

Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest

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Summary

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- Linking tree diversity to carbon storage can provide further motivation to conserve tropical forests and to design carbon-enriched plantations. Here, we examine the role of tree diversity and functional traits in determining carbon storage in a mixed-species plantation and in a natural tropical forest in Panama.
- We used species richness, functional trait diversity, species dominance and functional trait dominance to predict tree carbon storage across these two forests. Then we compared the species ranking based on wood density, maximum diameter, maximum height, and leaf mass per area (LMA) between sites to reveal how these values changed between different forests.
- Increased species richness, a higher proportion of nitrogen fixers and species with low LMA increased carbon storage in the mixed-species plantation, while a higher proportion of large trees and species with high LMA increased tree carbon storage in the natural forest. Furthermore, we found that tree species varied greatly in their absolute and relative values between study sites.
- Different results in different forests mean that we cannot easily predict carbon storage capacity in natural forests using data from experimental plantations. Managers should be cautious when applying functional traits measured in natural populations in the design of carbon-enriched plantations.

Introduction

To fully understand the effect of species loss within tropical ecosystems, we need to link measures of biodiversity to ecosystem functions, such as carbon sequestration. The relationship between diversity and ecosystem function has been most intensively studied in temperate grasslands, where a decline in species number has negative effects on plant productivity (Tilman *et al.*, 1996; Schwartz *et al.*, 2000; Spehn *et al.*, 2005). Similarly, tropical mixed-species plantations have greater total biomass and higher annual rates of carbon sequestration than monocultures (Erskine *et al.*, 2006; Healy *et al.*, 2008; Piotta, 2008). Moreover, the dominant species has been shown to partly determine carbon storage in tropical plantations and natural forests where, depending on its functional characteristics it can

increase or decrease carbon storage (Balvanera *et al.*, 2005; Kirby & Potvin, 2007; Ruiz-Jaen & Potvin, 2010).

There have been attempts to link tree diversity to carbon storage in tropical ecosystems using experimental plantations (Erskine *et al.*, 2006; Healy *et al.*, 2008) because they can allow for testing the mechanisms responsible for this link, but do not contain the natural variability that occurs in natural forests where species richness can vary by an order of magnitude or more (Scherer-Lorenzen *et al.*, 2005). Thus, we do not know if results found in mixed-species plantations can be extrapolated to predict what is found in natural forests. For example, the most diverse tropical plantations have an average of eight species in a quarter of a hectare (Scherer-Lorenzen *et al.*, 2005; Erskine *et al.*, 2006; Piotta, 2008), while natural tropical forests have an average of 26 species in a similar area but with an upper limit of up

to 300 or more species (Condit *et al.*, 2005). If we can find a similar relationship between tree diversity and carbon storage in natural forests and experimental plantations, we can generalize about the importance for conserving biodiversity in tropical forests.

In the present study, we examined the relationship between tree carbon storage, species diversity, and functional diversity in a well-studied natural tropical forest in central Panama and compared results with a mixed-species plantation nearby. We are interested in understanding what explains variation in tree carbon storage to identify carbon sinks and help to decrease atmospheric CO₂ concentrations (Malhi & Phillips, 2004; Houghton, 2005; Houghton *et al.*, 2009). Tropical forests store more than one-quarter of the terrestrial carbon (Bonan, 2008; Houghton *et al.*, 2009) and trees represent 90% of this (Kirby & Potvin, 2007). This carbon storage can be determined in part by species diversity (Balvanera *et al.*, 2005; Spehn *et al.*, 2005; Vila *et al.*, 2007). Functional traits have also been proposed as an improved way to understand forest dynamics in hyperdiverse tropical forests (Wright *et al.*, in press), because functional traits considered the redundancy in function of species. This function can group species according to their resource use and life history strategies (Grime, 2002). To link functional traits to a specific function, we need to select traits that are related to the ecosystem function of interest, in this case, carbon storage. Therefore, we chose wood density, maximum diameter at breast height (DBH), maximum height, leaf mass per area (LMA) and nitrogen fixers as functional traits related to tree carbon storage (Ishida *et al.*, 2008). Wood density partly determines aboveground biomass (Baker *et al.*, 2004) and correlates with growth rates and tree mortality (King *et al.*, 2005; Chave *et al.*, 2009), with high wood density being correlated with slow growth and longer-lived tree species. Maximum diameter is an indirect measure of the maximum aboveground biomass that can be attained by a species (Nelson *et al.*, 1999; Chave *et al.*, 2003) and a measure of light competition among species (Sheil *et al.*, 2006). Maximum height (H_{\max}) is also a measure of light competition among species (Poorter *et al.*, 2005; Moles *et al.*, 2009). Leaf mass per area (LMA) is leaf biomass invested to produce the light-capturing foliar area and it is negatively correlated to photosynthetic rates (Thomas & Winner, 2002; Rozendaal *et al.*, 2006; Poorter *et al.*, 2009). The presence of root nodules in some trees to fix atmospheric nitrogen can increase the overall carbon uptake by plants (Cornelissen *et al.*, 2003b; Hedin *et al.*, 2009).

With these data available, we asked the following question. Does species richness, functional trait diversity, species dominance and functional trait dominance similarly explain proportions of tree carbon storage in a mixed-species plantation and in a natural forest? We are also interested in exploring how functional traits vary between sites within

and among species. If functional traits can order species similarly in natural forest and mixed-species plantations, we can use the available information on functional traits from different natural forests to design plantations for carbon sequestration (Baroloto *et al.*, 2010). Therefore, our second question was: how are functional traits differently ranked within in tropical forests and in plantations? Plantations can act as carbon sinks in areas where deforestation is a threat for preserving native species and could provide an alternative source of timber (Canadell & Raupach, 2008; Paquette & Messier, 2010).

