journal of Vegetation Science 27, 283-294.

Muscarella, R., Uriarte, M., Erickson, D.L., Swenson, N.G., Zimmerman, J.K., Kress, W.J., 2014. A well-resolved phylogeny of the trees of Puerto Rico based on DNA barcode sequence data. PLoS ONE 9, e112843.

Nakagawa, S., Schielzeth, H., 2012. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4, 133-142.

Navas, M.L., Violle, C., 2009. Plant traits related to competition: how do they shape the functional diversity of communities? Community Ecology 10, 131-137.

Orme, D., Freckleton, R.P., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., 2011. caper: Comparative Analyses of Phylogenetics and Evolution in R (Imperial College, London, UK) Version 0.4.

Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877–884.

Patiño, S., Fyllas, N.M., Baker, T.R., Paiva, R., Quesada, C.A., Santos, A.J.B., Schwarz, M., ter Steege, H., Phillips, O.L., Lloyd, J., 2012. Coordination of physiological and structural traits in Amazon forest trees. Biogeosciences 9, 775-801.

Pennington, R.T., Lavin, M., Oliveira-Filho, A., 2009. Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. Annual Review of Ecology & Systematics 40, 437-457.

Pérez-Ramos, I.M., Roumet, C., Cruz, P., Blanchard, A., Autran, P., Garnier, E., 2012. Evidence for a 'plant community economics spectrum' driven by nutrient and water limitations in a Mediterranean rangeland of southern France. Journal of Ecology 100, 1315-1327.

Poorter, H., Niinemets, U., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 182, 565-588.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211-214.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.-C., Peña-Claros, M., Sterck, F.J., Villegas, Z., Sass-Klaassen, U., 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytologist 185, 481-492.

R Development Core Team, 2013. R: A language and environment for statistical computing., v 3.0 ed. R Foundation for Statistical Computing, Vienna, Austria.

Radulovich, R., Sollins, P., 1991. Nitrogen and phosphorus leaching in zero-tension drainage from a humid tropical soil. Biotropica 23, 84-87.

Reich, P.B., 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102, 275-301.

Reich, P.B., Walters, M.B., Ellsworth, D.S., 2007. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences 94, 13730-13734.

Rivera, O.A.M., 2009. Vascular flora of the Guánica dry forest, Puerto Rico, Biology. University of Puerto Rico, Mayagüez.

Roa-Fuentes, L.L., Campo, J., Parra-Tabla, V., 2012. Plant biomass allocation across a precipitation gradient: an approach to seasonally dry tropical forest at Yucatán, Mexico. Ecosystems 15, 1234-1244.

Russo, S.E., Davies, S.J., King, D.A., Tan, S., 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. Journal of Ecology 93, 879-889.

Ryan, M.G., Phillips, N., Bond, B.J., 2006. The hydraulic limitation hypothesis revisited. Plant Cell and Environment 29, 367-381.

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. BioScience 47, 235-242.

Sanchez, M.J., Lopez, E., Lugo, A.E., 2015. Chemical and physical analyses of selected plants and soils from Puerto Rico (1981-2000). Gen. Tech. Rep. IITF GTR-45. Rio Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 85 p.

Schuur, E., Matson, P., 2001. Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. Oecologia 128, 431-442.

Soil Survey Staff, 2015. Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database. Available online at http://sdmdataaccess.nrcs.usda.gov/.

Spasojevic, M.J., Suding, K.N., 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. Journal of Ecology 100, 652-661.

Sterck, F., Markesteijn, L., Toledo, M., Schieving, F., Poorter, L., 2014. Sapling performance along resource gradients drives tree species distributions within and across tropical forests. Ecology 95, 2514-2525.

Swenson, N.G., Enquist, B.J., 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. American Journal of Botany 94, 451-459.

Swenson, N.G., Enquist, B.J., Jason, P., Thompson, J., Zimmerman, J.K., 2006. The problem and promise of scale dependency in community phylogenetics. Ecology 87, 2418-2424.

Thomas, S.C., Bazzaz, F.A., 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology 80, 1607-1622.

Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., Murphy, L., Sabat, A.M., Fetcher, N., Haines, B.L., 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. Ecol. Monogr. 79, 423-443.

USFS, 2006. Forest inventory and analysis national core field guide: Caribbean version 3.0, in: USDA (Ed.). United States Forest Service.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.c.H., Hulshof, C., Jung, V., Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology & Evolution 27, 244-252.

Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24, 2098-2100.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33, 475-505.

Weeks, B.C., Claramunt, S., Cracraft, J., 2016. Integrating systematics and biogeography to disentangle the roles of history and ecology in biotic assembly. Journal of Biogeography 43, 1546-1559.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., Bentivenga, S., 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B-Biological Sciences 366, 2403-2413.

Weiher, E., Keddy, P., 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74, 159-164.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology & Systematics 33, 125-159.

Whittaker, R.H., 1967. Gradient analysis of vegetation. Biological Reviews 49, 207-264.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas,

S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821-827.

Wright, I.J., Westoby, M., Reich, P.B., 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology 15, 423-434.

Wright, S.J., Muller-Landau, H.C., Condit, R., Hubbell, S.P., 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology 84, 3174-3185.

Zhao, M., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000–2009. Science 329, 940-943.

Zimmerman, J.K., Iii, E.M.E., Waide, R.B., Lodge, D.J., Taylor, C.M., Brokaw, N.V.L., 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. Journal of Ecology 82, 911-922.
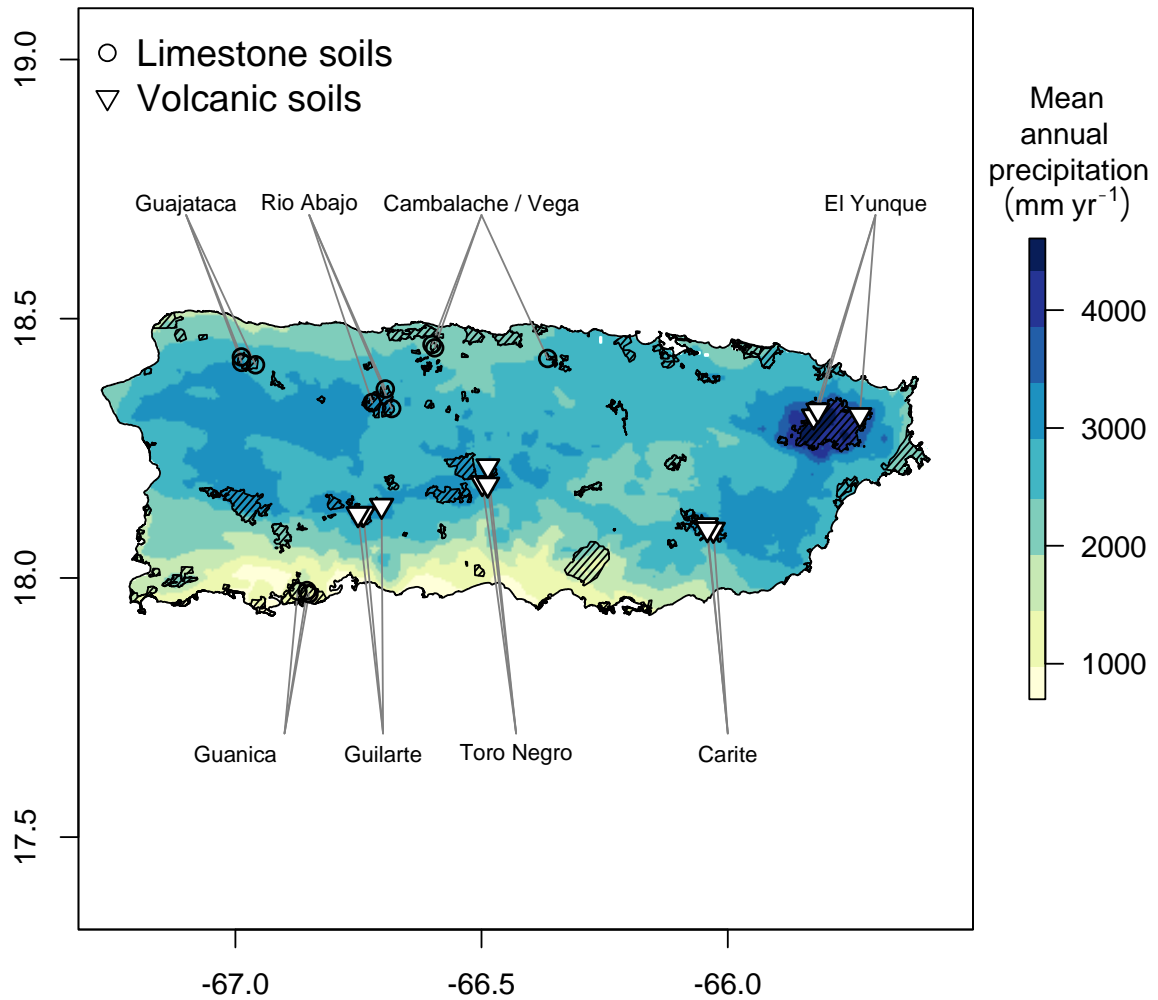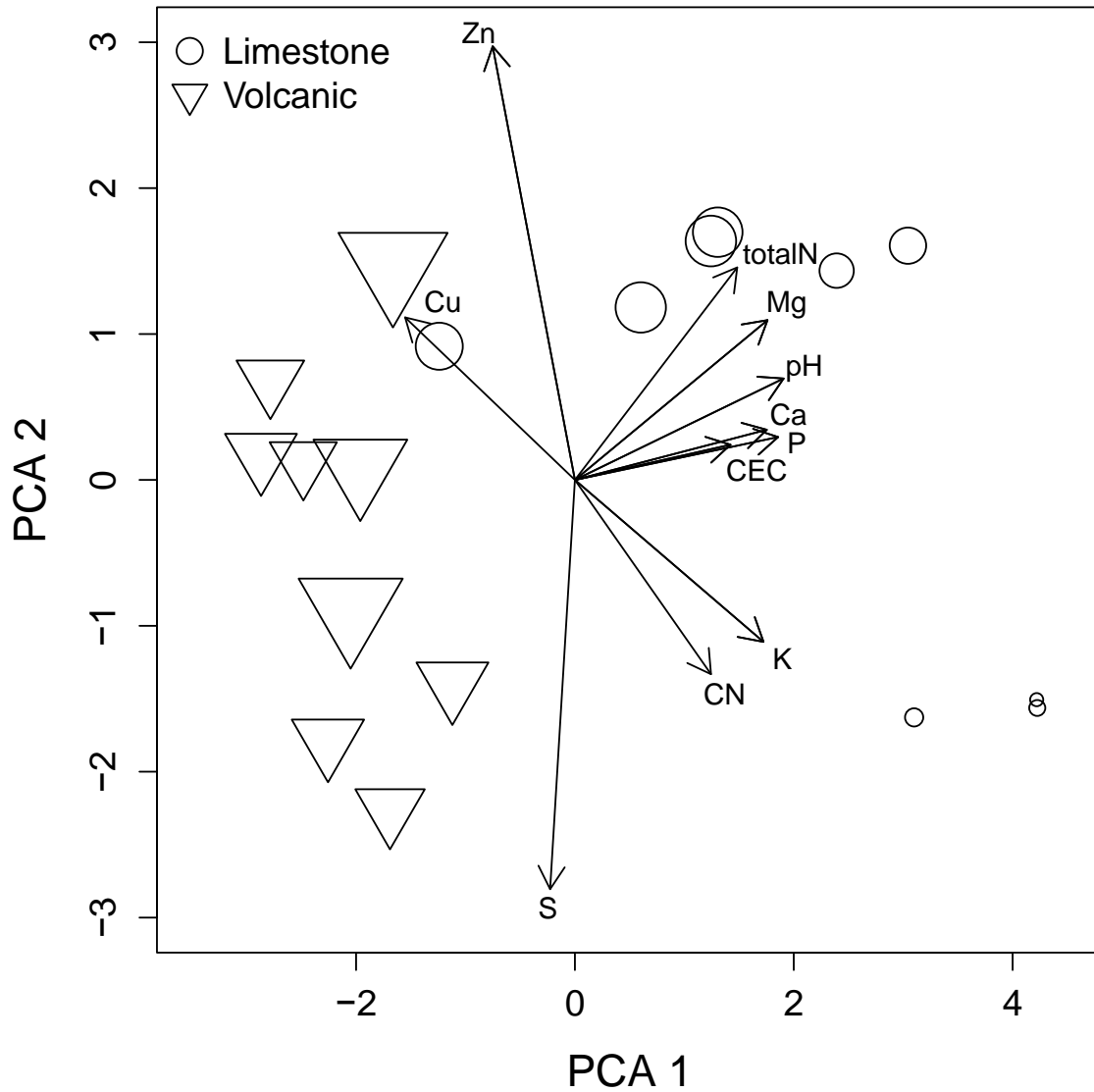
FIGURES

