Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2014)

Global Ecology and Biogeography A Journal of Macroecology

RESEARCH PAPER

Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale

Kyle C. Cavanaugh[1,2*], J. Stephen Gosnell[3], Samantha L. Davis[3], Jorge Ahumada[4], Patrick Boundja[5], David B. Clark[6], Badru Mugerwa[7], Patrick A. Jansen[8,9], Timothy G. O'Brien[10], Francesco Rovero[11,12], Douglas Sheil[7,13,14], Rodolfo Vasquez[15] and Sandy Andelman[4]

[1]Smithsonian Institution, 647 Contees Wharf Road, Edgewater, MD 21037-0028, USA, [2]Department of Ecology and Evolutionary Biology , Brown University, Providence, RI 02912, USA, [3]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA, [4]Tropical Ecology Assessment and Monitoring Network, Moore Center for Ecosystem Science and Economics, Conservation International, Arlington, VA, USA, [5]Tropical Ecology Assessment Monitoring Network, Nouabale-Ndoki National Park and Periphery, The Democratic Republic of the Congo, [6]University of Missouri-St Louis, St Louis, MO, USA, [7]Institute of Tropical Forest Conservation (ITFC), Mbarara University of Science and Technology (MUST), PO Box 44, Kabale, Uganda, [8]Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa Ancón, Republic of Panama, [9]Resource Ecology Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands, [10]Wildlife Conservation Society, 2300 Southern Blvd, Bronx, NY 10460, USA, [11]Tropical Biodiversity Section, MUSE – Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38123 Trento, Italy, [12]Udzungwa Ecological Monitoring Centre, Udzungwa Mountains National Park, PO Box 99 Mang'ula, Tanzania, [13]School of Environment, Science and Engineering, Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia, [14]Center for International Forestry Research, PO Box 0113 BOCBD, Bogor 16000, Indonesia, [15]Jardin Botanico de Missouri, Oxapampa, Pasco, Peru

*Correspondence: Kyle C. Cavanaugh, Smithsonian Institution, 647 Contees Wharf Road, Edgewater, MD 21037-0028, USA.
E-mail: cavanaughk@si.edu

ABSTRACT

Aim We examined (1) the relationships between aboveground tropical forest C storage, biodiversity and environmental drivers and (2) how these relationships inform theory concerning ecosystem function and biodiversity. Experiments have shown that there is a positive relationship between biodiversity and ecosystem functioning, but intense debate exists on the underlying mechanisms. While some argue that mechanisms such as niche complementarity increase ecosystem function, others argue that these relationships are a selection effect.

Location Eleven tropical forests in the Americas, Africa and Asia.

Methods We analysed the correlates of biodiversity and carbon storage in tropical forests using data from 59 1-ha tree plots from a standardized global tropical forest biodiversity-monitoring network. We examined taxonomic and functional diversity, aboveground C storage and environmental variables in order to determine the relationships between biodiversity and carbon storage in natural (non-plantation) tropical forests.

Results We found that aboveground C storage in tropical forests increased with both taxonomic diversity and functional dominance, specifically the dominance of genera with large maximum diameters, after potential environmental drivers were accounted for (final model $R^2 = 0.38$, $P < 0.001$).

Main conclusions Our results suggest that niche complementarity and the selection effect are not mutually exclusive: they both play a role in structuring tropical forests. While previous studies have documented relationships between diversity and C storage, these have largely been conducted on small scales in biomes that are relatively species poor compared with tropical forests (e.g. grasslands and temperate or boreal forests). Our results demonstrate that these positive biodiversity–ecosystem functioning relationships are also present in hyperdiverse systems on spatial scales relevant to conservation and management. This insight can be used to inform the conservation and management of tropical forests, which play a critical role in the global carbon cycle and are some of the biologically richest ecosystems on the planet.

Keywords
Aboveground carbon storage, Africa, Asia, biodiversity, functional diversity, functional dominance, Neotropics, niche complementarity, taxonomic diversity, tropical forest.

DOI: 10.1111/geb.12143
http://wileyonlinelibrary.com/journal/geb

INTRODUCTION

The relationship between biodiversity and ecosystem functioning has been a matter of debate for more than three decades (Grime, 1973; Adler *et al.*, 2011). The importance of a better understanding of this relationship and the underlying mechanisms is only increasing as habitat loss, species invasions and climate change alter biotic communities (Sax & Gaines, 2003). Manipulative experiments designed to control levels of local diversity have indicated that there are positive relationships between plant diversity and productivity at the plot scale in grassland systems (Tilman *et al.*, 1997; Hector *et al.*, 1999). However, meta-analyses of the biodiversity–ecosystem function (B-EF) relationship of natural systems have produced conflicting results (Jiang *et al.*, 2009). Some have found that hump-shaped relationships between species richness and biomass or productivity are most common (Mittelbach *et al.*, 2001), while others have argued that positive relationships dominate (Gillman & Wright, 2006). Critics of these comparative analyses have argued that variability of conclusions reflects methodological differences among the field studies, particularly differences in the size of the sampling unit and the spatial extent of the studies (Chase & Leibold, 2002; Whittaker & Heegaard, 2003). As a result, there have been calls to implement global networks using standard and consistent approaches to avoid such discrepancies (Condit, 1995; Adler *et al.*, 2011).

Much of the debate over the mechanisms behind observed B-EF relationships has centred on whether diversity effects are driven by niche partitioning and facilitation (i.e. the complementarity effect; Tilman *et al.*, 1997) or by the selection of one or more highly productive or high-biomass species (i.e. the selection effect; Loreau & Hector, 2001; Cardinale *et al.*, 2012). The complementarity effect hypothesis states that a diverse group of species has a greater variety of functional traits and can thus better utilize a pool of limiting resources, thereby increasing total ecosystem functioning, than a less diverse community. The selection effect hypothesis assumes that dominant species or traits drive ecosystem functioning and that positive B-EF relationships arise simply because diverse communities are more likely to include high-functioning species and traits. A better understanding of how diversity and dominance affect ecosystem function would help direct conservation and restoration strategies for threatened or exploited ecosystems.

