

Climate and Biodiversity Effects on Standing Biomass in Puerto Rican Forests

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Abstract - Carbon sequestration is a major ecosystem service provided by tropical forests. Especially in light of global climate change, understanding the drivers of forest productivity is of critical importance. Although abiotic conditions (e.g., precipitation) are known to influence forest productivity, ecological theory predicts that biodiversity may also have independent effects on productivity. We estimated standing aboveground biomass (AGB) in mature forests of Puerto Rico that span a strong precipitation gradient and 2 general soil types. With these data, we examined the independent and interactive effects of precipitation and 5 metrics of tree diversity (species richness, phylogenetic diversity, and three aspects of functional diversity) on spatial variation of AGB in forests on 2 soil types. Precipitation had a strong positive effect on AGB on both soil types, and we did not find evidence for an independent effect of diversity on AGB in either soil type. We found some evidence from plots on limestone soils that the increase in AGB along the precipitation gradient was less pronounced in plots where species richness was relatively high. We discuss our results in light of spatial scale and biodiversity–ecosystem function theory.

Introduction

Land managers and conservationists are increasingly tasked with ensuring the maintenance of key ecosystem services in addition to their more traditional focus on species conservation (Aerts and Honnay 2011, Naeem et al. 2012, Perring et al. 2011, Thompson and Starzomski 2007). For example, tropical forests harbor an enormous amount of biodiversity and provide a substantial contribution to carbon sequestration on a global scale (Bonan 2008, Pan et al. 2011). In addition to the effects of abiotic conditions (e.g., precipitation and soil) on tropical forest productivity (Brown and Lugo 1982, Laumonier et al. 2010, Vieira et al. 2004), research in the field of biodiversity and ecosystem function (BEF) suggests that diversity may independently affect productivity (Caspersen and Pacala 2001, Hooper et al. 2005). Especially in light of global climate change, establishing the relationships between productivity, abiotic conditions, and diversity may facilitate the integration of biodiversity in management plans (Thomas et al. 2013), elucidate the processes by

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which key ecosystem functions arise (Srivastava and Vellend 2005), and clarify the valuation of biodiversity (Hector et al. 2001, Schwartz et al. 2000).

From a BEF perspective, diversity can promote ecosystem functioning through two general mechanisms: complementarity and selection (Loreau 1998, 2000; Loreau and Hector 2001). Complementarity (or niche partitioning) arises when diversity increases overall resource-use efficiency, resulting in higher productivity and retention of nutrients (Loreau 2000, Tilman et al. 1997, Trenbath 1974). In the context of biomass production of tropical forests, diverse assemblages that contain species with different responses to spatial and temporal heterogeneity (e.g., light conditions or soil moisture) may store greater biomass than less diverse assemblages (Ruiz-Jaen and Potvin 2010). The second mechanism, selection, refers to situations where there is covariance between a species' local competitive dominance and its per capita contribution to function (Huston 1997, Loreau 2000, Tilman et al. 1997). For example, in light-limited environments, species that achieve a taller maximum height may contribute disproportionately to biomass production and also be competitively dominant (Ruiz-Jaen and Potvin 2011). The direction of selection effects depends on whether the competitively dominant species have a relatively positive or negative influence on the particular ecosystem function under consideration (Jiang et al. 2008, Loreau and Hector 2001).

Determining how these mechanisms link diversity with biomass production in natural forest systems presents numerous challenges (Balvanera et al. 2006, Godbold et al. 2011, Vilá et al. 2005). First, the majority of experimental and theoretical BEF studies have focused on relatively low-diversity grasslands (e.g., Hector and Bagchi 2007, Naeem and Wright 2003, Tilman et al. 1996). The comparably few studies in tropical forests have primarily focused on comparing monocultures with mixed-tree plantations that incorporate only a fraction of the diversity found in natural stands (Bruehlheide et al. 2013, Erskine et al. 2006, Piotto et al. 2010, Potvin et al. 2011, Ruiz-Jaen and Potvin 2010, Scherer-Lorenzen et al. 2005; but see Bunker et al. 2005, Ruiz-Jaen and Potvin 2011). Additionally, most experimental BEF studies occur at relatively small spatial scales ($\leq 500 \text{ m}^2$) where environmental conditions are presumed to be uniform. However, theoretical and empirical work suggests that BEF relationships are likely to vary along abiotic gradients (Cardinale et al. 2000, 2009; Loreau 1998; Ruiz-Jaen and Potvin 2011), so it is unclear whether results from experimental studies can be extrapolated to spatial scales relevant to management (Srivastava and Vellend 2005, Vellend et al. 2013).