Figure 1. (a) Theory and empirical results suggest that under low resource conditions, communities should be dominated by species with traits associated with conservative strategies (e.g., high WD, LMA and low H_{max}). Under high resource conditions, in contrast, species with traits associated with acquisitive strategies (e.g., low WD, LMA and high H_{max}) should dominate. (b) An often hypothesized shift in the relative importance of abiotic filtering to niche partitioning as the dominant assembly mechanism leads to the prediction that functional diversity should increase along a gradient of resource availability (solid line in (b)). However, competitive dominance hierarchies and alternative strategies to cope with abiotic stress can lead to the opposite pattern (dashed line in (b)). Note that panel (b) assumes that relevant functional traits are phylogenetically conserved (see introduction). Complicating these hypotheses about plant functional responses is the fact that, particularly at broad spatial scales, environmental gradients often comprise multiple axes of variation. For instance, we expect both (c) understory light availability and (d) nutrient availability to be negatively correlated with mean annual precipitation.
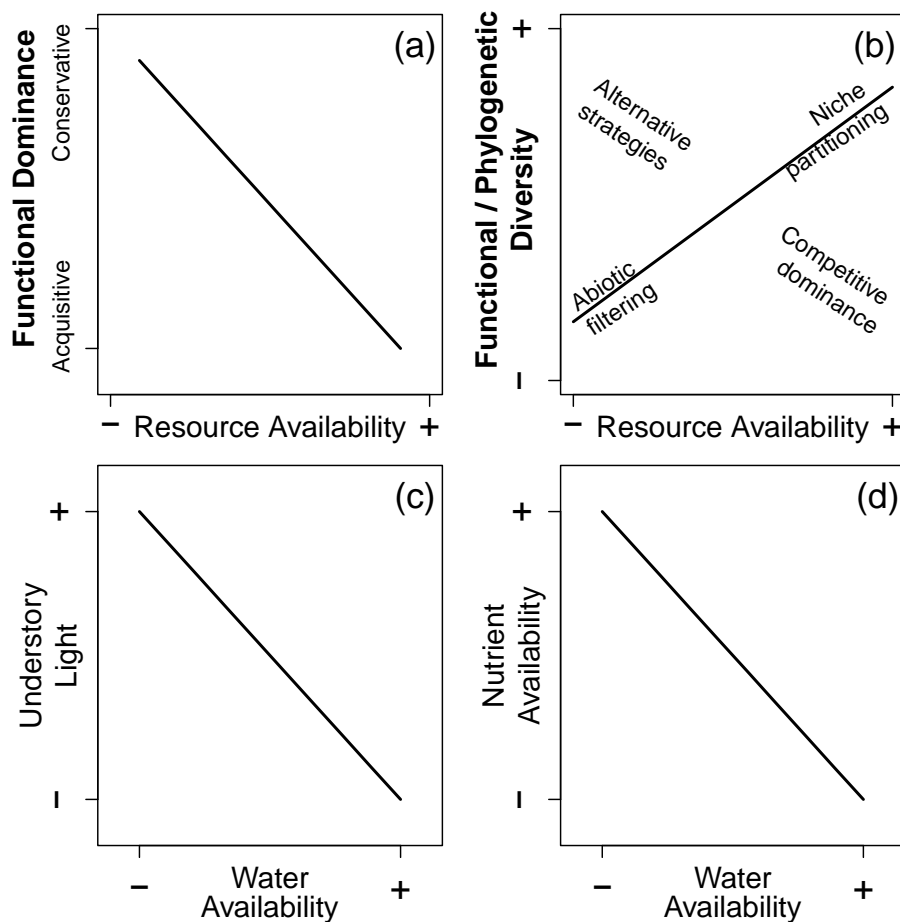
Figure 2. A map of Puerto Rico with the locations of 24, 0.25 ha tree census plots. Circles indicate plots on limestone soils and triangles indicate plots on volcanic soils. The background shows mean annual precipitation from Daly et al. (2003) and hatched polygons represent protected forests of mainland Puerto Rico (Gould et al., 2008). See Table S1 for additional details on plots.