A range of approaches have been used to examine B-EF relationships (specifically productivity and/or aboveground C storage for the following examples) in forests on continental scales. These approaches include studies of the contribution of individual species to total community function (Balvanera *et al.*, 2005), simulations of the response of ecosystem function to different local extinction scenarios (Bunker *et al.*, 2005), data resampling to examine the relationship between traits and function (Baker *et al.*, 2009) and multisite studies that correlate biodiversity or functional traits to ecosystem function (Baker *et al.*, 2004; Vilà *et al.*, 2007). Results have demonstrated mixed support for the hypothesized B-EF relationships in forests. There is some empirical evidence for a positive relationship between species richness and wood production in temperate and boreal forests (Vilà *et al.*, 2007; Paquette & Messier, 2011), and Caspersen & Pacala (2001) found that aboveground biomass was positively related to successional stage and species richness in temperate forests of the midwestern USA, supporting the complementarity mechanism. A study of 6 ha of old-growth forest in Panama found that tree species richness explained more variation in carbon storage than did tree dominance, also supporting the complementarity mechanism (Ruiz-Jaen & Potvin, 2010). However, simulations have demonstrated that changes in aboveground C storage depend on the characteristics of the species being removed (Bunker *et al.*, 2005), and stand-level basal area and wood density correlate with spatial patterns in aboveground biomass in the Amazon and Asia (Baker *et al.*, 2004; Slik *et al.*, 2010). These results support the selection effect hypothesis, with a few dominant species contributing disproportionately to C storage (Balvanera *et al.*, 2005). Other studies have found no general relationship between wood density and forest biomass (Stegen *et al.*, 2009) and suggested that relationships among diversity metrics and carbon storage may differ among even geographically close forests (Ruiz-Jaen & Potvin, 2011).

A concern with many of these multisite studies is that many potentially influential site factors such as local climate are not accounted for, which may mask the key relationships (Ma *et al.*, 2010). In addition, for logistical reasons, many multisite experimental and observational studies have small plot sizes and/or limited extents, which may cause the impact of diversity on ecosystem processes to be underestimated (Cardinale *et al.*, 2011). To better explore relationships among diversity and functioning, a standardized, global approach is needed. We used data from a standardized tropical forest monitoring effort, the Tropical Ecology Assessment and Monitoring (TEAM) Network, to examine the relationship between plot-level biodiversity and aboveground C storage, a key measure of ecosystem functioning. Our goal was to determine whether the relationship was general across the tropics, and assess whether it was driven by niche complementarity, the selection effect or a combination of the two. We used data from 59 1-ha plots at TEAM sites in Africa, Asia and tropical America that systematically span current and projected environmental and land-use gradients. We estimated aboveground C stocks at each plot and compared them with a number of potential explanatory variables to identify the major biotic and abiotic correlates of aboveground C storage. We addressed the following questions:

1. What are the most important environmental controls of taxonomic diversity, functional diversity and aboveground C storage in tropical forests?

2. Is there a positive relationship between taxonomic diversity, functional diversity or functional dominance and aboveground C storage, after accounting for environmental factors?

Our focus on B-EF in tropical forests enabled us to consider relationships between diversity and productivity in hyperdiverse areas where past work has suggested that saturating relationships between diversity, services (e.g. carbon storage) and niche space may minimize the importance of additional species

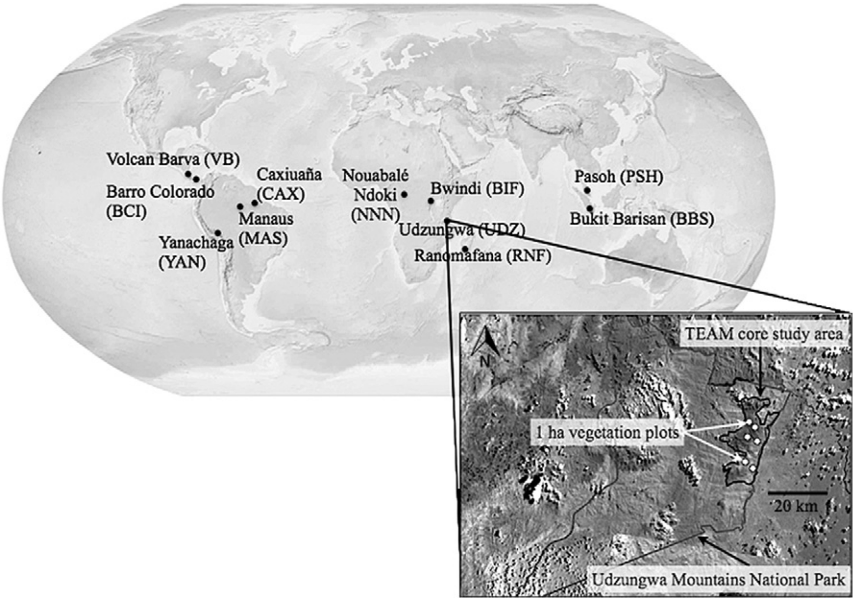

Figure 1 Map of TEAM sites used in this study: Bukit Barisan (BBS, Indonesia), Barro Colorado Island (BCI, Panama), Bwindi Impenetrable Forest (BIF Uganda), Caxiuanã (CAX, Brazil), Manaus (MAS, Brazil), Nouabalé Ndoki (NNN, Republic of Congo), Pasoh Forest Reserve (PSH, Malaysia), Ranomafana (RNF, Madagascar), Udzungwa (UDZ, Tanzania), Volcán Barva (VB, Costa Rica), Yanachaga Chimillén National Park (YAN, Peru). Inset gives an example of the distribution of plots at the Udzungwa site.

(Hooper *et al.*, 2005; Ruiz-Jaen & Potvin, 2011). This dataset also allowed us to examine the relationship between diversity and C storage in tropical forest systems which have historically received less attention due to a paucity of monitoring plots in these areas (e.g. Africa and Asia; Ciais *et al.*, 2008). We need to better understand the relationship between diversity and C storage in tropical forest systems across continents as both biodiversity and C storage are threatened by deforestation and climate change. Understanding the controls on C storage will help inform conservation policies intended to mitigate CO_2 emissions while preserving biodiversity.