We lack experimental BEF studies in natural forests over large spatial scales, but several recent observational studies have examined biodiversity effects on the productivity of (mostly temperate) forests across environmental gradients (Chisholm et al. 2013; Paquette and Messier 2011; Ruiz-Benito et al. 2013; Vilá et al. 2005, 2007, 2013). Although results are mixed, a common finding is that diversity–productivity relationships change by forest type or along abiotic gradients. For example, Vilá et al. (2005) reported a positive diversity–productivity relationship, but the effect was only evident in early successional or physiologically stressed forests. Paquette and Messier (2011) showed a positive effect of biodiversity on productivity in both

temperate and boreal forests, but the effect was stronger in more physiologically stressful boreal forests. These findings suggest that abiotic conditions can interact with diversity to affect the nature of BEF relationships (Cardinale et al. 2000, Mouquet et al. 2002, Warren et al. 2009). One potential explanation is that complementarity effects are relatively weak in favorable environments because increased competitive exclusion favors fewer highly productive, competitively dominant species (Warren et al. 2009). However, sites with strong abiotic filters (e.g., drought) are often comprised of functionally similar species (Cavender-Bares et al. 2004, Weiher and Keddy 1995). Thus, when the pool of species available to colonize a site is reduced through abiotic filtering, the potential for niche differentiation to generate positive biodiversity effects can be diminished (Mouquet et al. 2002). Evaluating how the relative strength of the factors that limit diversity vary along environmental gradients may help clarify the mechanisms underlying diversity–productivity relationships.

The multi-faceted nature of biodiversity may help disentangle the interactive effects of abiotic conditions and diversity (Cadotte et al. 2008, Flynn et al. 2011). Although species have long been considered the fundamental unit of diversity, the concept of biodiversity comprises numerous aspects including diversity of species, functional types, and evolutionarily distinct lineages. Compared to species diversity, functional diversity may be more strongly related to community-level processes when these are driven by niche differentiation along particular trait axes (Cadotte et al. 2009). By considering an integrated measure of evolutionary relatedness, phylogenetic diversity may better reflect the overall degree of functional similarity among species than either species diversity or functional diversity along any single trait axis (Cadotte et al. 2008, Maherali and Klironomos 2007).

We examined the relationship between different metrics of diversity and above-ground biomass (AGB) of trees in mature forests of Puerto Rico, spanning a broad precipitation gradient and two main soil types that differed in their water-holding capacity and nutrient availability. We relied on data collected in plots across these gradients to ask two primary questions:

First, how do the drivers of AGB differ for forests on the island's 2 main soil types? Primarily because of differences in water-holding capacity between soil types, we expected that the dominant axes of niche partitioning might differ for forests on limestone versus volcanic soils. Specifically, because forests on porous limestone soils face greater water stress, we expected precipitation to more strongly influence AGB on that substrate than in forests on volcanic soils with lower water stress. We also hypothesized that the relatively favorable conditions on volcanic soils would permit a stronger role for diversity effects on AGB through a reduced relative importance of abiotic filters.

Second, how does the relationship between diversity and AGB within each soil type vary with respect to precipitation? We predicted a stronger influence of precipitation in mediating the effects of biodiversity on AGB in forests on limestone soils because of their low precipitation and water-holding capacity. In contrast, we expected precipitation to play a weaker role in mediating biodiversity effects on AGB in forests on wetter volcanic soils. We expected this pattern to be most

pronounced for functional dimensions of biodiversity, which have strong direct links to hydrological conditions.

Field-site Description

Puerto Rico encompasses 6 Holdridge life zones ranging from subtropical dry forest to subtropical rainforest in an area of 8740 km² (Ewel and Whitmore 1973). These forests occur along a broad precipitation gradient from subtropical dry forests that receive ~800 mm yr⁻¹ of rainfall to lower montane rainforests that receive upwards of ~4500 mm yr⁻¹. The island's complex geologic history is reflected in its rugged topography (0–1338 m asl) and diverse soil parent materials, which include volcanic, limestone, alluvial, and ultramafic materials. Based on underlying geology (Bawiec 1998), the most extensive soil types are derived from limestone and volcanic materials which represent major differences in water-holding capacity and nutrient availability (Miller and Lugo 2009, Murphy and Lugo 1995). The topographic distributions of these soils compound their hydraulic properties; limestone soils occur at lower elevations that receive less rainfall while volcanic soils primarily occur at higher (and wetter) elevations (Govender et al. 2013). To confront the confounded effects of precipitation and soil type, we analyzed each soil type separately.

Methods

Tree-census plots

From May to August 2013, we established twenty-four 0.25-ha plots located in 8 protected forests in Puerto Rico, 12 in each soil type (Fig. 1, Table 1). We chose plots randomly in stands that were free from signs of former land-use (e.g., dominated by plantation species or species associated with coffee plantations) and natural disturbance (hurricanes). 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 estimated their height to the nearest 0.5 m. We used allometric equations

Table 1. Summary of the characteristics for Puerto Rican forests based on data from three 0.25-ha study plots in each forest. Precipitation data are from Daly et al. (2003), soil type (L = limestone, V = volcanic) is from Bawiec (1998), and aboveground biomass was calculated with allometric equations from Chave et al. (2005) including wood density, height, and forest type.