Materials and Methods

Study sites

This study was conducted in natural forest on Barro Colorado Island (BCI) and a mixed-species plantation in Sardinilla < 20 km apart with similar precipitation regimes (both locations are in Panama). We used the same sampling protocols to collect wood density, maximum diameter, maximum height and LMA for all the species present at both sites. In Sardinilla we used a high-diversity experimental plantation established in a pastureland (9°18'N, 79°38'W) in 2003; > 800 trees were planted in 24 plots of 18 × 18 m with treatments of 6, 9 or 18 species replicated 8 times (Scherer-Lorenzen *et al.*, 2005). These species were randomly drawn from a pool of 28 species found in the nearby natural forest of BCI based on how common they were in midstory to canopy layer (i.e. > 15 m of maximum height at maturity), their shade tolerance (i.e. light demanding, light intermediate and shade tolerant), and their timber value (Delagrange *et al.*, 2008). The maximum number of species planted in the experimental plantation was based on the average number of species larger than 10 cm DBH in 20 × 20 m found in BCI (Scherer-Lorenzen *et al.*, 2005). In this plantation, tree height, basal diameter at 10 cm from the ground and diameter at breast height of all individuals have been recorded yearly since its establishment. For statistical analysis, we used the data of the census in 2009. The topography of Sardinilla is almost uniformly flat, with a total elevation difference of 5 m (Potvin *et al.*, 2004). This plantation receives a mean annual precipitation of 2350 mm with very low rainfall reported during the months of January to March and with an annual mean temperature of 25°C (Scherer-Lorenzen, 2007). The soil is an Alfisols dominated by clay over a Tertiary limestone and other sedimentary rocks (Potvin *et al.*, 2004).

For natural forest, we used the nearby tropical moist forest of BCI that has a 50 ha permanent dynamic plot (9°09'N, 79°51'W). This site is a seasonal forest with a mean annual rainfall of 2600 mm with very dry periods during January–April (Leigh, 1999). Soils are weathered kaolinitic Oxisols composed mostly of red light clay (John

et al., 2007; Barthold *et al.*, 2008). In the 50 ha permanent plot, every individual > 1 cm DBH has been mapped and identified to species and has been censused every 5 yr since 1985 (Hubbell & Foster, 1987). For statistical analysis, we used data of the last available census on BCI, 2005.

To compare BCI with Sardinilla, we examined equivalent plot and tree sizes. For the plot size, we subdivided the 50-ha forest plot into plots of 20 × 20 m and excluded the ones along streams and with steep slopes (see Harms *et al.*, 2001 for habitat classification). The small plot size helps to control for the effect of habitat heterogeneity, even though it increases carbon storage variation among plots (Chave *et al.*, 2004). Moreover, the chosen plot size reflects the scale of individual tree competition, as neighbor effects are detected in radius of < 20 m (Hubbell *et al.*, 2001; Wiegand *et al.*, 2007). For tree size, we restricted our analysis to species with a maximum height at maturity of > 15 m, because the mixed-species plantation is composed only of midstory to canopy trees.

Tree carbon storage

We calculated the aboveground biomass (AGB) for individual trees using the following allometric regression for moist forest (Chave *et al.*, 2005):

$$\text{AGB} = \text{WD} \times \text{EXP}(-1.499 + 2.148 \log_e(\text{DBH}) + 0.207(\log_e(\text{DBH}))^2 - 0.0281(\log_e(\text{DBH}))^3).$$

(DBH is the diameter at breast height (1.30 m) in cm; WD is the wood density for each species in g cm⁻³). To determine the WD values in the experimental plantation, we collected wood cores of five individuals per species and followed the standardized protocols in Cornelissen *et al.* (2003b). The WD values for the natural forest were provided S.J. Wright (Wright *et al.*, in press). For those species with no WD values, we used the average wood density, 0.54 g cm⁻³ for moist forests in Panama (Chave *et al.*, 2003). For individuals with multiple stems, we calculated the AGB of each stem and summed them. The estimation of AGB in the natural forests was done using the biomass function in the CTFS package in R (Hall, 2006). Then, we estimated tree carbon (C) storage per plot using: C (Mg C ha⁻¹) = AGB × 0.46/plot area (Elias & Potvin, 2003).

Species and functional traits

We examined how species richness, functional diversity, and species dominance determined carbon storage in natural forest and mixed-species plantation. Species richness was estimated using rarefaction curves (Hurlbert, 1971), with the minimum number of stems in the mixed-species plantation (19 individuals) as the sample size. For functional

diversity, we calculated the dispersion for wood density, maximum DBH, H_{max} , LMA and potential for nitrogen fixers (NF) based on the trait value of the species present at each plot. Functional dispersion for each functional trait comes from a species–species distance matrix, where it calculates the species average distance from the centroid of each plot. We weighted species distance by the basal area of the species within each plot (Laliberté & Legendre, 2010). We estimated the functional diversity using the FD package in R using the function dbFD (Laliberté, 2009).

Wood density is the oven-dry mass divided by its fresh volume (Cornelissen *et al.*, 2003b) and was calculated from wood cores of five individuals of each species (Wright *et al.*, in press). In Sardinilla (25 species), we chose the largest individuals of each species within the study site, while for BCI (*c.* 300 species) we measured individuals close to the study site. Maximum DBH and H_{max} is the maximum size a species can reach at maturity. To calculate maximum DBH and H_{max} , we selected the six largest individuals of each species in Sardinilla and in the 50-ha plot of BCI based on previous census in 2009 and in 2005, respectively. The H_{max} was measured using a telescopic measuring pole for trees < 15 m and a laser rangefinder and a clinometer for trees > 15 m (Wright *et al.*, in press).

The LMA is the leaf oven-dry weight divided by its fresh area (Cornelissen *et al.*, 2003b) and was calculated from two leaves of five individuals per species in the mixed-species plantation and in the natural forests. Most of the leaves collected were exposed to full sunlight, as suggested by Cornelissen *et al.* (2003b). However, we collected leaves in the shade when a species did not have individuals that were fully exposed to the sun (for details see Wright *et al.*, in press). For nitrogen fixers, we assigned a one to species that had the potential to nodulate (i.e. observed having a symbiotic interaction with nitrogen fixing bacteria) based on field observation or existing literature. In the mixed-species plantation, we searched for active root-nodules from five individuals of each species identified as nitrogen fixers in previous studies (Cornelissen *et al.*, 2003b). In the natural forest, we classified nitrogen fixers based their potential for nodulation according to existing literature (De Faria *et al.*, 1984, 2010; Sprent, 2005).