METHODS

Study sites

Data from this study come from the TEAM Network (http://www.teamnetwork.org, dataset ID 20120620104615 3074), a global network of tropical forest monitoring sites designed to understand the effects of climate change and land use on biodiversity and ecosystem services. We examined tropical forest biodiversity and carbon storage in 59 1-ha plots at 11 TEAM sites in America, Africa and Asia (Fig. 1). These plots were selected from available TEAM data that had more than 80% of trees identified to the family level (Table 1). Of the plots meeting these criteria, 97% of trees were identifiable to genus and 98% of trees were identifiable to family. The 11 TEAM sites were all located in mature, relatively undisturbed tropical forests within protected areas. The sites covered pronounced gradients in climate, elevation and latitude (see Results). Some sites were designed to span elevation gradients within the site (e.g. Volcán Barva, Table 1), while others had little intrasite variation in elevation (e.g. Ranomafana, Table 1).

Data

Each TEAM site contained between one and eight 1-ha vegetation plots (the median number of plots was five). Within each 1-ha plot, all of the trees > 10 cm in diameter were identified and measured for diameter at 1.3 m (or above basal irregularities) at least once per year following standardized protocols (TEAM 2009). Lianas were not included in this study. We used the most recent sampling date at each site; this ranged from 2010 to 2012 depending on the site. We first classified the TEAM sites as 'dry' (< 1500 mm year^{-1} precipitation) or 'moist' (1500–3500 mm year^{-1}) (cf. Chave *et al.*, 2005), where mean annual precipitation for each site was obtained from the Climatic Research Unit, University of East Anglia, Norwich, UK (CRU) (see below for details regarding precipitation data). We then calculated aboveground biomass for individual, live trees using allometric equations for dry and moist forests from Chave *et al.* (2005):

$$\begin{aligned}\mathrm{AGB}_{\mathrm{dry}} = \mathrm{WD}\times\exp[&-0.667+1.784\ln D\\ &+0.207(\ln D)^2-0.0281(\ln D)^3]\end{aligned}$$

$$\begin{aligned}\mathrm{AGB}_{\mathrm{moist}} = \mathrm{WD}\times\exp[&-1.499+2.148\ln D\\ &+0.207(\ln D)^2-0.0281(\ln D)^3],\end{aligned}$$

where WD is the wood density for each genus in g cm^{-3} and D is the diameter at 1.3 m in cm. Aboveground biomass (AGB) was scaled to aboveground C storage by multiplying by a factor of 0.5 (as in Chave *et al.*, 2005). We used the same allometric regression models for both trees and palms (Chave *et al.*, 2008). We obtained wood density values for each genus from a publicly available wood density database (Zanne *et al.*, 2009). If a genus was missing from the database we used the mean family wood density. If family data on wood density was missing or a tree had not been identified to the family level, we used the mean wood

Table 1 Mean and coefficient of variation (CV; in parentheses) of carbon storage, taxonomic diversity (genus richness and Shannon diversity), functional diversity (Rao Q), functional dominance [community weighted mean (CWM) of wood density and maximum diameter], and environmental variables (elevation, mean precipitation, and coefficient of variation of mean monthly precipitation) for each TEAM site (see caption to Fig. 1 for the full name of each site). The CV for each variable was calculated across the plots of a site.

	Site										
Properties	MAS	CAX	YAN	BCI	VB	RNF	NNN	UDZ	BIF	PSH	BBS
Country	Brazil	Brazil	Peru	Panama	Costa Rica	Madagascar	Congo	Tanzania	Uganda	Malaysia	Indonesia
No. of plots	6	6	1	5	8	6	3	6	6	6	6
Stem density (trees ha^{-1})	684 (0.07)	485 (0.08)	718 (0.00)	521 (0.12)	510 (0.22)	1082 (0.22)	274 (0.11)	532 (0.17)	528 (0.29)	417 (0.31)	398 (0.23)
Aboveground C storage (Mg C ha^{-1})	191 (0.16)	285 (0.17)	113 (0.00)	174 (0.18)	150 (0.14)	226 (0.28)	232 (0.02)	151 (0.22)	113 (0.41)	138 (0.35)	146 (0.42)
Taxonomic diversity											
Genus richness	129 (0.05)	90 (0.09)	88 (0.00)	74 (0.10)	71 (0.34)	64 (0.14)	46 (0.09)	33 (0.33)	32 (0.21)	89 (0.19)	68 (0.17)
Shannon diversity	4.05 (0.03)	3.51 (0.08)	3.63 (0.00)	3.42 (0.07)	3.52 (0.10)	3.27 (0.10)	3.09 (0.05)	2.35 (0.30)	2.47 (0.19)	3.81 (0.07)	3.36 (0.11)
Functional diversity											
Rao *Q*	0.91 (0.13)	0.85 (0.12)	0.97 (0.00)	1.37 (0.38)	1.12 (0.33)	0.67 (0.21)	0.92 (0.04)	0.62 (0.55)	0.76 (0.47)	0.85 (0.49)	0.95 (0.37)
Functional dominance											
CWM wood density (g cm^{-1})	0.67 (0.04)	0.71 (0.03)	0.56 (0.00)	0.57 (0.07)	0.55 (0.06)	0.60 (0.03)	0.66 (0.01)	0.61 (0.05)	0.56 (0.07)	0.56 (0.07)	0.55 (0.07)
CWM diameter (cm)	50.96 (0.03)	67 (0.10)	36 (0.00)	46 (0.06)	52 (0.07)	71 (0.15)	91 (0.04)	79 (0.08)	63 (0.13)	55 (0.08)	57 (0.16)
Environment											
Elevation (m)	110 (0.25)	48 (0.08)	1273 (0.00)	128 (0.47)	712 (0.98)	1153 (0.05)	487 (0.05)	1283 (0.34)	1880 (0.19)	466 (0.50)	90 (0.82)
Mean annual precipitation (mm $year^{-1}$)	2192 (na)	2342 (na)	2197 (na)	2420 (na)	3462 (na)	1553 (na)	1662 (na)	1371 (na)	1239 (na)	2067 (na)	2871 (na)
CV monthly precipitation	0.43 (na)	0.57 (na)	0.44 (na)	0.61 (na)	0.39 (na)	0.69 (na)	0.46 (na)	0.91 (na)	0.32 (na)	0.29 (na)	0.15 (na)

na, not applicable.

density for that plot (as in Baker *et al*., 2004; Stegen *et al*., 2009). We were able to obtain genus-level wood density values for 76% of the stems and family- or genus-level values for 85% of the stems.