Forest	Mean annual precipitation (cm yr ⁻¹)	Soil type	Stem density (stems ha ⁻¹)	Estimated biomass (Mg ha ⁻¹)	Species richness (species 0.75 ha ⁻¹)
Cambalache Vega	155	L	4973	115.6	73
Guajataca	197	L	4256	186.9	92
Guánica	98	L	8463	97.9	66
Río Abajo	205	L	3625	165.0	92
Carite	205	V	1961	154.4	54
Guilarte	223	V	2400	107.9	51
El Yunque	352	V	1676	273.0	75
Toro Negro	214	V	1877	156.9	54

from Chave et al. (2005) to estimate AGB for each stem ($n = 32,182$) and aggregated AGB to the scale of 500 m^2 ($10 \text{ m} \times 50 \text{ m}$) subplots (5 per plot, $n = 120$). Chave et al. (2005) provide separate allometric equations for dry, moist, and wet forests. We calculated AGB using the corresponding equation based on the Holdridge life-zone classification of each plot (Ewel and Whitmore 1973).

Because variation in stem density precluded direct comparison of species-richness metrics across sites sampled in fixed areas (Gotelli and Colwell 2001), we used rarefied metrics of diversity in our analyses. Separately for each soil type, we used the RAREFY function in the R package VEGAN (Oksanen et al. 2013) to calculate rarefied species richness based on the number of stems found in the subplot with the fewest stems (limestone soils = 130; volcanic soils = 36). We rarefied differently for the two soil types because rarefying limestone plots to 36 stems strongly skewed richness values towards the maximum of 36 species.

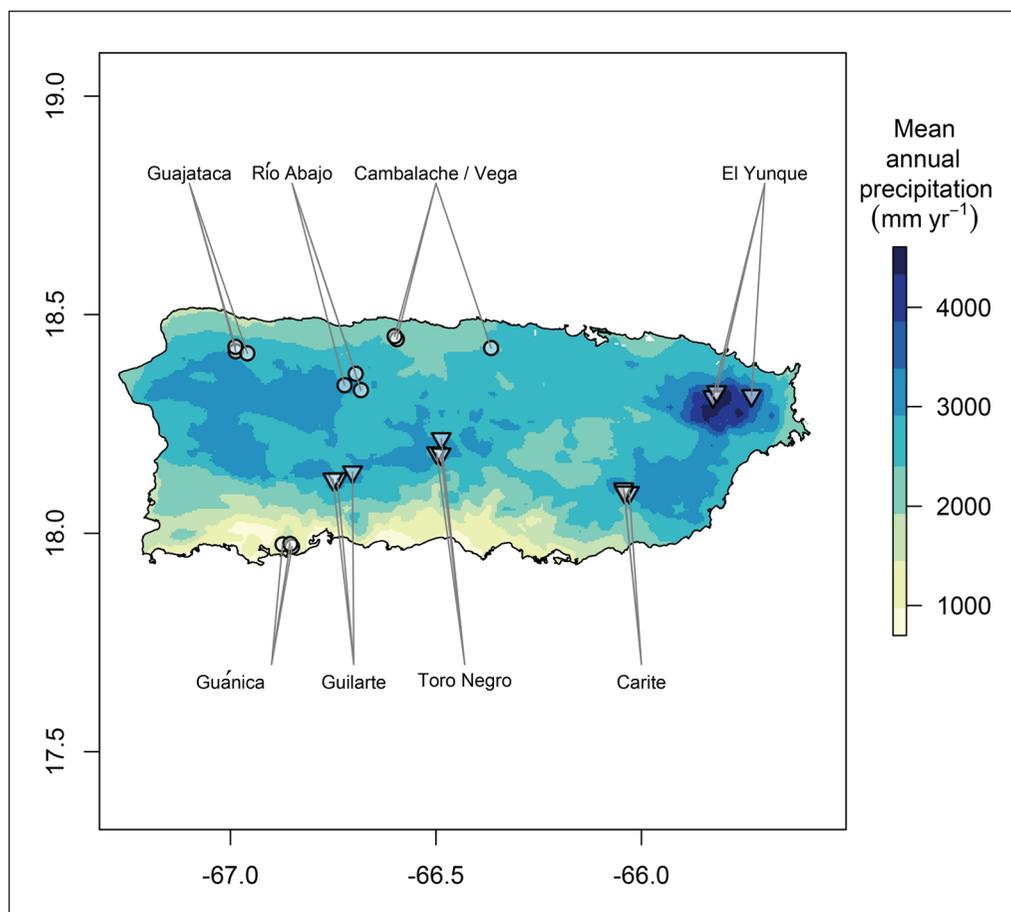


Figure 1. A map of Puerto Rico showing the locations of twenty-four 0.25-ha tree-census plots (each contains five 500-m^2 subplots) located in 8 protected forests (see Table 1 for forest details). Circles indicate plots on limestone soils and triangles indicate plots on volcanic soils. The background shows mean annual precipitation from Daly et al. (2003).