For species dominance, we calculated the relative basal area (BA) for all the species in a plot to account for the contribution to the total basal area of the species dominating the BA in the plot. Previous studies have shown that only a few species accounted for > 90% of total carbon storage (Walker *et al.*, 1999; Balvanera *et al.*, 2005). For functional dominance, we calculated the community weight mean (CWM) for wood density, H_{max} , LMA and nitrogen fixing. CWM is the mean of each species trait value weighted by the relative basal area of the species at each plot (Lavorel *et al.*, 2008). We estimated the CWM using the FD package in R (Laliberté, 2009).

Statistical analysis

Before the statistical analysis, we controlled for the variation in stem density and light availability among plots. Stem density has been related to tree carbon storage because stem density is a trade-off between stem size classes, where a high density of trees is related to smaller average stem size (Clark & Clark, 2000; DeWalt & Chave, 2004). Light availability in a plot can indicate the presence of a gap or can help to determine stand age. Different light levels can affect species traits (Rijkers *et al.*, 2000) and can enhance tree growth (King *et al.*, 2005). Light availability in the mixed-species plantation was measured taking hemispheric photographs at 1 m above the ground at the center of each plot and using the software, GAP LIGHT ANALYZER 2.0 (<http://www.ecostudies.org/gla/>), to obtain light availability. For the natural forest, we used existing data for light availability (Ruger *et al.*, 2009) that was calculated as a function of the vertical distribution of canopy density at six height intervals. We regressed tree carbon storage against stem density and light availability and used the model residuals as the dependent variable. To compare the mixed-species plantation in Sardinilla with the natural forest of BCI, we partitioned the variation of the dependent variable among: species richness, functional diversity, species dominance and functional dominance (Borcard *et al.*, 1992; Legendre, 2008). To estimate the variation explained by each independent matrix and assess model fit, we used adjusted R^2 , which controls for sample size and number of predictors (Peres-Neto *et al.*, 2006). We performed these analyses using the vegan package in R (Oksanen *et al.*, 2009). We selected independent variables using step-wise procedures to avoid multicollinearity and over-fitting the model (Crawley, 2007). We also used the variance inflator factor to select independent variables and excluded the ones with values > 10 (Oksanen *et al.*, 2009). After these variable selection procedures, we excluded diversity and dominance of wood density and maximum diameter and retained the relative basal area of two dominant species. To estimate functional trait variability between study sites, we compared species ranking based on four traits (wood density, maximum diameter, maximum height and LMA) for species shared in Sardinilla and BCI. According to Garnier *et al.* (2001), no change in species ranking among sites implies that there is no trait plasticity in different environments (e.g. plantation vs natural forests), or that all species responded similarly to the environment.

Results

Determinants of carbon storage

Tree carbon storage was highly variable at both study sites (Table 1). It ranged from 0.83 to 10.75 Mg C ha⁻¹ in Sardinilla and from 12.91 to 856.40 Mg C ha⁻¹ in BCI.

Table 1 Mean and coefficient of variation of tree carbon storage, stem density, light availability, species richness, functional diversity (standard deviation of maximum height (H_{\max}), leaf mass per area (LMA), and nitrogen fixers (NF)), species dominance (relative basal area (BA) of *Anacardium excelsum* and *Tabebuia rosea*), and functional dominance (community weight mean of H_{\max} , LMA and NF weighted by the BA) in the mixed-species plantation of Sardinilla and the natural forest of Barro Colorado Island (BCI) in Central Panama

Variables	Sardinilla ($n = 24$)	BCI ($n = 815$)
Carbon storage (Mg C ha ⁻¹)	5.44 (0.47)	146.80 (0.79)
Stem density (trees ha ⁻¹)	700.88 (0.18)	2371.73 (0.23)
Light availability (%)	0.10 (0.38)	0.01 (0.62)
Species richness	7.18 (0.28)	13.33 (0.14)
Functional diversity		
H_{\max} (m)	0.76 (0.22)	0.66 (0.28)
LMA (g m ⁻²)	0.51 (0.29)	0.58 (0.42)
NF	0.40 (0.47)	0.28 (0.23)
Species dominance ¹		
<i>Anacardium excelsum</i>	0.10 (0.92)	0.48 (0.64)
<i>Tabebuia rosea</i>	0.23 (0.38)	0.04 (2.04)
Functional dominance		
CWM H_{\max} (m)	28.26 (0.13)	28.82 (0.11)
CWM LMA (g m ⁻²)	69.64 (0.07)	72.81 (0.14)
CWM NF	0.29 (0.68)	0.09 (1.63)

¹Plots removed where these species were absent. CWM, community weight mean.

Not surprisingly, carbon storage was much higher in BCI because of the young age of Sardinilla. It is interesting to note, that after only 6 yr of growth some of the plantation plots had approached the minimum biomass observed in the forest plots. Nitrogen fixers represented 32% of the species in Sardinilla (from a total of 25 species) but 14% of the species in BCI (from a total of 157 species ≥ 15 cm DBH). Functional diversity and the CWM of H_{\max} , LMA, and N fixers had similar coefficient of variation at the plot level in both sites (Table 1).

Species richness, functional diversity, species dominance and functional dominance together explained 67% of the variation of carbon storage in Sardinilla and 49% for BCI, and their contribution to carbon storage variation differed between the two sites. Species richness explained most of the tree carbon storage variation in Sardinilla but did not contribute significantly to carbon in BCI (Fig. 1). By contrast, functional dominance explained most of the variation in the natural forest (Fig. 1) with CWM of H_{\max} as the variable most responsible for this pattern (Table 2). Another important source of variation was the interaction between species dominance and functional dominance; it explained 8% of carbon storage variation in Sardinilla and 12% in BCI. Functional diversity was only important for BCI, which explained 6% of carbon storage variation (Fig. 1; Table 2).