We measured three dimensions of tree diversity at each plot: taxonomic diversity, functional diversity and functional dominance. We evaluated all diversity metrics at the genus level because some of the individual trees were not identified to species; coverage was much more complete at the genus level (we had 97% coverage at the genus level). Previous work in diverse taxa has suggested that lower taxonomic resolution is an appropriate solution for analysing relationships among diversity and other factors when needed due to a lack of species-level identification or other constraints (expertise, information, etc.; Chainho *et al*., 2007; Bacci *et al*., 2009; Timms *et al*., 2013). Our taxonomic diversity metrics, genus richness and Shannon diversity, measure the variety of taxa in a plot. Genus richness was calculated as the number of distinct genera in each plot. We also calculated the Shannon diversity index at the genus level for each plot (Magurran, 1988). We used wood density and maximum diameter for our analyses of functional diversity and dominance as these traits are closely related to differences in life-history strategies (Whitmore, 1998). Wood density is a good indicator of whether a species allocates its growth into fast growth and early reproduction or slow growth and resistance to environmental hazards (Tilman, 1988; Chave *et al*., 2006). Typically fast-growing species have a higher light demand and lower wood density than slow-growing shade-tolerant species (Whitmore, 1998). Maximum diameter can serve as a proxy for potential height, which is considered an important indicator of the light capture strategy (Falster & Westoby, 2005; Kraft *et al*., 2008). Functional diversity refers to the variability of functions or characteristics of the trees in a plot. As a functional diversity metric, we calculated the Rao quadratic entropy (Rao *Q*) of each plot using data on wood density and maximum diameter with the FD package in R (Laliberté & Legendre, 2010; Laliberté & Shipley, 2011). The Rao *Q* is a multitrait functional diversity metric that incorporates both the relative abundances of species and the pairwise functional difference between species (Botta-Dukát, 2005). Maximum diameter was determined from within the dataset, with values assigned equal to the largest diameter value in the data set for a given genus at a given site (to account for possible environmental variation). Whereas functional diversity measures the variety of characteristics of the trees in a plot, functional dominance measures the degree to which a trait is more numerous than other traits. For functional dominance, we estimated the community weight mean (CWM) for wood density and maximum diameter, again using the FD package in R (Laliberté & Shipley, 2011). Plot CWM was calculated as the mean trait value of each genus weighted by the relative abundance of the genus in a given plot.

In order to characterize the environmental variability across plots we estimated the mean annual precipitation and the coefficient of variation (CV) of mean monthly precipitation for each site from 1900–98 from a historic global gridded monthly precipitation dataset provided by the CRU (Hulme, 1992). The CV of mean precipitation across months measures the month-to-month variability in rainfall and so is a measure of rainfall seasonality. Sites with pronounced wet and dry seasons will have a high CV of mean monthly precipitation. The global precipitation dataset had a spatial resolution of 5°, so we were unable to resolve plot-scale precipitation variability. We estimated the mean elevation of each 1-ha plot using 225-m resolution digital elevation model data from the USGS Global Multiresolution Terrain Elevation Data 2010 product (Danielson & Gesch, 2011).

Statistical analysis

We used generalized linear mixed models (Zuur, 2009) to examine the relationships between individual environmental variables (elevation, mean annual precipitation and CV of mean monthly precipitation) and taxonomic diversity, functional diversity and aboveground carbon storage at the plot scale. We included site as a random effect in our models, since plots within a given site may be expected to be similar and should not be considered independent. Due to the potential for communities within a site to change along elevational gradients, errors were also considered to be correlated along elevation at each site using a Gaussian spatial correlation structure (Zuur, 2009). By using mixed models we took advantage of both plot-scale and site-scale variability in most factors when analysing the relationships between environmental drivers, biodiversity and C storage. Using the same random effects and covariance structure, we also examined the relationship between taxonomic diversity (genus richness and Shannon diversity) and functional diversity (Rao *Q*).

We next evaluated the combined effects of environmental drivers (mean annual precipitation, CV of mean monthly precipitation, elevation) on taxonomic diversity (Shannon diversity and genus richness) and functional diversity (Rao *Q*). Finally, we explored the combined effects of environmental drivers, taxonomic diversity (genus richness), functional diversity and functional dominance (community weighted means of maximum diameter and wood density) on aboveground C storage. Optimal models were selected using stepwise regression procedures. Models fitted by maximum likelihood methods were compared using likelihood ratio tests; parameters retained in the final models were all significant at the $P < 0.05$ level according to Type III ANOVA. For the final model we quantified the variance explained using the R^2 measures developed for fixed effects in linear mixed models (Edwards *et al*., 2008). To aid in visualization and interpretation, we plotted the bivariate relationships between the predictor and response variables for the final models of taxonomic diversity, functional diversity and aboveground C storage.

Although wood density and stem diameter were both used to estimate aboveground C storage at the stem level, we assumed that plot CWMs of these variables could still be considered to be relatively independent predictors of plot C storage (following Baker *et al*., 2004; Ruiz-Jaen & Potvin, 2011). Essentially we are comparing community traits with estimates of carbon storage

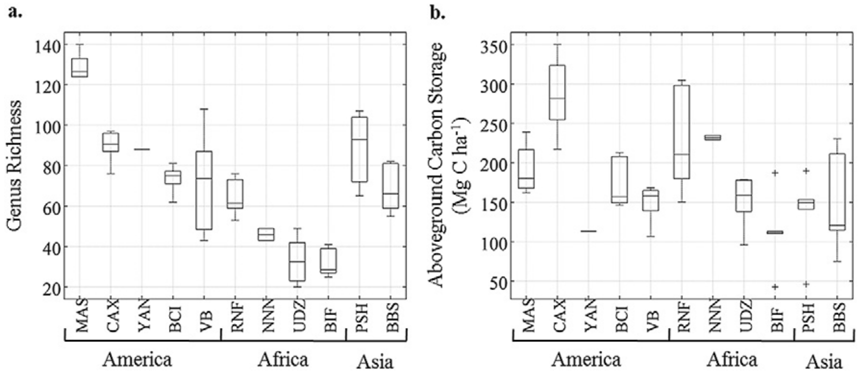

Figure 2 Distribution of plot (a) genus richness and (b) aboveground carbon storage at each TEAM site. See caption to Fig. 1 for the full name and country of each site.

determined by individual tree values. For example, the plot CWM of maximum diameter represents the potential height of the community in a given plot, whereas C storage is calculated from the actual diameter of each tree. Maximum potential diameter will not necessarily be correlated with actual stem diameter. In fact, the relationship between the maximum diameter of species and the actual diameter of their stems was extremely weak (linear regression $R^2 = 0.02$).