Functional diversity

We collected data on 3 functional traits from multiple individuals of each species using standardized methods (Cornelissen et al. 2003). Wood density (g cm^{-3}) is a key aspect of the wood economics spectrum, which corresponds to a trade-off between relative growth rate and survival (Chave et al. 2009, Kraft et al. 2010, Poorter et al. 2008, Swenson and Enquist 2007, Wright et al. 2010) and is strongly associated with hydraulic capacity; trees that occur in drought-prone areas tend to have high wood density. Leaf area (cm^2) is related to light-capture strategies, water balance, and thermal regulation. Low water and nutrient availability generally result in selection for smaller leaves because of the costs of supplying adequate water for transpiration (Givnish 1986, 1987; Westoby et al. 2002). Maximum height (m) is associated with overall plant size and competitive ability in light-limited environments (Givnish 1995, Thomas and Bazzaz 1999). In general, maximum height is positively associated with increasing precipitation and soil nutrients.

After log-transforming leaf area to improve normality, we quantified abundance-weighted functional dispersion (FDis; Laliberté and Legendre 2010) of each subplot separately for each trait using the dbFD function in the R package FD (Laliberté and Shipley 2011). FDis quantifies the average distance to the centroid of trait values (the mean for single traits) among individuals (among species if using presence-absence data) in an assemblage; larger values indicate more dispersed assemblages. For each subplot, we calculated the mean FDis from 100 rarefied assemblages for each subplot that comprised the minimum number of stems per subplot in each soil type.

Phylogeny

To quantify phylogenetic diversity, we used three regions of chloroplast DNA (*rbcl*, *matK*, and *trnH-psbA*) to infer a phylogenetic hypothesis for 529 native and naturalized trees of Puerto Rico (Kress et al. 2010, Muscarella et al. 2014). This phylogeny contains 89% of the tree flora of the island. We calculated the abundance-weighted mean phylogenetic species variability (PSV; Helmus et al. 2007) from the same 100 rarefied assemblages described above using the PSV function in the R package PICANTE (Kembel et al. 2010). PSV summarizes the phylogenetic relatedness of individuals in an assemblage, ranging from 0 to 1 with increasing relatedness.

Statistical analyses

We used generalized linear mixed models (GLMMs) to characterize the relationship between AGB, precipitation, and the 5 diversity metrics mentioned above. Because of strong covariance between precipitation and soil types, we analyzed subplots on each soil type using separate but identical models:

$$\text{estimated (AGB)}_i = b_0 + b_1 \times \text{ppt}_i + b_2 \times \text{div}_i + b_3 (\text{ppt}_i \times \text{div}_i) + p_i + e \quad (\text{eq. 1})$$

Estimated AGB in 500- m^2 subplot i is a function of mean annual precipitation, one of the 5 rarefied diversity metrics (species richness, PSV, and FDis for three traits), and the interaction between precipitation and diversity, giving a total of 10 models

(2 soil types \times 5 diversity metrics). We interpreted the main-effect coefficients as the relative strength of precipitation versus diversity to drive variation in AGB (question 1). We interpreted the interaction between precipitation and diversity as evidence for how the diversity–AGB relationship changed along the precipitation gradient within each soil type (question 2). To account for autocorrelation among subplots within each plot, we included a random plot effect, p , in the GLMMs. Random effects in mixed models account for the non-independence of observations by modeling the covariance structure of grouped data; this is a commonly used strategy to avoid issues of pseudoreplication (Crawley 2012, Gelman and Hill 2006). All variables were centered and standardized within soil types prior to analyses by subtracting their mean and dividing by their standard deviation (Gelman and Hill 2006). This standardization process facilitates the direct comparison of the magnitude and direction of covariate effects based on their estimated coefficients (Schielzeth 2010). Analyses were conducted with R v3.0 (R Development Core Team 2013) with the lme4 package used to fit GLMMs and sample posterior distributions of parameters (Bates et al. 2013). We determined statistical significance when the 95% confidence intervals for a parameter estimate did not overlap zero. We used the MuMIn package (Bartoń 2013) to calculate both marginal R^2_{GLMM} (R^2_{M} ; the proportion of variance explained by fixed factors alone) and conditional R^2_{GLMM} (R^2_{C} ; proportion of variance explained by both the fixed and random factors) following Nakagawa and Schielzeth (2012).

Results

Subplots varied widely in the amount of AGB they contained. Estimated AGB ranged from 57.0 Mg ha⁻¹ to 457.6 Mg ha⁻¹ (mean \pm SD = 147.1 Mg ha⁻¹ \pm 74.4) on limestone soils and 59.2 Mg ha⁻¹ to 496.9 Mg ha⁻¹ (mean \pm SD = 175.2 Mg ha⁻¹ \pm 98.6) on volcanic soils. Observed species richness in 500-m² subplots ranged from 17 to 48 (mean \pm SD = 33.0 \pm 7.1) on limestone soil and from 11–36 (mean \pm SD = 22.2 \pm 4.6) on volcanic soil (Table 2). Once rarefied, the species richness range = 16.2–36.7 (rarefied to 130 individuals, mean \pm SD = 25.3 \pm 4.5) on limestone soils and 8.6–20.7 (rarefied to 36 individuals, mean \pm SD = 13.8 \pm 2.3) on volcanic soils (Table 2, Fig. 2).

