

Tree Diversity Explains Variation in Ecosystem Function in a Neotropical Forest in Panama

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ABSTRACT

Many experimental studies show that a decline in species number has a negative effect on ecosystem function, however less is known about this pattern in natural communities. We examined the relative importance of environment, space, and diversity on ecosystem function, specifically tree carbon storage in four plant types (understory/canopy; trees/palms), in a tropical forest in central Panama. The objectives of this study were to detect the relationship between tree diversity and carbon storage given the environmental and spatial variation that occur in natural forests and to determine which species diversity measure is more important to tree carbon storage: richness or dominance. We used redundancy analyses to partition the effect of these sources of variation on tree carbon storage. We showed that together, environment, space, and diversity accounted for 43 percent of tree carbon storage, where diversity (19%) alone is the most important source of variation and explained more variation than space (13%) and environment (1%) together. Therefore, even in natural forests where substantial environment and spatial variation can be found, it is still possible to detect the effect of diversity on ecosystem function at scales relevant to conservation. Moreover, both richness and dominance are important to explain the variation on tree carbon storage in natural forests suggesting that these two diversity measures are complementary. Thus, tree diversity is important to predict tree carbon storage in hyperdiverse forests.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>

Key words: dominance; environment; principal coordinates of neighbor matrices (PCNM); redundancy analyses (RDA); space; species richness; tree carbon storage.

WHILE SPECIES DIVERSITY CONDITIONS ECOSYSTEM FUNCTIONING in natural communities like grasslands (Loreau & Hector 2001, Tilman *et al.* 2006), the relationship between diversity and ecosystem function in complex and hyperdiverse ecosystems like tropical forests is unclear (Srivastava & Vellend 2005). This relationship has been explored in the tropics either through simulations (Balvanera *et al.* 2005, Bunker *et al.* 2005) or by using native tropical tree plantations (Erskine *et al.* 2006, Healy *et al.* 2008). Simulations suggest that, in tropical forests, aboveground carbon stocks depend on species composition and on the identity and characteristics of the species being lost (Bunker *et al.* 2005) with a few species contributing disproportionately to carbon storage (Balvanera *et al.* 2005). Furthermore, tropical mixed species plantations tend to produce higher biomass than monocultures (Erskine *et al.* 2006, Healy *et al.* 2008).

In natural forests, the effect of diversity on ecosystem function could be masked by the variability of environment and space (Huston & McBride 2002, Vila *et al.* 2005). Studies have often shown that abiotic factors such as soil and topographic characteristics (hereafter referred to as the environment) play a major role for species distribution (Tuomisto *et al.* 2003, John *et al.* 2007, Russo *et al.* 2008). Moreover, space has been shown to be more important than environment in determining woody plant species distribution (Svenning *et al.* 2004). Therefore to understand the role of species diversity in natural landscapes, we need to factor out the effects of environment and space (Chesson *et al.* 2002, Cardinale *et al.* 2004).

In a tree diversity plantation established in Panama, the effect of environment on tree biomass was greater than that of tree diver-

sity (Healy *et al.* 2008), a result that corroborates earlier findings by Huston (1997) for temperate grasslands. We build on these results to explore the relationship between diversity and ecosystem function in a natural tropical forest of Panama that harbors *ca* 240 tree species. We used aboveground tree carbon storage as our measure of ecosystem function, since trees account for > 90 percent of carbon in aboveground biomass (AGB) (Nascimento & Laurance 2002, Chave *et al.* 2003, Kirby & Potvin 2007) and 35–85 percent of total ecosystem carbon storage (Kraenzel *et al.* 2003, Kirby & Potvin 2007). Our analysis focused on four plant groups (understory/canopy; trees/palms), because it has often been suggested that grouping of plants into functional types would improve the ability to detect a relationship between diversity and ecosystem function, because certain functional traits are related to specific ecosystem function (Scherer-Lorenzen *et al.* 2007, De Deyn *et al.* 2008). We used partial redundancy analysis (Borcard *et al.* 2004, Healy *et al.* 2008) to answer the following questions: (1) does the environment and spatial variation in plant abundance mask the true relationship between diversity and tree carbon storage in four plant groups? If we can detect a relationship, (2) which diversity measure is more important to explain tree carbon storage, species richness, or dominance? Answering these questions contributes to one of ecology's most pressing challenges: What is the role of species diversity in determining ecosystem function in complex, diverse ecosystems?