RESULTS

Precipitation, elevation and latitude varied widely among sites (Table 1). Mean annual rainfall ranged from 1239 to 3462 mm and the CV of mean monthly rainfall (a measure of seasonality) ranged from 0.15 to 0.91 (Table 1). Elevation ranged from 48 m above sea level (Caxiuaña, Brazil) to 1880 m (Bwindi Impenetrable Forest, Uganda). Some sites covered large elevation gradients (e.g. plots at the Volcán Barva site ranged from 68 to 1997 m), while others (e.g. Ranomafana and Caxiuaña) had only slight intrasite differences in elevation.

The number of genera per plot ranged from 20 to 140 (Fig. 2a). On average, the Neotropical sites had more than twice as many genera per plot as the African sites (89.8 vs. 43.2; two-sample *t*-test: $t = 6.81$, d.f. = 38, $P < 0.0001$), but there was no significant difference in genus richness between the Neotropical and Asian sites (89.8 vs. 78.6; $t = 1.32$, d.f. = 36, $P = 0.20$). The amount of aboveground carbon was highly variable across sites, ranging from 50 to 350 t ha^{-1} (Fig. 2b). There were no large differences in aboveground C biomass between continents, although the Asian plots had slightly lower C on average, 141.8 ± 15.2 Mg C ha^{-1} (mean ± SE), than had the Neotropical, 193.8 ± 12.3 Mg C ha^{-1}, and African sites, 170.1 ± 14.5 Mg C ha^{-1}.

Table 2 Mixed-model bivariate relationships between environmental variables and genus richness, Shannon diversity, Rao *Q*, and carbon storage. Precipitation seasonality was calculated as the coefficient of variation across months of mean monthly precipitation.

Variable	Coefficient	R^2	P
Genus richness			
Mean annual precipitation	1.9×10^{-2}	0.04	0.11
Precipitation seasonality	−34.64	0.01	0.38
Elevation	-2.0×10^{-2}	0.16	0.00
Latitude	0.38	0.00	0.69
Longitude	-1.4×10^{-1}	0.02	0.24
Shannon diversity			
Mean annual precipitation	4.30×10^{-4}	0.07	0.04
Precipitation seasonality	−1.01	0.03	0.16
Elevation	-3.10×10^{-4}	0.09	0.02
Latitude	0.01	0.01	0.51
Longitude	0	0.01	0.38
Functional diversity (Rao *Q*)			
Mean annual precipitation	2.0×10^{-4}	0.12	0.01
Precipitation seasonality	−0.28	0.01	0.35
Elevation	-2.0×10^{-4}	0.10	0.02
Latitude	0.02	0.16	0.01
Longitude	-2.0×10^{-3}	0.07	0.04
Aboveground C storage			
Mean annual precipitation	-1.0×10^{-3}	0.00	0.96
Precipitation seasonality	90.00	0.02	0.21
Elevation	-3.0×10^{-3}	0.00	0.78
Latitude	−1.28	0.01	0.46
Longitude	−0.18	0.01	0.41

Analyses of bivariate relationships indicated that taxonomic and functional diversity were correlated with certain environmental variables but aboveground C storage was not. Taxonomic diversity (genus richness) was significantly negatively correlated with elevation, while Shannon diversity was significantly positively correlated with mean annual precipitation and negatively correlated with elevation (Table 2). Functional diversity (the Rao *Q* of wood density and maximum diameter) was also positively correlated with mean annual precipitation and negatively correlated with elevation. The Rao *Q* was positively correlated with latitude and negatively correlated with longitude. As expected, genus richness was highly correlated with Shannon diversity ($R^2 = 0.70$, $P < 0.001$); for this reason we considered only genus richness as the taxonomic diversity predictor of C storage in the final model. However, neither genus richness nor Shannon diversity was significantly associated with functional diversity ($R^2 < 0.01$, $P = 0.55$ and $R^2 < 0.01$, $P = 0.55$, respectively).

Only elevation was a significant predictor of taxonomic diversity, explaining 10% of the variation in Shannon diversity and

Table 3 Results of full mixed models of genus richness, Rao *Q*, and carbon storage.

Variable	d.f.	X^2	*P*
Genus richness			
Elevation	1	11.4	< 0.001
Intercept	1	123.7	< 0.001
Rao *Q*			
Mean annual precipitation	1	10.8	< 0.001
Intercept	1	11.1	< 0.001
Aboveground C storage			
Genus richness	1	21.4	< 0.001
CWM maximum d.b.h.	1	29.8	< 0.001
Intercept	1	5.8	0.01

CWM, community weighted mean.

16% of the variation in genus richness (Table 3). Functional diversity (the Rao *Q* of wood density and maximum diameter) was only explained by mean precipitation, which explained 11% of the variation in the Rao *Q* (Table 3). Taxonomic diversity (genus richness) and functional dominance (CWM of maximum diameter) together explained 38% of the variance in carbon storage (Table 3). These findings were not qualitatively affected by inclusion of stem density in the models (the same parameters retained to explain 25% of variation). Figure 3 shows the bivariate relationships between each significant predictor and its corresponding response variable for the final models of taxonomic diversity, functional diversity and aboveground C storage.

DISCUSSION

We found that aboveground C storage was positively associated with both functional dominance and taxonomic diversity in tropical forests, after site effects were accounted for and the impact of potential environmental drivers was considered. This provides empirical evidence that producer biomass increases with diversity, even in hyperdiverse ecosystems such as tropical forests. We accounted for environmental variability among sites, but did not find any direct relationships between our climate/environmental variables and aboveground C storage.