We used the coefficients of main terms from our regression models to determine the relative strength of precipitation and diversity in driving AGB (question 1). Among subplots on limestone soils, precipitation had the strongest independent (positive) effect on AGB and the effect was significant in all models except for the model including phylogenetic variability (Fig. 3, Table 3). None of the diversity metrics had significant independent effects on AGB for subplots on limestone soils. Among subplots on volcanic soils, the effect of precipitation was also positive and significantly different from zero in all 5 models. None of the independent diversity effects were significant in these models (Fig. 3, Table 3).

We used the coefficients of the interaction between precipitation and diversity to evaluate how precipitation mediated the effect of diversity on AGB (question 2). Out of all 10 models, the interaction between precipitation and species richness on

Table 2. Mean \pm standard deviation of diversity statistics across fifteen 500-m² subplots in each forest. Soil types: L=limestone, V=volcanic. Diversity metrics are rarefied to 130 stems for subplots on limestone soils and 36 stems for subplots on volcanic soils. FD_{WSG} , FD_{LA} , and FD_{MAXHT} correspond to functional dispersion of wood density, leaf area, and maximum height, respectively. PSV = phylogenetic species variability (Helmus et al. 2007). See main text for additional details on diversity calculations.

Forest	Soil Type	Observed richness	Rarefied n	Rarefied richness	Shannon diversity	FD_{WSG}	FD_{LA}	FD_{MAXHT}	PSV
Cambalache/Vega	L	29.9 \pm 4.28	130	23.2 \pm 3.42	2.42 \pm 0.34	-0.57 \pm 0.86	0.29 \pm 0.57	-0.75 \pm 0.58	0.22 \pm 0.55
Guajataca	L	20.7 \pm 5.87	130	13.4 \pm 1.38	2.74 \pm 0.18	-0.11 \pm 0.70	-0.20 \pm 1.14	0.48 \pm 0.36	0.95 \pm 0.45
Guánica	L	34.3 \pm 8.55	130	26.5 \pm 4.01	2.54 \pm 0.23	-0.56 \pm 0.66	-0.80 \pm 0.61	-0.56 \pm 0.69	-1.32 \pm 0.34
Río Abajo	L	21.8 \pm 2.70	130	12.5 \pm 1.34	2.73 \pm 0.35	1.01 \pm 0.88	0.71 \pm 0.92	0.83 \pm 1.17	0.15 \pm 0.82
Carite	V	33.4 \pm 3.48	36	23.6 \pm 2.07	2.25 \pm 0.14	0.18 \pm 1.47	0.20 \pm 1.00	-0.55 \pm 0.78	0.67 \pm 0.76
Guilarte	V	26.1 \pm 4.36	36	16.5 \pm 1.74	2.14 \pm 0.15	0.18 \pm 0.73	-0.43 \pm 0.60	-0.01 \pm 0.77	0.28 \pm 0.84
El Yunque	V	34.2 \pm 9.98	36	28.0 \pm 6.18	2.53 \pm 0.17	0.02 \pm 0.80	-0.33 \pm 0.66	1.12 \pm 0.46	-0.74 \pm 0.76
Toro Negro	V	20.5 \pm 3.48	36	12.9 \pm 2.42	2.16 \pm 0.31	-0.38 \pm 0.81	0.55 \pm 1.32	-0.56 \pm 0.89	-0.21 \pm 1.08