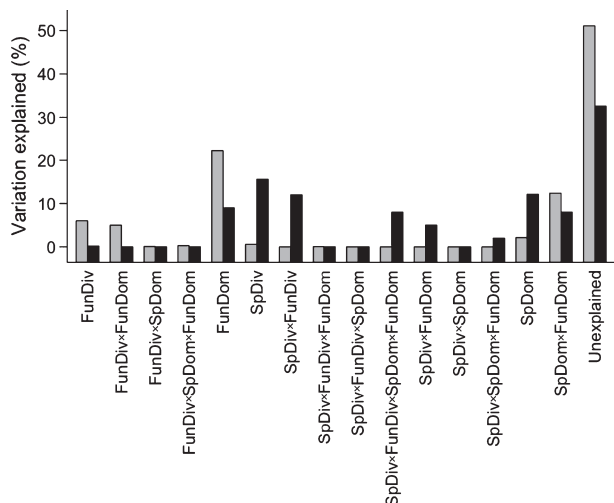


Fig. 1 Proportion of tree carbon storage variation explained after controlling for stem density and light availability in the mixed-species plantation of Sardinilla (black bars) and the natural forest of Barro Colorado Island (grey bars) located in Central Panama. Independent matrices were: species richness (SpDiv), functional diversity (FunDiv), species dominance (SpDom) and functional dominance (FunDom).

Species dominance explained the higher proportion of tree carbon storage variation in Sardinilla (12%) than in BCI (2%). The two species chosen after forward selection were nonpioneer species and allocated carbon differently (Tables 2 and 3). *Anacardium excelsum* has higher investment producing more branches than *Tabebuia rosea*, which invests in vertical growth (Table 3). In BCI, *T. rosea* is more abundant (0.23% of the stems) than *A. excelsum* (0.02% of the stems), but achieved smaller DBH sizes (10.5 cm and 105.6 cm average DBH, respectively). In Sardinilla, these two species along with five others contributed more than half of the basal area (Fig. 2a). For BCI, *A. excelsum*, along with 12 other species, contributed half of the basal area and *T. rosea* was ranked as the 49th largest contributor to basal area (Fig. 2b).

Table 3 Description of the two tree species used to explain the variation of carbon storage in the mixed-species plantation, Sardinilla, and the natural forest of Barro Colorado Island (BCI) located in Central Panama

Description	<i>Anacardium excelsum</i>		<i>Tabebuia rosea</i>	
	Sardinilla	BCI	Sardinilla	BCI
Family	Anacardiaceae		Bignoniaceae	
Wood density (g cm^{-3})	0.31 (0.24)	0.42 (0.06)	0.39 (0.21)	0.49 (0.14)
Maximum diameter at breast height (mm)	171.82 (0.14)	1775.67 (0.08)	149.62 (0.17)	752.20 (0.13)
Maximum height (m)	10.45 (0.02)	35.11 (0.09)	10.20 (0.04)	40.42 (0.07)
LMA (g m^{-2})	82.82 (0.12)	98.26 (0.14)	116.06 (0.09)	101.15 (0.22)
Economic use ¹	Timber value		High timber value and ornamental	

Traits values represented the average of the six largest individuals and values in parenthesis are the coefficient of variation (Wright *et al.*, in press). LMA, leaf mass per area.

¹Information taken from Delagrangé *et al.* (2008).

Table 2 Pearson correlations (r) between tree carbon storage controlled by stem density and light availability with species richness, functional diversity, species dominance and functional dominance in the mixed-species plantation of Sardinilla and the natural forest of Barro Colorado Island (BCI) in Central Panama

	Carbon storage (Mg C ha^{-1})	
	Sardinilla ($n = 24$)	BCI ($n = 751$)
Species richness	0.544**	-0.084*
Functional diversity		
H_{max}	0.053ns	-0.315***
LMA	0.490*	-0.004ns
NF	0.343*	-0.001ns
Species dominance		
<i>Anacardium excelsum</i>	-0.485*	0.171***
<i>Tabebuia rosea</i>	-0.494*	0.008ns
Functional dominance		
CWM H_{max}	-0.523**	0.628***
CWM LMA	-0.450*	0.130***
CWM NF	0.397*	0.098**

Abbreviations: H_{max} , maximum height (m); LMA, leaf mass per area (g m^{-2}); NF, nitrogen fixers; CWM, community weight mean weighted by basal area.

Significance level: ns, nonsignificant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Species trait ranking

None of the traits gives a consistent ranking of species between sites. Wood density and H_{max} values were consistently lower in Sardinilla than BCI (Fig. 3a,c). For maximum DBH and LMA, trait values increased or decreased depending on the tree species (Fig. 3b,d). There was a large range of LMA values in BCI; by contrast, values were low to medium in Sardinilla (Fig. 3d).

Based on species ranking by traits, we can identify species that perform very differently in the mixed-species plantation of Sardinilla and in the natural forest of BCI. For example, *Astronium graveolens* (AG), *Dipteryx oleifera* (DO) and *Ormosia macrocalyx* (OM) were consistently lower in