METHODS

STUDY SITE.—Our study site is a lowland wet tropical forest located in San Lorenzo National Park on the Caribbean coast of Panama ($9^{\circ}17' N$, $79^{\circ}58' W$), locally known as Fort Sherman. The forest

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receives a mean annual precipitation of 3100 mm with a short dry season (January–March; Santiago & Mulkey 2005). The soil is a Saprist (Histosol) with rich organic material lying on sedimentary substrate from Chagres Sandstone parent material (Pyke *et al.* 2001, Santiago *et al.* 2005). In comparison with other forests in the Panama Canal Watershed, the soils have high percent of carbon (C) and nitrogen (N) and low pH and bulk density (Santiago *et al.* 2005). The site includes a 5.95 ha L-shape forest dynamics plot where all stems ≥ 1 cm diameter at breast height (dbh) have been identified to species, measured and mapped in 1999 by the Center for Tropical Forest Science (CTFS; <http://www.ctfs.si.edu/site/Sherman>). Most of the plot (4.96 ha) is covered with *ca* 200 yr old growth forest, while the rest is covered by secondary forest. To homogenize forest age as much as possible, we selected the old growth forest portion of the CTFS plot and subdivided it into 124 subplots of 20×20 m for sampling purposes.

RESPONSE MATRIX: TREE CARBON STORAGE.—We chose aboveground tree carbon storage as an important measure of ecosystem function in tropical ecosystems, since they store one quarter of terrestrial carbon (Bonan 2008). To estimate the variance among subplots' tree carbon storage, we first calculated the AGB of individual trees using the allometric regression equation for wet tropical forests in Chave *et al.* (2005). This equation multiplies the wood specific gravity (WSG) with the wood volume. Where the wood volume is estimated from relationships of volume and dbh. For WSG values, we used published (Santiago *et al.* 2004, Chave *et al.* 2006) and unpublished (S. J. Wright, unpubl. data) material. When the WSG was not known for a species, we used 0.54 g/cm^3 (Chave *et al.* 2003). We used the same allometric regression models for both trees and palms individuals (Chave *et al.* 2008). We included the values of all trees (≥ 1 cm dbh) to avoid underestimation of total AGB in subplots (DeWalt & Chave 2004). For individuals with multiple stems, we calculated AGB of each stem and summed them. We then calculate tree carbon content, which is approximated 50 percent of the AGB (Hugues *et al.* 1999). Because tree carbon storage may simply be a function of stem density within a subplot, previous to the analysis, we determined the effect of total stem abundance and total tree carbon storage and found a non-significant relationship (Fig. S1).

For the statistical analysis, we separated tree carbon storage in four plant types akin to functional groups with different capacity to store carbon aboveground (DeWalt & Chave 2004) and with different responses to environment and space (Vormisto *et al.* 2000, de Castilho *et al.* 2006). First, we separated palms from trees, since palms are an important component of the forest community in Fort Sherman (13% of total individuals). We further separated understory from canopy trees/palms based on species maximum height at maturity, since forests in Fort Sherman have a high proportion of understory stems (Santiago *et al.* 2004). This forest has an average canopy height of 36 m (Kurzel *et al.* 2006), thus, the vertical stratification was done at 10 m, where understory trees were species < 10 m height at maturity and canopy trees were the remainders of the species. Each species maximum height was based on the CTFS classification of species in the Fort Sherman plot

(S. J. Wright, unpubl. data). Hereafter, we will use the term TREE carbon storage to refer to the carbon storage aboveground of trees and palms in the understory and canopy layer.

EXPLANATORY MATRICES.—Three sets of explanatory variables: environment, space, and diversity were used as independent variables to explain variation in TREE carbon storage. Each of the three sets of independent variables served to construct an explanatory matrix, which is described below.