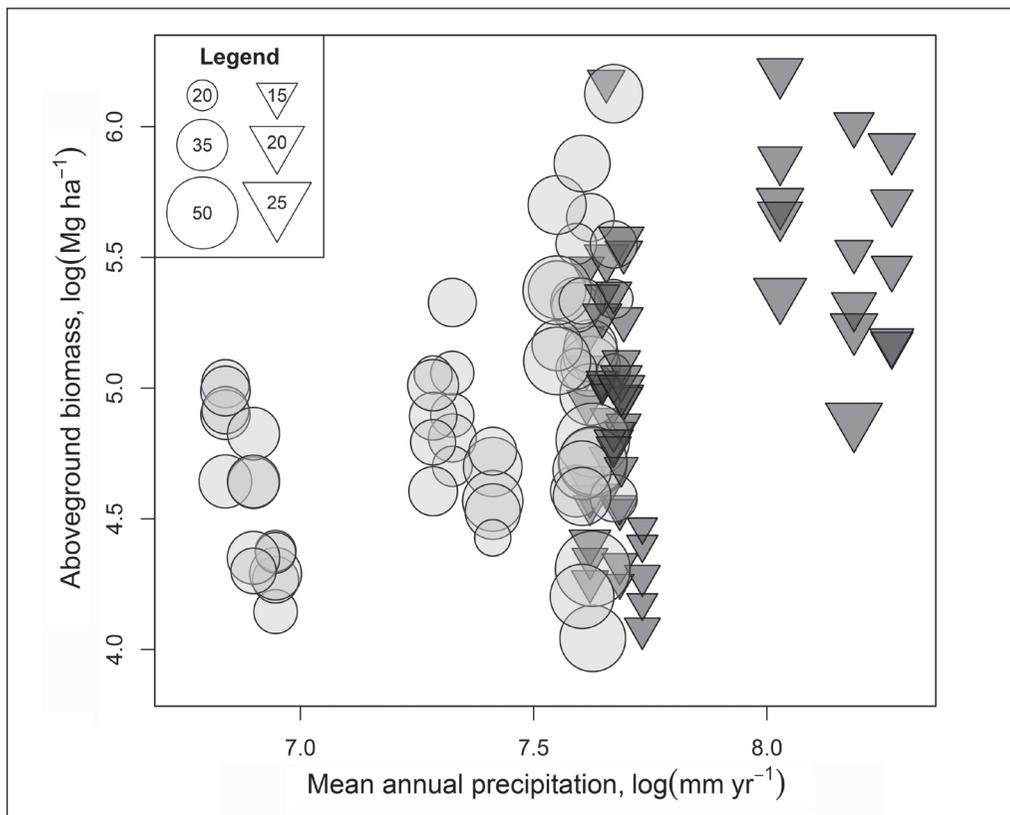


Figure 2. Estimated aboveground biomass (AGB) and (log) mean annual precipitation in one hundred-twenty 500-m² subplots located in protected forests throughout Puerto Rico. Size of symbols is proportional to rarefied species richness (see legend). Note that species richness was rarefied differently for the 2 soil types (see main text for details). Light grey circles represent subplots on limestone soil; dark grey triangles represent subplots on volcanic soil.

Table 3. Results from GLMMs from subplots on limestone and volcanic soils. Marginal and conditional values of R^2_{GLMM} (R^2_M and R^2_C) correspond to the proportion of variance explained by fixed factors alone. R^2_M is and the proportion of variance explained by both the fixed and random factors (R^2_C) (Nakagawa and Schielzeth 2012).

Model/coefficient	Estimate	SD	t value	R^2_M	R^2_C	AIC
Limestone soil subplots						
log(AGB)~ppt + richness + ppt * R + (1 plot)						
Intercept	0.062	0.186	0.331	0.206	0.441	165.88
ppt	0.420	0.189	2.222			
R	-0.040	0.174	-0.231			
ppt * R	-0.192	0.213	-0.900			
plot (random)	-	0.494	-			
log(AGB)~ppt + PSV + ppt * PSV + (1 plot)						
Intercept	0.002	0.251	0.009	0.166	0.485	166.62
ppt	0.398	0.317	1.257			
R	0.037	0.214	0.174			
ppt * R	-0.003	0.219	-0.015			
plot (random)	-	0.593	-			

Table 3. Continued.

Model/coefficient	Estimate	SD	<i>t</i> value	R^2_M	R^2_C	AIC
log(AGB)~ppt + FD _{WD} + ppt * FD _{WD} + (1 plot)						
Intercept	-0.002	0.214	-0.009	0.171	0.479	167.32
ppt	0.464	0.214	2.170			
R	-0.075	0.156	-0.480			
ppt * R	0.004	0.191	0.021			
plot (random)	-	0.579	-			
log(AGB)~ppt + FD _{LA} + ppt * FD _{LA} + (1 plot)						
Intercept	0.007	0.209	0.036	0.222	0.535	163.78
ppt	0.532	0.23	2.315			
R	-0.279	0.162	-1.728			
ppt * R	-0.019	0.185	-0.102			
plot (random)	-	0.596	-			
log(AGB)~ppt + FD _{MAXHT} + ppt * FD _{MAXHT} + (1 plot)						
Intercept	0.095	0.207	0.457	0.205	0.458	165.38
ppt	0.450	0.210	2.139			
R	-0.079	0.188	-0.420			
ppt * R	-0.187	0.208	-0.897			
plot (random)	-	0.516	-			
Volcanic soil subplots						
log(AGB)~ppt + richness + ppt * R + (1 plot)						
Intercept	0.177	0.212	0.832	0.289	0.669	147.17
ppt	0.638	0.227	2.810			
R	0.127	0.121	1.049			
ppt * R	-0.300	0.118	-2.541			
plot (random)	-	0.642	-			
log(AGB)~ppt + PSV + ppt * PSV + (1 plot)						
Intercept	0.025	0.206	0.122	0.248	0.62	153.24
ppt	0.509	0.215	2.369			
R	-0.073	0.124	-0.586			
ppt * R	0.065	0.127	0.514			
plot (random)	-	0.632	-			
log(AGB)~ppt + FD _{WD} + ppt * FD _{WD} + (1 plot)						
Intercept	0.000	0.205	0.001	0.242	0.629	153.80
ppt	0.516	0.207	2.488			
R	-0.041	0.109	-0.373			
ppt * R	0.061	0.114	0.533			
plot (random)	-	0.651	-			
log(AGB)~ppt + FD _{LA} + ppt * FD _{LA} + (1 plot)						
Intercept	0.034	0.205	0.169	0.253	0.634	152.12
ppt	0.568	0.209	2.720			
R	0.099	0.118	0.839			
ppt * R	0.145	0.12	1.203			
plot (random)	-	0.643	-			
log(AGB)~ppt + FD _{MAXHT} + ppt * FD _{MAXHT} + (1 plot)						
Intercept	0.181	0.241	0.750	0.257	0.656	150.15
ppt	0.874	0.300	2.912			
R	-0.212	0.143	-1.477			
ppt * R	-0.275	0.184	-1.493			
plot (random)	-	0.666	-			

volcanic-soil subplots was the only significant interaction effect, indicating that the positive effect of precipitation on AGB was relatively diminished in subplots with high species richness (Fig. 3, Table 3).