Figure 3. Principal components analysis of soil variables (see Table S2). Red circles indicate plots on limestone-derived soils and triangles indicate plots on volcanic-derived soils. Point size is proportional the log of mean annual precipitation. Loadings of individual soil variables are shown as arrows.

Figure 4. The relationships between mean annual precipitation and (a) percent canopy openness (as a measure of understory light availability) and (b) the first PCA axis of soil variables (as a measure of soil fertility) across in Puerto Rico. Red circles indicate plots on limestone-derived soils and triangles indicate plots on volcanic-derived soils. Marginal R^2 values were calculated among points within soil types. Marginal R^2 is shown for significant relationships; complete model results are provided in Tables S3.
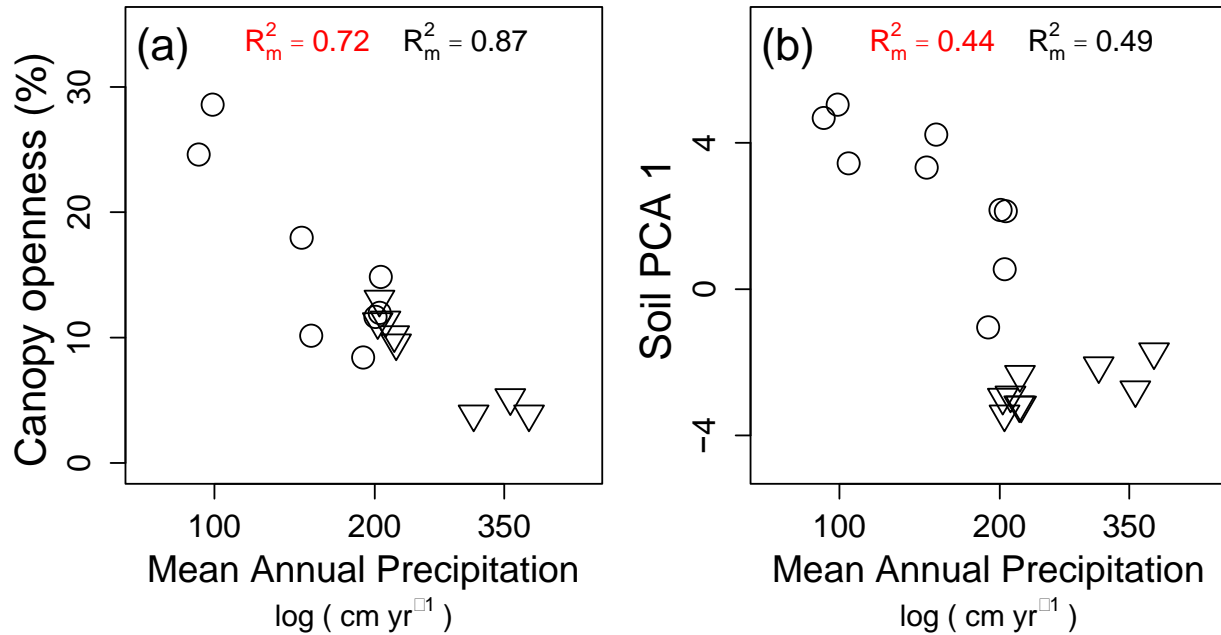
Figure 5. Community-weighted mean functional trait values for 24 0.25-ha plots in forests of Puerto Rico. In left side panels, red circles and grey triangles represent plots on limestone and volcanic soils, respectively, and the x-axis shows mean annual precipitation. Regression lines and marginal R^2 values are shown when a linear mixed model fit to plots within soil types had a significant slope. Box plots in right side panels compare the six plots on each soil type that have similar levels of mean annual precipitation (*see main text*). Marginal R^2 is shown for significant relationships; complete model results are provided in Tables S6-7.