To characterize the environment, we chose five abiotic variables that were measured, at the center, and at 5 m east and west from the center for each subplot. These values were averaged to obtain one entry per subplot for each abiotic variable. To characterize topography, we classified slopes in a quadrant as flat (1), gentle (2), and steep slope (3). Slope determined changes in AGB (Chave *et al.* 2003, de Castilho *et al.* 2006) and stand structure of tropical forests (Robert & Moravie 2003). We measured soil depth to have an estimate of tree growth belowground. We used a calibrated iron pole of 1.5 m, since most of the root biomass is present at this soil depth (Jackson *et al.* 1996). To characterize other soil physical properties, we measured the following variables at 0–10 cm depth: bulk density, texture, and color using standard protocols (see Table S1 for details in methodology). Soil bulk density is the measure of soil compaction and can decrease root density in the topsoil (Watson & Kelsey 2006). Soil texture can affect soil water retention and carbon storage (Silver *et al.* 2000). Soil color provides information of the mineral, organic, texture composition, and can be used as a surrogate of soil fertility (Ketterings & Bigham 2000, Fontes & Carvalho 2005). For example, soil color has been correlated with Fe oxides content (Fontes & Carvalho 2005), which is negatively correlated with phosphorous availability in soils (Agbenin 2003). Environmental variables were obtained for 117 of the 124 subplots, since two were around a canopy crane and five others were with large treefalls. These plots were excluded from the analysis (see Fig. 1 for the location of these plots).

To remove the methodological artifact of space and detect any spatially structured pattern, we estimated the spatial variation with principal coordinates of neighbor matrices (PCNM) analyses (Borcard *et al.* 2004). This method generates a set of orthogonal sine waves constructed from a truncated matrix of Euclidean distances among sampling units using the x and y coordinates from the center of each subplot (Fig. 1). Because our study site was sampled irregularly (see Fig. 1), we filled the empty space by adding points where it was needed to avoid disruption of the sine waves (Borcard & Legendre 2002). PCNM reconstruct spatial patterns from fine to broad scales among the study site. For this study, the PCNM wavelengths ranged from 20 to 340 m. It is important to note that PCNM scores allow us to detect spatial structure of environment, diversity and TREE carbon storage and to interpret these results; we need to graph these scores against the sampling sites coordinates. We generated the spatial variables (*i.e.*, eigenvectors) by using the spacemakeR package in R (R Development Core Team 2008).

We considered two components of diversity: richness (Hooper *et al.* 2005) and dominance (Hillebrand *et al.* 2008). For richness, we calculated the number of species for each four-plant type, since

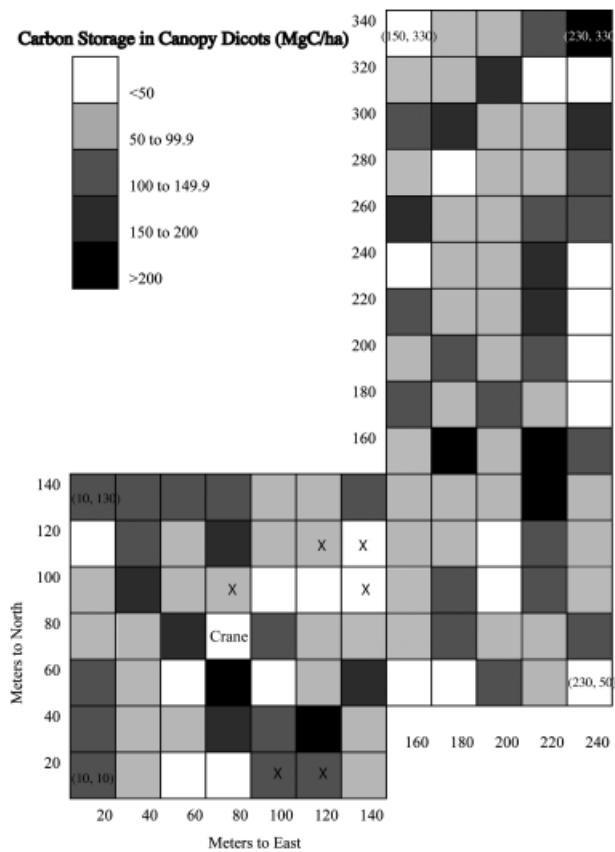


FIGURE 1. Tree carbon storage in canopy trees distributed across the 124 20 × 20 m² subplots in Fort Sherman, Panama. In parenthesis are the x and y coordinates used for the spatial analyses. Subplots marked with an X were not included in the statistical analysis.

we expected that the relationship between richness and ecosystem function might be very different between palms and trees due to intrinsic differences in growth pattern, morphology, and density. For dominance, we calculated the relative basal area (BA) of all species in a subplot and identified the species with the highest value, and selected the species that dominated the BA in more than eight subplots. Then, we determined the effect of both relative BA dominance and the identity of the dominant species by using the relative BA of six identified dominant species.