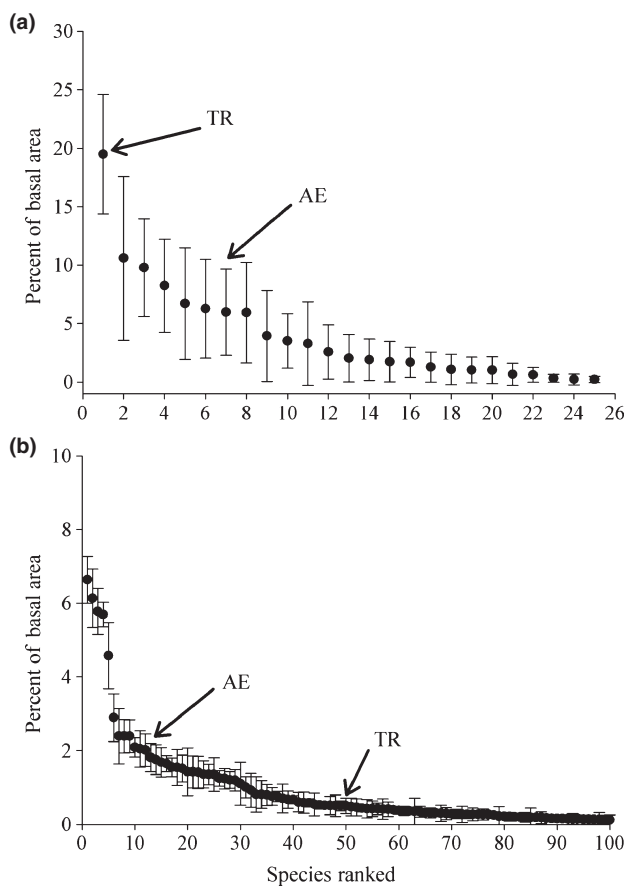


Fig. 2 Species ranked by their dominance in the relative basal area in the mixed-species plantation of Sardinilla (a) and the natural forest of Barro Colorado Island (BCI; b), Central Panama. Values are average per cent of basal area (BA) by species in each plot. Lines are 95% confidence intervals. Note that only the first 100 species of the natural forests are included, the rest are rare species that contribute very little to total BA in each plot. AE, *Anacardium excelsum*; TR, *Tabebuia rosea*.

the species ranking from BCI to Sardinilla (Fig. 3a–d). By contrast, *Colubrina glandulosa* (CG), *Guazuma ulmifolia* (GU), *Inga punctata* (IP), and *Terminalia amazonia* (TA) improved their species ranking from BCI to Sardinilla.

Discussion

Sources of variation for carbon storage

Tree carbon storage in the mixed-species plantation was mainly explained by species richness and in the natural forests by functional trait diversity. For example, species richness only mattered in Sardinilla, where increasing the number of species also increased carbon storage. This relationship was expected because trees were planted according to different species functions, including shade tolerance and nutrient acquisition ability (Scherer-Lorenzen *et al.*, 2005). By contrast, we found no relationship between species

richness and carbon storage in the BCI forest. One explanation of the lack of relationship is that carbon storage in the natural forest may have reached saturation in species richness, an effect that can be found in high species richness treatments in experimental grasslands (Silver *et al.*, 1996; Wright, 1996; Hooper *et al.*, 2005). In those systems, < 15 species are needed to reach the highest values of plant productivity (Hector *et al.*, 2001; Balvanera *et al.*, 2005). Saturation between species number and carbon storage can vary among sites and will depend on the niche overlap among species. Previous studies on BCI have found that most species have overlapping ecological niches along an environmental gradient within the same forest type (Wright, 1996; Harms *et al.*, 2001; Cardinale *et al.*, 2007).

Functional dominance explained most of the variation of tree carbon storage on BCI; more specifically, we found that the more a canopy tree dominates (i.e. higher CWM of H_{\max}) a plot, the greater the increase in carbon storage. Canopy trees have a higher probability of survival and can grow faster owing to asymmetry in the size relative to their neighbors' (Hubbell *et al.*, 2001; Potvin & Dutilleul, 2009). Plots with low H_{\max} diversity, where most trees have similar H_{\max} , had higher tree carbon storage. By contrast, we can expect that sites with more variation in H_{\max} are associated with younger forests and forest gaps but this could also be a result of greater liana loads (Schnitzer & Carson, 2001), which reduces carbon storage.

The diversity and the proportion of nitrogen fixers enhanced carbon storage only in the mixed-species plantation in Sardinilla. Nitrogen content in the soil was lower and less variable in Sardinilla (15.56 mg kg⁻¹ N; Zeugin *et al.*, 2010) than in BCI (25.92 mg kg⁻¹ N; John *et al.*, 2007). In Sardinilla, the previous presence of pasturelands has altered the nitrogen cycle by reducing nitrogen content in the soil after forest cutting (Jordan, 1985; Silver *et al.*, 2005). Thus, an increase in the proportion and diversity of nitrogen fixers in Sardinilla has increased carbon storage through soil improvement in these nutrient poor sites. Nitrogen fixers have been found to be facultative, where nitrogen fixation occurs in disturbed sites such as in Sardinilla or in forest gaps (Barron *et al.*, 2010). The high nitrogen soil-content BCI could suppress nitrogen fixation by trees, by reducing the relative advantage of symbiotic fixation over direct uptake (Barron *et al.*, 2010; Hedin *et al.*, 2009). Moreover, preliminary data along a forest chronosequence have shown that younger stands, such as Sardinilla, have a higher occurrence of nodulation than old-growth forest (S. Batterman *et al.*, unpublished).

In both sites, the effect of LMA diversity on carbon storage was generally lower than that found for H_{\max} and nitrogen fixers. In the experimental plantation, we found that plots dominated by trees with low LMA have higher carbon storage. In general, species that have lower LMA have higher growth rates because of their fast resource acquisition (Reich