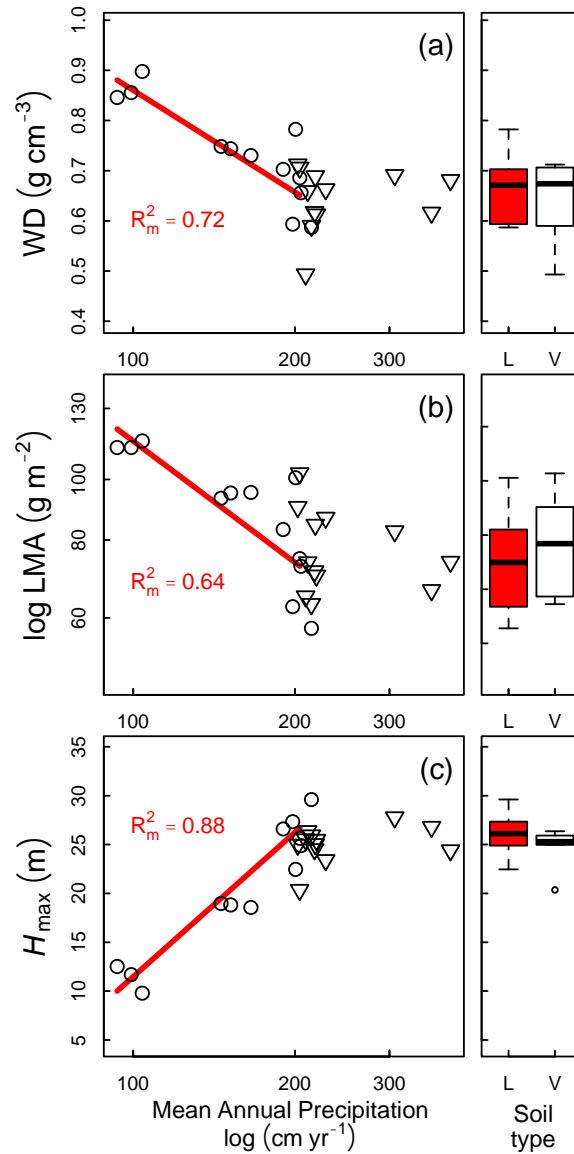
Figure 6. Standardized mean pairwise functional distance (SES.MPD$_{FUN}$) for WD (a), LMA (b), H_{max} (c), and standardized mean pairwise phylogenetic distance (SES.MPD$_{PHY}$; d) among individuals in 24 Puerto Rican forest plots. In left side panels, red circles and grey triangles represent plots on limestone and volcanic soils, respectively. The x-axis shows mean annual precipitation for each plot on a log scale. Regression lines are shown when the linear mixed model between SES.MPD and precipitation (within soil types) had a significant slope. Right side panel box plots compare the six plots on each soil type that receive similar levels of precipitation (*see main text*). An asterisk is shown if there was a significant difference between plots across soil types based on a mixed model. In all cases, negative values indicate functional (a-c) or phylogenetic (d) clustering whereas positive values indicate functional (a-c) or phylogenetic (d) evenness (or, 'overdispersed'). Marginal R^2 is shown for significant relationships; complete model results are provided in Tables S6-7.