DATA ANALYSES.—We first reduced the covariation among environmental variables and examined their variability at the study site using a principal component analyses (PCA). We then quantify the proportion of the variation in TREE carbon storage explained by environment, space, and diversity. To do so, we selected subsets of space and diversity variables that exerted a significant effect on TREE carbon storage using forward selection with 999 random permutations (Blanchet *et al.* 2008). Forward selection chooses from a set of explanatory variables a parsimonious subset of variables to model multivariate response data. Then, using partial redundancy analyses (RDA; Borcard *et al.* 1992, Healy *et al.* 2008), we partitioned the variation in TREE carbon storage explained by

environment, space, and/or diversity. RDA is the canonical extension of a multiple regression that analyzes multivariate response data (Legendre & Legendre 1998). To test for multicollinearity (*i.e.*, correlation) among the explanatory variables in the RDA models, we used the vif.cca function in the vegan package in R (Oksanen *et al.* 2009). This function calculates the variance inflation factors for each variable in the model. For example, if variables are linear combinations or have an inflation factor of > 10, they are removed from the estimation.

Entries for the response matrix were (1) C of understory trees, (2) C of canopy trees, (3) C of understory palms, and (4) C of canopy palms. The explanatory matrices used after the forward selection were (a) environment expressed as the scores for the first four axis obtained in the principal components analysis, (b) space (13 PCNM scores), and (c) diversity (understory tree richness, understory palm richness, canopy palms richness, canopy tree richness, relative BA of six tree species as dominance). Entries in the explanatory matrices were centered and standardized when necessary.

The significant relative contribution of these three sources of variation was tested by a series of seven RDAs: (1) with all three explanatory subsets with no covariables; (2) for each explanatory matrix, using the other two explanatory matrices as covariables (*e.g.*, environment was analyzed using space and diversity as covariables); and (3) with two subsets of explanatory matrices. To estimate the variation explains by each explanatory matrix, we used adjusted R^2 to reduce the R^2 biased toward sample size and number of predictors (Peres-Neto *et al.* 2006). Moreover, the significance of each RDA model was determined after 999 permutations using the anova.cca function in the vegan package in R (Oksanen *et al.* 2009).

RESULTS

TREE CARBON STORAGE.—TREE carbon storage at the subplot level ranged from 26.1 to 284 MgC/ha; most of this carbon was distributed among the canopy trees that on average represented 87 percent (94.2 ± 47.5 MgC/ha with a coefficient of variation [CV] of 50%; Fig. 1) of carbon storage, followed by understory trees that, on average, represented 11 percent (10.9 ± 15.0 MgC/ha with a CV of 138%) of carbon storage. Palms were the smallest component of TREE carbon storage. Understory palms carbon storage was 0.17 ± 0.12 MgC/ha with a CV of 74 percent, while canopy palms was 2.10 ± 1.25 MgC/ha with a CV of 59 percent.

ENVIRONMENT AND SPACE.—The first four PCA axes explained 75 percent of the environmental variation in Fort Sherman (Table S2). These principal components separated subplots by clay to sandy clay soils for axis 1 (29% of variance). Axis 2 separated subplots from low to high redness factor (soil color) and from shallow to deep soils (17% of variance). Axis 3 separated subplots from flat to steppe slopes (15% of variance), and axis 4 separated subplots from compacted to soil with higher aeration (bulk density; 13% of variance; see Table S1 for values of soil physical variables). For space, subplots coordinates generated 113 orthogonal variables. After forward selection, we retained 13 PCNM variables that were significant to the TREE carbon storage. These PCNM variables were

TABLE 1. Variation partitioning results from the Redundancy analyses (RDA) on tree carbon storage of trees and palms in Fort Sherman. Lower case letters represent single fractions of variation: (a) environment (E), (b) space (S), (c) diversity (D), (d) $E \times S$, (e) $S \times D$, (f) $E \times D$, and (g) $E \times S \times D$. df is the degrees of freedom for each RDA model. Because of the bias associated with R^2 values, we reported the adjusted R^2 . The F-ratio and P-values were obtained after 999 permutations.