The CWM of wood density appeared to be unimportant as a factor explaining aboveground C storage. This result argues against the hypothesis that aboveground forest biomass is generally related to the dominance of trees with either high or low wood densities (cf. Stegen *et al.*, 2009). However, the positive relationship between CWM of maximum diameter, a measure of functional dominance, and C storage suggests that characteristics of the dominant trees in a plot (specifically their maximum potential diameter) do influence aboveground C storage in mature forests. This result agrees with previous studies that have found that the traits of dominant species (i.e. wood density and diameter) have a large effect on aboveground C storage (Balvanera *et al.*, 2005; Ruiz-Jaen & Potvin, 2010) and productivity (Healy *et al.*, 2008). Brown & Lugo (1992) found that the relative abundance of tree stems >70 cm diameter was positively correlated with estimates of aboveground biomass in the Brazilian Amazon, further demonstrating the importance of large trees in plot biomass estimates. Baker *et al.* (2004) and Slik *et al.* (2010) also found that forest basal area explained a significant amount of between-site variation in aboveground biomass in Amazonian and Asian tropical forests. These findings support the selection-effect hypothesis, which emphasizes the importance of these dominant species in maintaining ecosystem function (Smith & Knapp, 2003; Loreau & Hector, 2001; Cardinale *et al.*, 2012). All of the aforementioned studies that have linked functional dominance to C storage and productivity have had local (100s of metres; e.g. Healy *et al.*, 2008; Ruiz-Jaen & Potvin, 2010) to regional extents (100s to 1000s of kilometres; e.g. Baker *et al.*, 2004; Slik *et al.*, 2010). Our study was global in its extent, and therefore our results demonstrate that the positive relationship between aboveground C storage and the dominance of trees with large potential diameters is apparent both across and within continents. This relationship thus appears to be consistent across a variety of scales.

However, taxonomic diversity (genus richness) was still positively associated with aboveground C storage after functional dominance was accounted for. This indicates that niche complementarity, the ability of a diverse assemblage of species to more efficiently utilize a pool of limiting resources, may also be operating in diverse tropical forests. Previous studies have suggested that the niche complementarity effect may be less important in stable and productive environments, where competition is often the most common form of species interaction, than in unstable and stressful environments (Paquette & Messier, 2011). This hypothesis is supported by Ruiz-Jaen & Potvin (2011), who found that functional dominance explained most of the variation in aboveground C storage in an old-growth tropical forest in Panama while there was no relationship between species richness and C storage. They suggested that the relationship between taxonomic diversity and C storage saturated in this species-rich forest. In contrast, we found that taxonomic diversity was nearly as important as functional dominance in explaining aboveground C storage in diverse tropical rain forests (Table 3). This discrepancy may be partially explained by the size of our vegetation plots. Our 1-ha plots were more than an order of magnitude larger than plots used in the aforementioned forest B-EF studies (e.g. 0.07 ha in Vilà *et al.*, 2007, 0.04 ha in Paquette & Messier, 2011, 0.004 ha in Ruiz-Jaen & Potvin, 2011). Larger plot size may have enhanced our ability to detect B-EF relationships, as there is evidence that diversity effects are more apparent at larger spatial scales because more heterogeneity and niche opportunities are captured (Cardinale *et al.*, 2011). Moreover, the global extent of our study may also have contributed to the positive relationship we found between genus richness and aboveground C storage. It has been suggested that variation in C storage and productivity increases with the extent of a study, and this increased variation can result in a larger overall response to species richness (Mittelbach *et al.*, 2001). In addition, all of our plots were located in mature forests, and there is evidence that

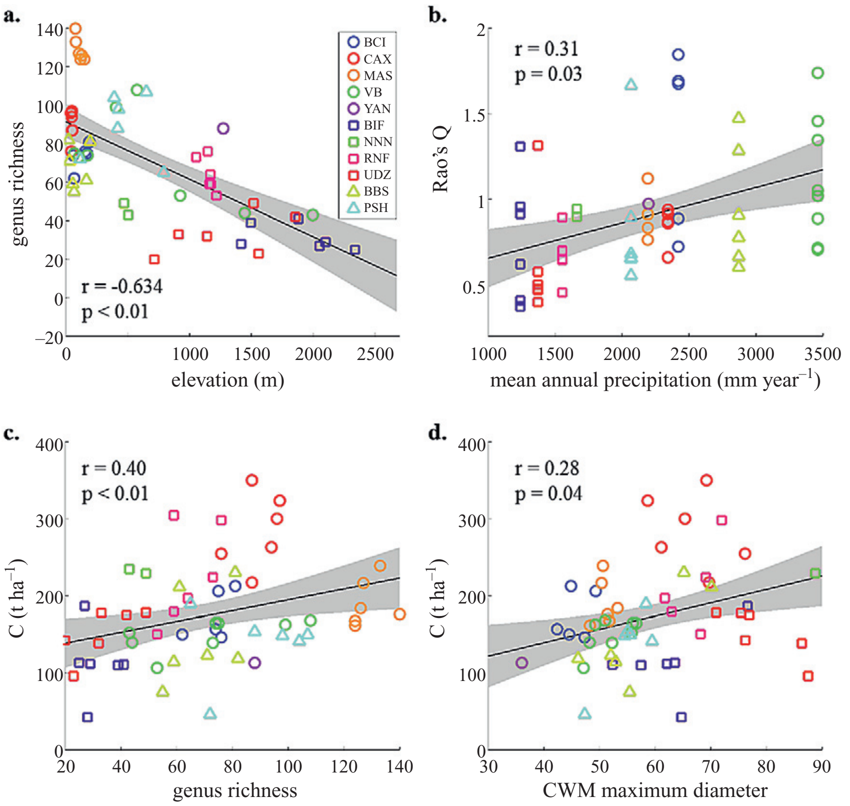

Figure 3 Plots of bivariate relationships for the variables in the final models (the variables listed in Table 3) of (a) genus richness, (b) functional diversity (Rao Q), and (c, d) C storage. In all panels, sites are identified by colour and continents are identified by symbols (circles, America; squares, Africa; triangles, Asia). Statistics from bivariate Pearson correlation analyses are given, but note that the statistics from Table 3 are from generalized linear mixed models. Shaded area gives the 95% confidence intervals for each relationship. See caption to Fig. 1 for the full name and country of each site. CWM, community weighted mean.

the effects of complementarity increase over time, especially in communities of long-lived organisms such as forests (Cardinale *et al.*, 2007). Our overall results are consistent with a recent meta-analysis of manipulative studies which found that, on average, selection and niche complementarity effects both contribute about 50% to the B-EF relationship (Cardinale *et al.*, 2011). We demonstrate that the coexistence of these two effects is not only apparent when many ecosystems are examined together; they can both contribute to biomass storage in a single, hyperdiverse ecosystem.