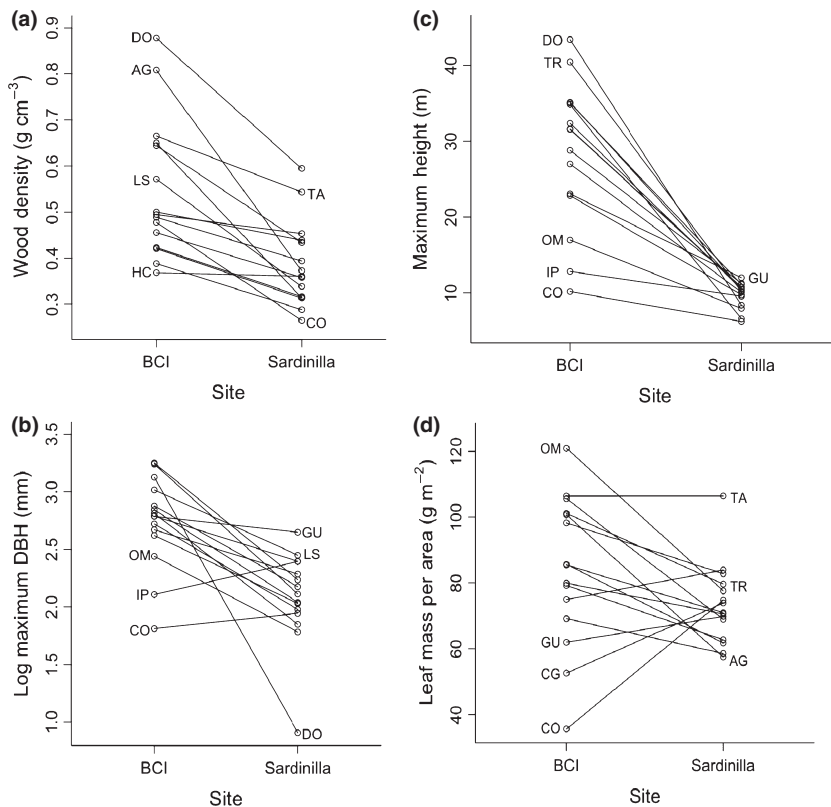


Fig. 3 Species ranking comparison based on four functional traits of the species shared across the mixed-species plantation (Sardinilla) and the natural forest (Barro Colorado Island). Traits are: wood density (WD; a), log maximum diameter at breast height (DBH; b), maximum height (c) and leaf mass per area (LMA; d). Species abbreviations: AG, *Astronium graveolens*; CO, *Cedrela odorata*; CG, *Colubrina glandulosa*; DO, *Dipteryx oleifera*; GU, *Guazuma ulmifolia*; HC, *Hura crepitans*; IP, *Inga punctata*; LS, *Luehea seemannii*; OM, *Ormosia macrocalyx*; TR, *Tabebuia rosea*; TA, *Terminalia amazonia*.

et al., 2007; Poorter *et al.*, 2009), these are also the species that have greater aboveground biomass in the experimental plantations. Thus, when they dominate the plot, there is more tree carbon storage. We found the opposite relationship in the natural forests, as the old-growth forest canopy is mostly dominated by late successional species with high LMA. Similarly, LMA values have been shown to increase with tree height (Rijkers *et al.*, 2000; Poorter *et al.*, 2009).

The dominance of a given species alone is not a strong determinant for tree carbon storage. However, we still found significant effect of a species and this effect depends on the basal area each species occupied. For example, the positive effect of *A. excelsum* on carbon storage in the natural forest results mostly from its capacity to reach large DBH even though it has a low wood density. In natural forests, aboveground biomass in trees has been mostly determined by their diameter size and not by their wood density (Chave *et al.*, 2004).

Species trait ranking

There is little interspecific trait consistency among species present at both study sites. Others studies have found that their high intraspecific trait variability provides no clear pattern (Rozendaal *et al.*, 2006; Albert *et al.*, 2010). Changes in interspecific trait ranking have been observed from seedlings grown in a glasshouse with plants found in natural

environments (Cornelissen *et al.*, 2003a). Species ranking based on single functional traits can be attributed to ontogenetic changes between study sites and to different responses of species to the environment (Garnier *et al.*, 2001; Cornelissen *et al.*, 2003a). For example, there are changes in wood density and LMA at different ontogenetic stages in other tropical forests (Rozendaal *et al.*, 2006; Ollivier *et al.*, 2007), where low wood density at early stages is associated with a higher proportion of sapwood relative to heartwood (Chave *et al.*, 2009). We would have expected to observe lower values for most of the functional traits in Sardinilla than in BCI due to ontogeny because this plantation has only been established for 6 yr. However, we were surprised to see no clear pattern in the species ranking by all functional traits between study sites.

The convergence in the LMA values observed in Sardinilla can be explained by the higher light availability for each individual compared with the forest of BCI (Table 1). Similarly, some species in Sardinilla invested more in growing horizontally (i.e. achieved higher values for maximum DBH than H_{max}) than vertically. Investing in tree height is a response of light competition in tropical forests (Poorter *et al.*, 2005; Kooyman & Westoby, 2009). Thus, if light is not a limiting resource, tree species will not invest in height, but in growing branches.

Species that reached larger sizes in the mixed-species plantation of Sardinilla showed no clear similarities among

their functional traits. However, we found that these species had low LMA and low wood density in natural forest. These characteristics are associated with pioneer species, which have a trade-off between high growth and low carbohydrate storage (Poorter & Kitajima, 2007; Chave *et al.*, 2009). By contrast, the species that could be considered good carbon storers (e.g. *D. oleifera* and *A. graveolens*), based on their high wood density and H_{\max} in the natural forest, had low carbon storage in Sardinilla, even though these species have high growth rates relative to their wood density (i.e. growth rate is negatively correlated to wood density) and are light-demanding species (Condit *et al.*, 2006). Wishnie *et al.* (2007) found that these two species grow poorly in other mixed-species plantations in Panama.

Can we use plant functional traits to design carbon-enriched plantations? We have to be cautious if we want to use information on functional traits from natural forest plots to design experimental high-carbon plantations. However, some species have been identified as having potential for mixed-species plantations, as they can grow to larger sizes, are good for timber (Kirby & Potvin, 2007) and can store carbon for long periods of time (Chambers *et al.*, 1998). Despite the poor grouping of species based on functional traits, we can recommend the use of *C. glandulosa*, *G. ulmifolia*, *Hura crepitans*, *T. rosea* and *T. amazonia*. Most of these have been reported to grow well in both diameter and height in mixed-species plantations (Wishnie *et al.*, 2007) and, more specifically, *T. amazonia* and *I. punctata* have been used to reduce degraded areas dominated by grasslands (Kim *et al.*, 2008; Craven *et al.*, 2009).

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References

Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P, Lavorel S. 2010. Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* **98**: 604–613.

- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF *et al.* 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology* **10**: 545–562.
- 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.
- Baroloto C, Marcon E, Morneau F, Pavoine S, Roggy JC. 2010. Integrating functional diversity into tropical forest plantation designs to study ecosystem processes. *Annals of Forest Science* **67**: 303.
- Barron AR, Purves DW, Hedin LO. 2010. Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. *Oecologia*, in press.
- Barthold FK, Stallard RF, Elsenbeer H. 2008. Soil nutrient-landscape relationships in a lowland tropical rainforest in Panama. *Forest Ecology and Management* **255**: 1135–1148.
- Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**: 1444–1449.
- Borcard D, Legendre P, Drapeau P. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**: 1045–1055.
- Canadell JG, Raupach MR. 2008. Managing forests for climate change mitigation. *Science* **320**: 1456–1457.
- Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava D, Loreau M, Weis JJ. 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.
- Chambers JQ, Higuchi N, Schimel JP. 1998. Ancient trees in Amazonia. *Nature* **391**: 135–136.
- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Folster H, Fromard F, Higuchi N, Kira T *et al.* 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**: 87–99.
- Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R. 2004. Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society of London: Biological Series* **359**: 409–420.
- Chave J, Condit R, Lao S, Caspersen JP, Foster RB, Hubbell SP. 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *Journal of Ecology* **91**: 240–252.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**: 351–366.
- Clark DB, Clark DA. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* **137**: 185–198.
- Condit R, Ashton P, Balslev H, Brokaw N, Bunyavejchewin S, Chuyong G, Co L, Dattaraja HS, Davies S, Esufali S *et al.* 2005. Tropical tree α -diversity: results from a worldwide network of large plots. *Biologiske Skrifter* **55**: 565–582.
- Condit R, Ashton P, Bunyavejchewin S, Dattaraja HS, Davies S, Esufali S, Ewango C, Foster R, Gunatilleke I, Gunatilleke CVS *et al.* 2006. The importance of demographic niches to tree diversity. *Science* **313**: 98–101.
- Cornelissen JHC, Cerabolini B, Castro-Diez P, Villar-Salvador P, Montserrat-Marti G, Puyravaud JP, Maestro M, Werger MJA, Aerts R. 2003a. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science* **14**: 311–322.
- Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA *et al.* 2003b. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335–380.
- Craven D, Hall J, Verjans JM. 2009. Impacts of herbicide application and mechanical cleanings on growth and mortality of two timber species in

- Saccharum spontaneum* grasslands of the Panama Canal Watershed. *Restoration Ecology* 17: 751–761.
- Crawley M. 2007. *The R book*. Chichester, UK: John Wiley & Sons.
- De Faria SM, Diedhiou AG, de Lima HC, Ribeiro RD, Galiana A, Castilho AF, Henriques JC. 2010. Evaluating the nodulation status of leguminous species from the Amazonian forest of Brazil. *Journal of Experimental Botany* 61: 3119–3127.
- De Faria SM, Franco AA, De Jesus RM, Menandro MS, Baitello JB, Mucci ESF, Dobreiner J, Sprent JJ. 1984. New nodulating legume trees from South-East Brazil. *New Phytologist* 98: 317–328.
- Delagrèze S, Potvin C, Messier C, Coll L. 2008. Linking multiple-level tree traits with biomass accumulation in native tree species used for reforestation in Panama. *Trees – Structure and Function* 22: 337–349.
- DeWalt SJ, Chave J. 2004. Structure and biomass of four lowland Neotropical forests. *Biotropica* 36: 7–19.
- Elias M, Potvin C. 2003. Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species. *Canadian Journal of Forest Research* 33: 1039–1045.
- Erskine PD, Lamb D, Bristow M. 2006. Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management* 233: 205–210.
- Garnier E, Laurent G, Bellmann A, Debain S, Berthelot P, Ducout B, Roumet C, Navas ML. 2001. Consistency of species ranking based on functional leaf traits. *New Phytologist* 152: 69–83.
- Grime JP. 2002. *Plant strategies, vegetation processes and ecosystem properties*. Chichester, UK: John Wiley and Sons.
- Hall P. 2006. CTFS: the CTFS large plot forest dynamics analyses. In: *R package, version 1.00* [WWW document]. URL <http://CRAN.R-project.org/src/contrib/Archive/CTFS/> [accessed on 30 September 2010].
- Harms KE, Condit R, Hubbell SP, Foster RB. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.
- Healy C, Gotelli NJ, 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, Joshi J, Lawler SP, Spehn EM, Wilby A. 2001. Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia* 129: 624–628.
- Hedin LO, Brookshire ENJ, Menge DNL, Barron AR. 2009. The nitrogen paradox in tropical forest ecosystems. *Annual Review of Ecology, Evolution and Systematics* 40: 613–635.
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3–35.
- Houghton RA. 2005. Aboveground forest biomass and the global carbon balance. *Global Change Biology* 11: 945–958.
- Houghton RA, Hall F, Goetz SJ. 2009. Importance of biomass in the global carbon cycle. *Journal of Geophysical Research-Biogeosciences* 114: G00e03.
- Hubbell SP, Ahumada JA, Condit R, Foster RB. 2001. Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research* 16: 859–875.
- Hubbell SP, Foster R. 1987. Large-scale spatial structure of a Neotropical forest. *Revista de Biología Tropical* 35: 7–22.
- Hurlbert SH. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–586.
- Ishida A, Nakano T, Yazaki K, Matsuki S, Koike N, Lauenstein DL, Shimizu M, Yamashita N. 2008. Coordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant angiosperms. *Oecologia* 156: 193–202.
- John R, Dalling JW, Harms KE, Yavitt JB, Stallard RF, Mirabello M, Hubbell SP, Valencia R, Navarrete H, Vallejo M *et al.* 2007. Soil nutrients influence spatial distributions of tropical trees species. *Proceedings of the National Academy of Sciences, USA* 104: 864–869.
- Jordan CF. 1985. *Nutrient cycling in tropical forest ecosystems*. Chichester, UK: John Wiley & Sons.
- Kim TJ, Montagnini F, Dent D. 2008. Rehabilitating abandoned pastures in Panama: control of the invasive exotic grass, *Saccharum spontaneum* L., using artificial shade treatments. *Journal of Sustainable Forestry* 26: 192–203.
- King DA, Davis SJ, Nur Supardi MN, Tan S. 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology* 19: 445–453.
- Kirby KR, Potvin C. 2007. Variation in carbon storage among trees species: implications for the management of small-scale carbon sink project. *Forest Ecology and Management* 246: 208–221.
- Kooyman RM, Westoby M. 2009. Costs of height gain in rainforest saplings: main-stem scaling, functional traits, and strategy variation across 75 species. *Annals of Botany* 104: 987–993.
- Labiberté E. 2009. FD: measuring functional diversity from multiple traits. In: *R package version 1.0* [WWW document]. URL <http://CRAN.R-project.org/web/packages/FD/index.html> [accessed on 30 September 2010].
- Labiberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.
- Lavorel S, Grigulis K, McIntyre S, Williams NSG, Gardén D, Dorrough J, Berman S, Quetier F, Thebault A, Bonis A. 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology* 22: 134–147.
- Legendre P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology* 1: 3–8.
- Leigh EG. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford, UK: Oxford University Press.
- Malhi Y, Phillips OL. 2004. Tropical forests and global atmospheric change: a synthesis. *Philosophical Transactions of The Royal Society of London Series B—Biological Sciences* 359: 549–555.
- Moles A, Warton D, Warman L, Swenson N, Laffan S, Zanne A. 2009. Global patterns in plant height. *Journal of Ecology* 97: 923–932.
- Nelson BW, Mesquita R, Pereira JLG, de Souza SGA, Batista GT, Couto LB. 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *Forest Ecology and Management* 117: 149–167.
- Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2009. *vegan: community ecology package, version 1.15-4* [WWW document]. URL <http://CRAN.R-project.org/package=vegan> [accessed on 30 September 2010].
- Ollivier M, Baroloto C, Marcon E. 2007. A trait database for Guianan rain forest trees permits intra- and inter-specific contrasts. *Annals of Forest Science* 64: 781–786.
- Paquette A, Messier C. 2010. The role of plantations in managing the world's forests in the Anthropocene. *Frontiers in Ecology and the Environment* 8: 27–34.
- Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614–2625.
- Piotto D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest Ecology and Management* 255: 781–786.
- Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Poorter L, Bongers F, Sterck FJ, Woll H. 2005. Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. *Journal of Ecology* 93: 256–267.
- Poorter L, Kitajima K. 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology* 88: 1000–1011.