| Sources of variation | Fractions included | df | Adj. R^2 | F-ratio | P-values |
|---|--------------------|----|------------|---------|----------|
| E+S+D | [a+b+c+d+e+f+g] | 27 | 0.43 | 4.20 | < 0.005 |
| S+D | [b+c+d+e+f+g] | 23 | 0.42 | 4.39 | < 0.005 |
| E+D | [a+c+d+e+f+g] | 14 | 0.30 | 3.64 | < 0.005 |
| E+S | [a+b+d+e+f+g] | 17 | 0.24 | 2.46 | < 0.005 |
| Decomposed variation (single fractions) | | | | | |
| D controlled for E and S | [c] | 10 | 0.19 | 4.30 | < 0.005 |
| S controlled for E and D | [b] | 13 | 0.13 | 2.76 | < 0.005 |
| E controlled for S and D | [a] | 4 | 0.01 | 1.37 | 0.3 |
| Unexplained | | | 0.57 | | |

arbitrarily divided in broad (> 150 m apart), medium (50–150 m apart), and fine scales (< 50 m apart) based on their spatial pattern detected in relation to the x and y coordinates along the study site (see Fig. S2 for an example the spatial patterns detected by the PCNM scores at the three scales).

DIVERSITY.—Total species richness ranged from 30 to 61 species per plot (400 m^2), with an average of 52. Richness of understory trees ranged from seven to 29 species and had an average of 17 species in a subplot and a CV of 25 percent. For the trees with the potential to reach the canopy, their richness varied from 19 to 43 species, with an average of 30 species and a CV of 14.8 percent. Palms were less species-rich than trees, but varied greatly among subplots. Understory palms richness ranged from one to seven species, with an average of three species and a CV of 41 percent. For canopy palms, we only found three species, with an average of 2.2 for subplot and a CV of 35.2 percent.

The six dominant species in terms of their relative BA were all canopy trees with dominance values as high as 60 percent of total BA. The species with the highest relative BA were *Aspidosperma spruceanum* Benth. Ex Mull. Arg. ($N = 12$ subplots, average dominance = 31% of BA, range = 20–50%, Apocynaceae, high wood density), *Brosimum utile* (Kunth) Pittier ($N = 36$ subplots, average dominance = 34% of BA, range = 22–60%, Moraceae, medium wood density), *Calophyllum longifolium* Willd. ($N = 9$ subplots, average dominance = 35% of BA, range = 20–60%, Clusiaceae, medium wood density), *Manilkara bidentata* (A. DC.) A. Chev. ($N = 11$ subplots, average dominance = 32% of BA, range = 19–59%, Sapotaceae, high wood density), *Tapirira guianensis* Aubl. ($N = 8$ subplots, average dominance = 31% of BA, range = 23–45%, Anacardiaceae, low wood density), and *Vochysia ferruginea* Mart. ($N = 9$ subplots, average dominance = 32% of BA, range = 21–49%, Vochysiaceae, low wood density).

VARIATION PARTITIONING.—Together the variables of environment, space, and diversity that we retained explained 44 percent of the total variation in TREE carbon storage (Table 1). Notwithstanding, diversity alone is the most important source of variation, explaining more TREE carbon storage variation than environment and space

together (Table 1). The first canonical axis of the RDA model with the diversity matrix factoring out environment and space showed that carbon storage in canopy palms and trees increased with canopy palm richness ($r = 0.68$) and when *B. utile* ($r = 0.38$), *C. longifolium* ($r = 0.25$), and *M. bidentata* ($r = 0.53$) dominated BA, but decreased when *T. guianensis* dominated BA ($r = -0.34$; Fig. 2A). For the second RDA axis, carbon storage in understory palms increased in subplots with high richness of understory palms ($r = 0.73$) and trees ($r = 0.36$), but decreased when *V. ferruginea* dominated BA ($r = -0.25$). In general, species richness had higher correlation coefficients with TREE carbon storage than the identity of the dominant species and its dominance values based on basal area.