While taxonomic diversity was positively associated with aboveground C storage, we did not find a significant relationship between functional diversity and C storage, which is in disagreement with the niche complementarity hypothesis (Tilman *et al.*, 1997). A possible explanation is that the traits that were most important to complementary resource allocation were not included in our functional diversity metric (Petchey & Gaston, 2006). While wood density and maximum diameter capture variability in important life-history traits, other traits for which we did not have data (e.g. maximum height, leaf mass per area and nitrogen fixing capabilities) might have better characterized potential competition among species.

We were not able to detect significant relationships between aboveground C storage and any of the climate or environmental variables (Tables 2 & 3). A direct relationship between climate/environmental variables and estimated aboveground C stocks could have been obscured by limitations in the accuracy of our estimates of aboveground C and our climate data. Estimating plot-level aboveground biomass through the use of allometric scaling equations (as we have done here) is a common practice, but comprehensive accuracy assessments of these plot-scale estimates have not been conducted (Clark & Kellner, 2012). The accuracy of our climate data (CRU gridded data) is dependent on the density of climate stations near our sites and the quality of the interpolation methods used. Interpolated precipitation data can have poor accuracy in mountainous areas due to high local variability in rainfall. In addition, areas with a low population density typically have fewer climate stations. Finally, while our 1-ha size plots are large relative to many other empirical forest B-EF studies (e.g. Vilà *et al.*, 2007; Paquette & Messier, 2011; Ruiz-Jaen & Potvin, 2011), there is still fine-scale variation in forest biomass that could add uncertainty to our empirical relationships between environmental variables and aboveground C storage.

It is important to note that relationships between environmental variables and biodiversity can vary among continents (Parmentier *et al.*, 2007; Ghazoul & Sheil, 2010). For example, African forests generally have higher biomass and low diversity compared with Amazonian forests (Parmentier *et al.*, 2007; Ghazoul & Sheil, 2010). Tropical forests in parts of Asia (e.g. Borneo) also tend to have high aboveground biomass compared with forests from the Neotropics (Paoli *et al.*, 2008). These patterns are probably influenced by a suite of factors including disturbance histories, historical climate, botanical effects and geological and soil characteristics. Some of the influence of these factors is probably accounted for by the random 'site' effect in the mixed model. We also found that aboveground C storage was still positively associated with taxonomic diversity and functional dominance when continent was included as a fixed effect in the model. However, we did not have enough sites to perform the above analyses entirely for each continent or appropriately consider interactions. As a result we were not able to fully examine how the relationships between environmental factors, biodiversity and aboveground C storage vary across continents. As coordinated global networks such as TEAM increase in size, future studies will be able to more accurately evaluate the impact of regional effects on the relationships between biodiversity and C storage.

While causality cannot be demonstrated from observational studies such as this one, our results do suggest that biodiversity is positively related to aboveground C storage in natural, hyperdiverse systems. This positive relationship appears to be driven both by individual, dominant species and some form of complementarity among species, mirroring conclusions from recent multisystem meta-analyses of manipulative studies (Cardinale *et al*., 2011, 2012). Most of the other observational studies that have linked biodiversity to biomass or productivity in forests have been conducted in relatively species-poor temperate and boreal forests (e.g. Caspersen & Pacala, 2001; Vilà *et al*., 2007, Paquette & Messier, 2011). Much less is known about these relationships in highly diverse tropical forests. In general, few observational studies have demonstrated improved function at high levels of species richness (Schwartz *et al*., 2000). Our results demonstrate that biodiversity has a significant impact on aboveground C storage in diverse tropical forests at large spatial scales that are relevant to management and conservation. This insight can help increase the relevance of B-EF research to tropical forest conservation and management research. For example, our results highlight the importance of conserving trees with large potential sizes in order to increase the C storage of forest plots. However, they also indicate that protecting or planting species with high wood density may not necessarily be a good management strategy for increasing carbon storage (cf. Stegen *et al*., 2009). Finally, the positive relationship we found between genus richness and C storage supports the feasibility of efforts to reduce C emissions from forested lands while conserving biodiversity (e.g. REDD+; Huston & Marland, 2003). Improving the conservation and management of tropical forests is of critical importance. These ecosystems are the biologically richest places on the planet and they play a disproportionately large role in the global carbon cycle; however, they face significant threats that range in scale from local deforestation to global climate change.

ACKNOWLEDGEMENTS

All data in this publication were provided by the TEAM Network, a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution and the Wildlife Conservation Society, and partially funded by these institutions, the Gordon and Betty Moore Foundation and other donors. We thank Darley Calderado Leal Matos, Johanna Hurtado, Richard Condit, Leandro Valle Ferreira, Ieda Amaral, Nurul Winarni, Meyner Nusalawo, Emanuel Martin, David Kenfack, Christine Dawn Fletcher, Jean Claude Andrianantenaina and all the field staff at the following TEAM sites for their hard and invaluable work: Bukit Barisan, Barro Colorado Island, Bwindi Impenetrable Forest, Caxiuanã, Manaus, Nouabalé Ndoki, Pasoh Forest Reserve, Ranomafana, Udzungwa, Volcán Barva and Yanachaga Chimillén National Park. Fieldwork for the Costa Rican plots was partially supported by NASA grants TE08-0037 and TE11-0100. Thanks to SERNANP-PNYCh for their support. This research was supported by a Graduate Distributed Seminar Series made possible by a National Science Foundation Dimensions of Biodiversity grant (1050680) to SA and Julia Parish.

REFERENCES

Adler, P.B., Seabloom, E.W., Borer, E.T. *et al*. (2011) Productivity is a poor predictor of plant species richness. *Science*, **333**, 1750–1753.

Bacci, T., Trabucco, B., Marzialetti, S., Marusso, V., Lomiri, S., Vani, D. & Virno Lamberti, C. (2009) Taxonomic sufficiency in two case studies: where does it work better? *Marine Ecology*, **30**, 13–19.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Silva, J.N.M., Martinez, R.V. (2004) Variation in wood density determines spatial patterns in Amazon forest biomass. *Global Change Biology*, **10**, 545–562.

Baker, T.R., Phillips, O.L., Laurance, W.F., Pitman, N.C.A., Almeida, S., Arroyo, L., DiFiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Nascimento, H., Monteagudo, A., Neill, D.A., Silva, J.N.M., Malhi, Y., Lopez Gonzalez, G., Peacock, J., Quesada, C.A., Lewis, S.L., Lloyd, J. (2009) Do species traits determine patterns of wood production in Amazonian forests? *Biogeosciences*, **6**, 297–307.