- Potvin C, Dutilleul P. 2009. Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. *Ecology* **90**: 321–327.
- Potvin C, Whidden E, Moore T. 2004. A case study of carbon pools under three different land-uses in Panama. *Climatic Change* **67**: 291–307.
- Reich PB, Wright IJ, Lusk CH. 2007. Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. *Ecological Applications* **17**: 1982–1988.
- Rijkers T, Pons TL, Bongers F. 2000. The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Functional Ecology* **14**: 77–86.
- Rozendaal DMA, Hurtado VH, Poorter L. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* **20**: 207–216.
- Ruger N, Huth A, Hubbell SP, Condit R. 2009. Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology* **97**: 1360–1368.
- Ruiz-Jaen MC, Potvin C. 2010. Tree diversity explains variation in ecosystem function in a Neotropical forest in Panama. *Biotropica* doi: 10.1111/j.1744.7429.2010.00631.x.
- Scherer-Lorenzen M. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos* **116**: 2108–2124.
- Scherer-Lorenzen M, Potvin C, Koricheva J, Schmid B, Hector A, Bornik Z, Reynolds G, Schulze ED. 2005. The design of experimental tree plantations for functional biodiversity research. In: Scherer-Lorenzen M, Korner C, Schulze ED, eds. *Forest diversity and function: temperate and boreal systems*. Heidelberg, Germany: Springer, 347–376.
- Schnitzer A, Carson WP. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* **82**: 913–919.
- Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**: 297–305.
- Sheil D, Salim A, Chave J, Vanclay J, Hawthorne WD. 2006. Illumination-size relationships of 109 coexisting tropical forest tree species. *Journal of Ecology* **94**: 494–507.
- Silver WL, Brown S, Lugo AE. 1996. Effects of changes in biodiversity on ecosystem function in tropical forests. *Conservation Biology* **10**: 17–24.
- Silver WL, Thompson AW, Reich A, Ewel JJ, Firestone MK. 2005. Nitrogen cycling in tropical plantation forests: potential controls on nitrogen retention. *Ecological Applications* **15**: 1604–1614.
- Spehn EM, Hector A, Joshi J, Scherer-Lorenzen M, Schmid B, Bazeley-White E, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG *et al.* 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs* **75**: 37–63.
- Sprent JI. 2005. Nodulated legume trees. In: Werner D, Newton WE, eds. *Nitrogen fixation in agriculture, forestry, ecology, and the environment*. Dordrecht, the Netherlands: Springer, 113–141.
- Thomas SC, Winner WE. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology* **22**: 117–127.
- Tilman D, Wedin D, Knops J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718–720.
- Vila M, Vayreda J, Comas L, Ibanez JJ, Mata T, Obon B. 2007. Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters* **10**: 241–250.
- Walker B, Kinzing AP, Langridge J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2**: 95–113.
- Wiegand T, Gunatilleke CVS, Gunatilleke I, Huth A. 2007. How individual species structure diversity in tropical forests. *Proceedings of the National Academy of Sciences, USA* **104**: 19029–19033.
- Wishnie MH, Dent DH, Mariscal E, Deago J, Cedeño N, Ibarra D, Condit R, Ashton PMS. 2007. Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. *Forest Ecology and Management* **243**: 39–49.
- Wright SJ. 1996. Plant species diversity and ecosystem functioning in tropical forests. In: Orians GH, Dirzo R, Cushman JH, eds. *Biodiversity and ecosystem processes in tropical forests*. Berlin, Germany: Springer-Verlag, 11–31.
- Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davis SJ, Diaz S *et al.* in press. Functional traits and the growth-mortality tradeoff in tropical trees. *Ecology* doi: 10.1890/09-2335.1.
- Zeugin F, Potvin C, Jansa J, Scherer-Lorenzen M. 2010. Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation? *Forest Ecology and Management* **260**: 1424–1433.