The environment–space RDA controlling the effect of diversity explained the variation of carbon storage in understory and canopy palms in the first axis and understory and canopy trees in the second axis (Fig. 2B). Understory palms carbon storage was high in sandy clay soils ($r = -0.29$) located at steeper slopes ($r = -0.22$) and varied spatially at medium scales (PCNM 42; $r = 0.28$; PCNM 72; $r = 0.21$; Fig. 2B). Canopy palms carbon storage was high in sites with deep soils with high redness factor (i.e., nutrient poor sites; $r = 0.30$) and flat slopes ($r = 0.22$) and varied at broad scales (PCNM 18; $r = -0.50$). Understory tree carbon storage increased spatially at medium scales (PCNM 84; $r = 0.33$), but decreased at fine scales (PCNM 106; $r = -0.44$ and PCNM 113; $r = -0.47$). Carbon storage in canopy trees decreased spatially at medium (PCNM 29; $r = -0.22$) to fine (PCNM 106; $r = -0.44$) scales. In summary, spatial variables best explained the variation in the carbon storage in trees, while environmental factors are the best to explain carbon storage in palms.

DISCUSSION

DOES THE ENVIRONMENT AND SPATIAL VARIATION IN PLANT ABUNDANCE MASK THE TRUE RELATIONSHIP BETWEEN DIVERSITY AND TREE CARBON STORAGE IN FOUR PLANT GROUPS?—To answer this question, we partition the variation of TREE carbon storage and show that diversity and space explained the highest proportions. Thus, the answer to our question is that, even in natural forests where