Discussion

In addition to species conservation, resource and land management decisions increasingly involve consideration of critical ecosystem functions, such as carbon sequestration (Naeem et al. 2012). Although BEF studies focused on natural systems spanning broad environmental gradients are scarce (Naeem and Wright 2003), several recent studies have used forest-inventory data from temperate regions to evaluate the links between diversity and productivity (e.g., Messier et al. 2010, Paquette and Messier 2011, Ruiz-Benito et al. 2013, Vilá et al. 2007). We quantified variation of AGB in mature Puerto Rican forests that span broad abiotic gradients,

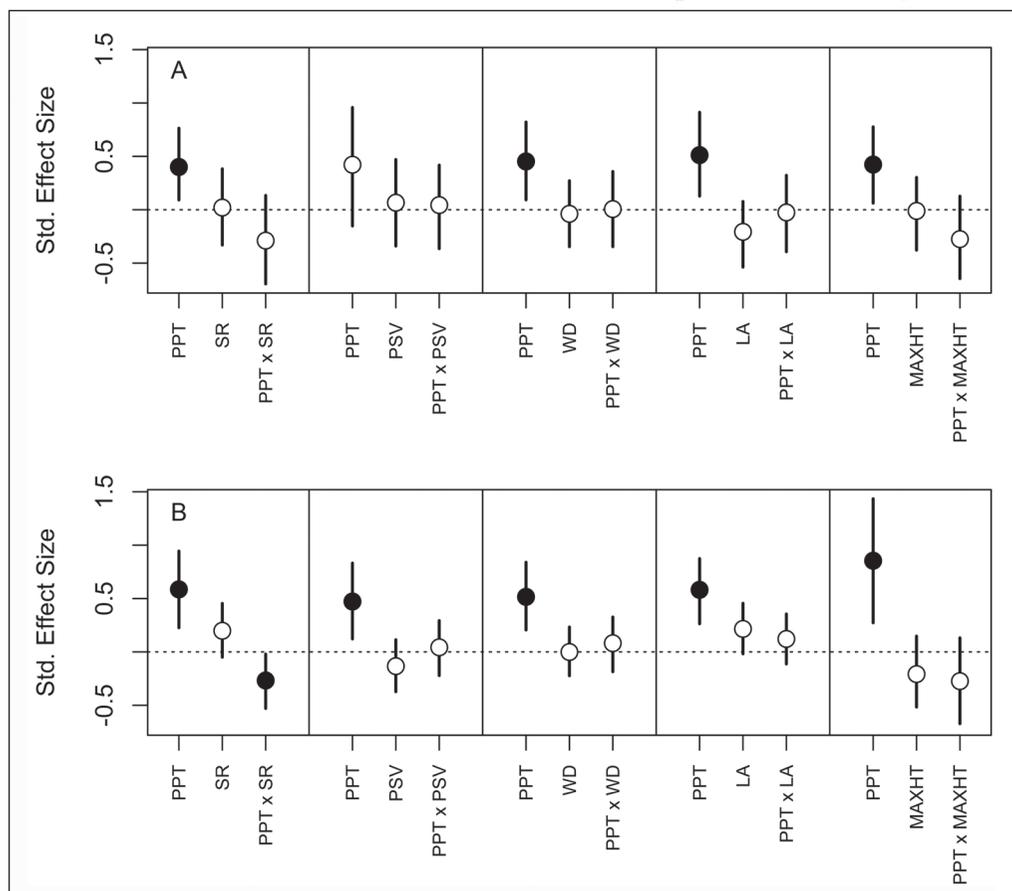


Figure 3. Panels show estimated parameter coefficients and 95% confidence intervals from GLMMs of limestone (A) and volcanic (B) soil subplots with 5 diversity metrics in each subpanel. Rarefied diversity metrics: SR = species richness, PSV = phylogenetic species variability, WD = functional dispersion (FDIs) of wood density, LA = FDIs of leaf area, and MAXHT = FDIs of maximum height. Open circles have 95% confidence intervals that overlap with zero; black circles are significantly different from zero.

and related it to 5 metrics of biodiversity. In mature forests of Puerto Rico, AGB varied substantially along abiotic gradients, and abiotic factors appear to be the strongest drivers of this variation.

Question 1: How do the drivers of AGB differ for the island's two main soil types?

A primary goal of our study was to determine which metrics of biodiversity are most strongly associated with AGB, and how these may differ in forests on different soil types. Although the broad categories we used here subsume finer-scale variation in soil type, the different geologic substrates should capture major differences in edaphic conditions (A.H. Johnson, University of Pennsylvania, Philadelphia, PA, USA, pers. comm.). Water-holding capacity of limestone soils is low, and relatively small increases of precipitation are likely to have a strong effect on plant growth and maximum size. In contrast, all of the volcanic soil plots received $>200 \text{ cm yr}^{-1}$ of precipitation. As a result, we expected precipitation to be a stronger driver of variation in AGB among limestone plots, which are more water limited. Contrary to our prediction, we found no evidence that the influence of precipitation on AGB differed between soil types.