Balvanera, P., Kremen, C. & Martinez-Ramos, M. (2005) Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecological Applications*, **15**, 360–375.

Botta-Dukát, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, **16**, 533–540.

Brown, S. & Lugo, A.E. (1992) Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia Caracas*, **17**, 1, 8–18.

Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M., Naeem, S. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310**, 1029–1031.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences USA*, **104**, 18123–18128.

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Conner, M.I., Gonzalez, A.

(2011) The functional role of producer diversity in ecosystems. *American Journal of Botany*, **98**, 572–592.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Caspersen, J. & Pacala, S. (2001) Successional diversity and forest ecosystem function. *Ecological Research*, **16**, 895–903.

Chainho, P., Lane, M.F., Chaves, M.L., Costa, J.L., Costa, M.J. & Dauer, D.M. (2007) Taxonomic sufficiency as a useful tool for typology in a poikilohaline estuary. *Hydrobiologia*, **587**, 63–78.

Chase, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature*, **416**, 427–430.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.

Chave, J., 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**, 6, 2356–2367.

Chave, J., Condit, R., Muller-Landau, H.C. *et al.* (2008) Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biology*, **6**, 3, e45.

Ciais, P., Piao, S.L., Cadule, P., Friedlingstein, P. & Chédin, A. (2008) Variability and recent trends in the African carbon balance. *Biogeosciences*, **5**, 3497–3532.

Clark, D.B. & Kellner, J.R. (2012) Tropical forest biomass estimation and the fallacy of misplaced concreteness. *Journal of Vegetation Science*, **23**, 1191–1196.

Condit, R. (1995) Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution*, **10**, 18–22.

Danielson, J.J. & Gesch, D.B. (2011) *Global multi-resolution terrain elevation data 2010 (GMTED2010)*. USGS Open file report 2011-1073.

Edwards, L.J., Muller, K.E., Wolfinger, R.D., Qaqish, B.F. & Schabenberger, O. (2008) An R^2 statistic for fixed effects in the linear mixed model. *Statistics in Medicine*, **27**, 6137–6157.

Falster, D.S. & Westoby, M. (2005) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology*, **93**, 521–535.

Ghazoul, J. & Sheil, D. (2010) *Tropical rain forests: ecology diversity and conservation*. Oxford University Press, Oxford, UK.

Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, **87**, 1234–1243.

Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.

Healy, C., Gotelli, N. & Potvin, C. (2008) Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. *Journal of Ecology*, **96**, 903–913.

Hector, A., Schmid, B., Beierkuhnlein, C. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123–1127.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 1, 3–35.

Hulme, M. (1992) A 1951–80 global land precipitation climatology for the evaluation of general circulation models. *Climate Dynamics*, **7**, 57–72.

Huston, M.A. & Marland, G. (2003) Carbon management and biodiversity. *Journal of Environmental Management*, **67**, 77–86.

Jiang, L., Wan, S. & Li, L. (2009) Species diversity and productivity: why do results of diversity-manipulation experiments differ from natural patterns? *Journal of Ecology*, **97**, 603–608.

Kraft, N.J., Valencia, R. & Ackerly, D.D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, **322**, 580–582.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Laliberté, E. & Shipley, B. (2011) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.

Ma, W., He, J.-S., Yang, Y., Wang, X., Liang, C., Anwar, M., Zeng, H., Fang, J., Schmid, B. (2010) Environmental factors covary with plant diversity–productivity relationships among Chinese grassland sites. *Global Ecology and Biogeography*, **19**, 233–243.

Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.

Paoli, G.D., Curran, L.M. & Slik, J.W.F. (2008) Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia*, **155**, 287–299.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

Parmentier, I., Yadvinder, M., Senterre, B. *et al.* (2007) The odd man out? Might climate explain the lower tree α-diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology*, **95**, 1058–1071.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.

Ruiz-Jaen, M.C. & Potvin, C. (2010) Tree diversity explains variation in ecosystem function in a Neotropical forest in Panama. *Biotropica*, **42**, 638–646.

Ruiz-Jaen, M.C. & Potvin, C. (2011) Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *The New Phytologist*, **189**, 978–987.

Sax, D.F. & Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution*, **18**, 561–566.

Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. & Van Mantgem, P.J. (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, **122**, 3, 297–305.

Slik, J.W.F., Aiba, S., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E. & van Valkenburg, J.L.C.H. (2010) Environmental correlates of tree biomass, basal area, wood specific gravity, and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, **19**, 50–60.

Smith, M.D. & Knapp, A.K. (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, **6**, 509–517.

Stegen, J.C., Swenson, N.G., Valencia, R., Enquist, B.J. & Thompson, J. (2009) Above-ground forest biomass is not consistently related to wood density in tropical forests. *Global Ecology and Biogeography*, **18**, 617–625.

TEAM Network (2009) *Vegetation protocol implementation manual, v. 1.5 tropical ecology, assessment and monitoring network*. Center for Applied Biodiversity Science, Conservation International, Arlington, VA.

Tilman, D. (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.

Timms, L.L., Bowden, J.J., Summerville, K.S. & Buddle, C.M. (2013) Does species-level resolution matter? Taxonomic sufficiency in terrestrial arthropod biodiversity studies. *Insect Conservation and Diversity*, **6**, 453–462.

Vilà, M., Vayreda, J., Comas, L., Ibáñez, J., Mata, T. & Obon, B. (2007) Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters*, **10**, 241–250.

Whitmore, T.C. (1998) *An introduction to tropical rain forests*. Oxford University Press, Oxford.

Whittaker, R. & Heegaard, E. (2003) What is the observed relationship between species richness and productivity? comment. *Ecology*, **84**, 3384–3390.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson N.G., Wiemann M.C., Chave J. (2009) Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. doi:10.5061/dryad.234 (accessed 2 February 2012).

Zuur, A.F. (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York.

BIOSKETCHES

Kyle Cavanaugh is a post-doctoral research fellow at the Smithsonian Environmental Research Center in Edgewater, MD. His research interests focus on macroscale patterns in population dynamics.

J. Stephen Gosnell is a post-doctoral research associate at Florida State University Coastal and Marine Laboratory. He is a community ecologist interested in exploring patterns, causes and consequences of diversity in order to determine how populations and communities may respond to environmental change.

Editor: Peter van Bodegom