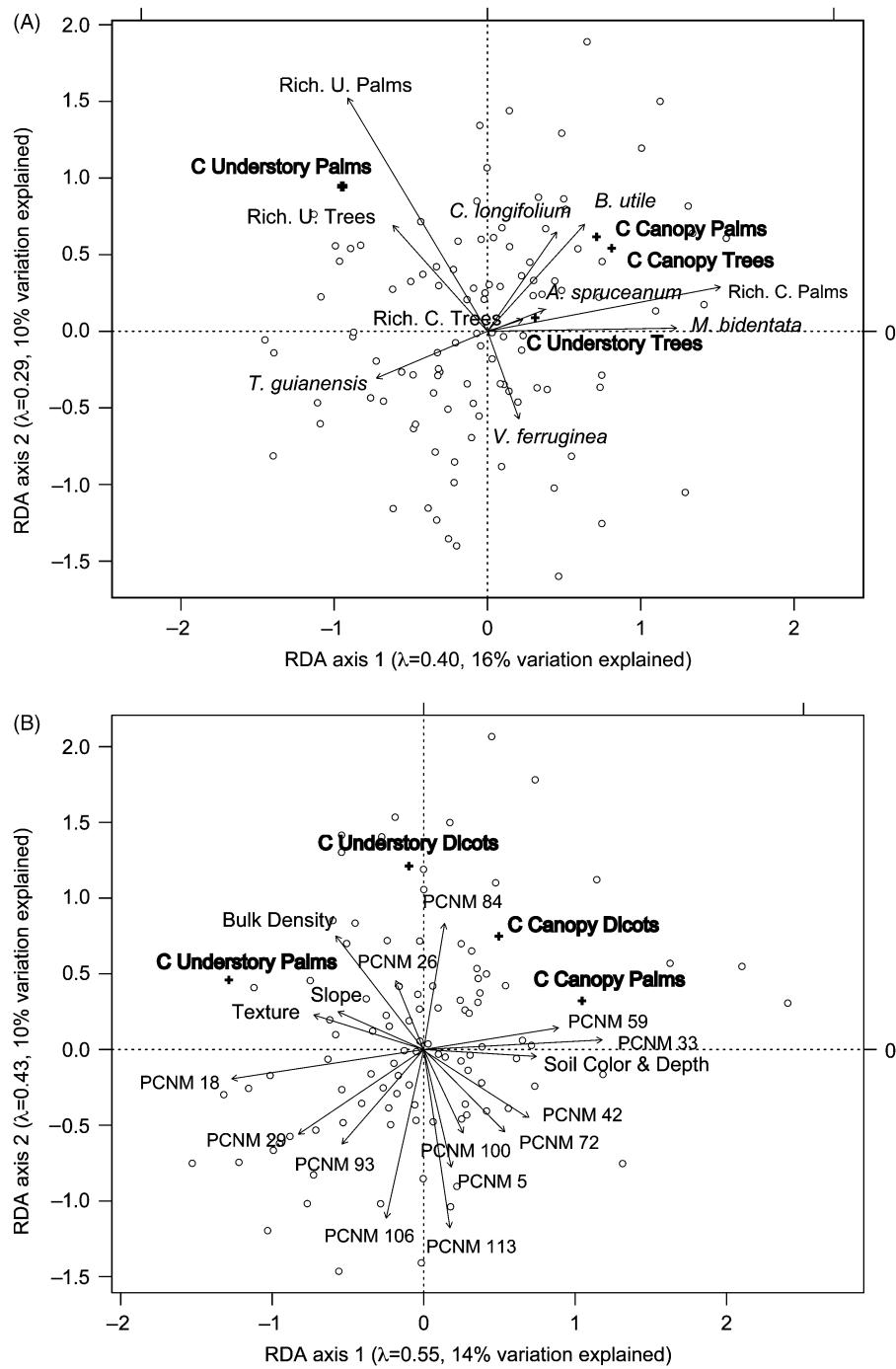


FIGURE 2. Correlation biplots from Redundancy Analysis of tree carbon storage in understory trees and palms and canopy trees and palms constrained by the explanatory matrices of (A) diversity and (B) environment and space (arrows) in Fort Sherman, Panama (see Table S3 for details in explanatory variables). Circles indicate the subplots ($N=117$). Crosses indicate the centroids of the response variables. Angles between tree carbon storage (variables in bold) and arrows of explanatory variables reflect their correlations. If the projection of tree carbon storage from the center of the axis is parallel to an arrow of an explanatory variable, then they are related. Arrow size is positively related to its effect level.

substantial environment and spatial variation can be found, it is still possible to detect the effect of diversity on ecosystem function at scales relevant to conservation. Our results support the hypothesis that tree diversity is spatially structured and is driven in part by the

environment. For example, environment only affected the carbon storage in palms (Andersen *et al.* 2010), where slope (Svenning 1999, Goldsmith & Zahawi 2007) and soil texture (Costa *et al.* 2009) have been identified as the strong predictors. In Fort

Sherman, understory palms dominates along riparian forest, which is characterize for steep slopes and sandy clay soils. When we factor out space and diversity, however, environment is not significant to explain TREE carbon storage. This finding runs contrary to previous studies that suggest that habitat heterogeneity is the main driver of ecosystem function in local communities or across larger scales (Healy *et al.* 2008, Jiang *et al.* 2009).

A salient feature of the present analysis is the high proportion of variation explained by space, which suggests that ecosystem function is spatially structured (Borcard *et al.* 2004). This spatial structure could be caused by the interaction of space–environment and space–diversity (Table 1) and these interactions vary with the scale. Carbon storage in trees was affected at fine scales. This can be explained by the light guild of the neighboring trees that could reduce or increase individual tree carbon sequestration through competition or facilitation. For example, competition for light could occur if neighbors have similar light guilds (Uriarte *et al.* 2004). Another example of fine scale process is the distribution of treefall gaps creating stands of different ages (Jones *et al.* 2008). These create differences in light environments within the forest and are important for AGB dynamics (Feeley *et al.* 2007). The presence of a gap can skew the dbh size class of different species according to their light growth requirement (Wright *et al.* 2003) and can promote the presence of palms (Svenning 1999). The change in carbon storage of palms at medium and broad scales could be explained by the spatially structured distribution of soil nutrients (Paoli *et al.* 2008) that can play a major role in determining AGB. The variation of tree carbon storage at medium to broad scales could be explained by the presence of large trees along the forest. Large trees are usually rare in Neotropical forests yet they account for a large proportion of AGB (Clark & Clark 1996, Chave *et al.* 2003). Moreover, seed dispersal would also affect the spatial distribution of species of trees and palms (Svenning 1999, Andersen *et al.* 2010) at medium to broad scales. Biodiversity–ecosystem functions experiments have likewise highlight the spatial component of this relationship (Weigelt *et al.* 2007, Potvin & Dutilleul 2009) suggesting that spatial heterogeneity needs to be incorporated as a key explanatory factor of biodiversity.