The influence of precipitation on AGB is most strongly apparent in its control on overall tree size and forest structure (Murphy and Lugo 1986a). Our study area covered a wide precipitation gradient; precipitation differences among our limestone plots were $>100 \text{ cm yr}^{-1}$ and differences among plots on volcanic soils were $\sim 200 \text{ cm yr}^{-1}$. Considering this range of variation, perhaps it is not surprising that precipitation is the primary driver of variation in AGB in these forests. However, a previous study of plots in the subtropical wet forest of Puerto Rico (Vance-Chalcraft et al. 2010) found only limited evidence for a linear AGB diversity relationship.

By including phylogenetic diversity and metrics of functional diversity based on traits with well-established responses to abiotic gradients (Westoby et al. 2002, Wright et al. 2004), we aimed to evaluate how diversity along particular axes of life-history variation were related to storage of AGB. In this study, however, none of the diversity metrics had significant direct explanatory power for AGB beyond that captured by precipitation. It is possible that the strong effect of precipitation on productivity precluded our ability to detect more subtle diversity effects. Additional sampling may reveal diversity effects that are detectable at finer scales where the effect of precipitation may be less likely to swamp out a diversity signal.

The forests we sampled varied dramatically in their stem density, and this variation was strongly correlated with precipitation. As a result, raw species richness among subplots was not directly comparable (Gotelli and Colwell 2001). We accounted for this issue by calculating diversity metrics based on rarefied assemblages, thereby controlling for differences in the number of individuals sampled among subplots. Our results would have differed had we not used rarefied metrics. In fact, preliminary analyses based on raw diversity metrics (i.e., not rarefied) suggested a significant role for diversity effects on AGB (data not shown). However, when we removed the positive correlation between stem density and raw diversity metrics through rarefaction, these effects disappeared.

Our results are consistent with a recent global-scale study (Chisholm et al. 2013). When variation in stem density was not considered, Chisholm et al. (2013) found strong positive effects of tree species richness on AGB. After accounting for variation in stem density, the richness effect was largely reduced and in some cases switched sign from positive to negative. The importance of considering stem density depended on the spatial resolution of the analysis; variation in stem density had a strong effect on results of analyses at small grain size (0.04 ha) but it was less important for analyses at larger grain size (1 ha). Greater consideration of this type of sampling issue is essential for evaluating BEF relationships across broad environmental gradients.

Question 2: How does precipitation mediate the relationship between diversity and AGB within each of the two main soil types?

Overall, we found limited evidence that precipitation mediates diversity effects on AGB in Puerto Rican forests. With one exception, none of the interaction terms in our models were statistically significant. The exception was a negative interaction between species richness and precipitation in volcanic soil subplots indicating that, although AGB increased along the precipitation gradient, the effect was diminished in subplots with higher species richness. One possible explanation is that, in these plots, complementary effects become relatively weaker and positive selection effects were acting on a relatively small number of dominant species. We caution against an over-interpretation of this result, however, because it is not supported by the results of models including functional diversity metrics.

It is important to note that the proportion of biomass stored above versus belowground has been shown to vary with respect to abiotic gradients. For example, Murphy and Lugo (1986b) reported that ~50% of total tree biomass occurred belowground in a Guanica dry forest. In comparison, Brown and Lugo (1982) reported that belowground biomass in moist and wet tropical forests accounted for ~16% of total biomass. Understanding how abiotic factors affect different pools of carbon storage will be an important aspect of future work (e.g., Tang et al. 2012).

Three additional caveats warrant discussion. First, although the functional-diversity metrics examined here were not significantly associated with AGB, our analysis only included a static measure of AGB, which is not a proxy for plant primary productivity. Diversity effects on standing AGB may be more strongly related to primary productivity or biomass accumulation over time, and the long-term effects of diversity on carbon sequestration require additional study (Potvin et al. 2011). Furthermore, dynamic processes other than plant productivity (e.g., biomass loss as a result of hurricane damage) are likely to simultaneously influence the amount of standing AGB in our plots. Long-term studies of forest dynamics across environmental gradients will be required to address these limitations and to refine our understanding of the processes governing biomass dynamics in Puerto Rican forests. Second, spatial patterns of biodiversity result from complex interactions among many ecological and evolutionary processes that are intrinsically linked to environmental conditions. Although we found only limited evidence for effects

of biodiversity on AGB in this study, we were not able to assess the direction of causality between diversity and ecosystem function. This issue remains a key area of biodiversity and ecosystem-function research that requires attention. Finally, forests provide many ecosystem services in addition to carbon sequestration (e.g., water purification, wildlife habitat). Simultaneously evaluating multiple ecosystem services provided by forests will provide a more complete picture of the link between biodiversity and ecosystem function (Gamfeldt et al. 2008, Naeem et al. 2012). From a conservation perspective, evaluations of ecosystem services will be better informed by an increased understanding of how different metrics of biodiversity correspond with overall ecosystem function.

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