WHICH DIVERSITY MEASURE IS MORE IMPORTANT TO EXPLAIN TREE CARBON STORAGE, SPECIES RICHNESS OR DOMINANCE?—Our results indicate that species richness increases TREE carbon storage among subplots. We suggest that the increase in carbon storage in understory palms occurring with the increase in understory tree and understory palm richness may be due to an increase in light availability. Most of the understory palms species in Fort Sherman have clonal growth and their number of ramets increases with light availability (Chazdon 1986, Svenning 2000). High canopy palm richness could also increase light availability in the canopy, which might also explain why plots with high palm richness have high carbon storage in canopy trees. It has been shown that the mixture of tree and palm in the canopy layer creates different light environments that may enhance tree growth (Bohlman & O'Brien 2006). Overall, our results support the niche complementarity hypothesis (Loreau & Hector 2001) and suggest that among different resources (*e.g.*, nutrients, light, and water; Wright 2002), light might

play a crucial role in carbon sequestration. Several authors had previously suggested that the niche complementary hypothesis should be prevalent in tropical natural systems where a high number of species with weak species–species effects (Paine *et al.* 2008) coexist in a small area (Tylianakis *et al.* 2008) and in mature stands (Cardinale *et al.* 2007, Fargione *et al.* 2007).

Beyond the effect of niche complementarity, the identity of the dominant species also explained subplot TREE carbon storage in Fort Sherman. This result is consistent with previous studies showing that the identity of dominant species, thus species-specific traits of the dominant species, ultimately has a large effect on carbon storage (Balvanera *et al.* 2005, Kirby & Potvin 2007) and productivity (Healy *et al.* 2008), thus playing a key role in maintaining ecosystem functions (Smith & Knapp 2003). We propose that the effect of the dominant species depends on the distribution of the dbh size classes of the species in the study site and of key functional traits such as wood density (Baker *et al.* 2004). For example, *Tapirira guianensis* is a low wood density species with the dbh size classes skewed toward lower sizes, thus when it dominates a subplot, the overall carbon storage is likely to be low (Fig. S3). In contrast, subplots dominated by *Brosimum utile* are likely to have high carbon storage due to both its skewed size classes distribution toward large trees as well as its medium wood density values (Fig. S3). The occurrence of large trees along the landscape has been previously identified as good predictors for AGB in tropical ecosystems (Clark & Clark 1996). Thus, our results also support the mass ratio hypothesis that predicts that ecosystem properties are controlled by the dominant species (Grime 1998, Smith & Knapp 2003). This hypothesis should occur in natural landscapes because some species become dominant along the mosaic of environmental patches through habitat specialization (Chesson *et al.* 2002, Cardinale *et al.* 2004).

Our results suggest that species richness (niche complementarity hypothesis) had a greater explanatory power than dominance (mass ratio hypothesis) on TREE carbon storage (*i.e.*, ecosystem function). The importance of these two components on ecosystem function has been a debate. For example, the properties of the dominant species have been the primarily mechanism to explain ecosystem function (Cardinale *et al.* 2006); however, as the forest stands get older, complementarity of species richness gain more relevance (Cardinale *et al.* 2007). We found that in an old growth natural forest with high species diversity, these two hypotheses are not mutually exclusive.

CONCLUSION.—While a vast literature examines the relationship between biodiversity and ecosystem function in grasslands and microcosms (Hooper *et al.* 2005, Balvanera *et al.* 2006), our analysis presents the first empirical results for the relationship between diversity and ecosystem function in a natural tropical forest. Our analyses allowed us to rank the sources of variation for TREE C storage in terms of their importance and we found that diversity and space were the two most important factors. We also highlight different responses of trees and palms to these independent variables. The distinction between these functional groups is often omitted despite the importance of palms in tropical forests (DeWalt & Chave 2004). Thus, future work in diverse natural

forests should define different functional groups to determine the role of diversity in the ecosystem function.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Soil physical variables measured at the 20 × 20 m² subplots in Sherman, Panama.*

TABLE S2. *Correlations found among environmental variables with the first four ordination axes of a Principal Component Analyses.*

TABLE S3. *Description of environmental, spatial, and diversity variables used for the partial redundancy analyses. These entries were retained after forward selection.*

FIGURE S1. TREE carbon storage is not related to total stem abundance in Fort Sherman.

FIGURE S2. Spatial variation detected by the principal component of the neighboring matrix.

FIGURE S3. Logarithmic distribution found for the dbh size classes for the six canopy tree species that dominates the basal area in Fort Sherman, Panama.

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