



Diversity enhances carbon storage in tropical forests

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ABSTRACT

Aim Tropical forests store 25% of global carbon and harbour 96% of the world's tree species, but it is not clear whether this high biodiversity matters for carbon storage. Few studies have teased apart the relative importance of forest attributes and environmental drivers for ecosystem functioning, and no such study exists for the tropics.

Location Neotropics.

Methods We relate aboveground biomass (AGB) to forest attributes (diversity and structure) and environmental drivers (annual rainfall and soil fertility) using data from 144,000 trees, 2050 forest plots and 59 forest sites. The sites span the complete latitudinal and climatic gradients in the lowland Neotropics, with rainfall ranging from 750 to 4350 mm year⁻¹. Relationships were analysed within forest sites at scales of 0.1 and 1 ha and across forest sites along large-scale environmental gradients. We used a structural equation model to test the hypothesis that species richness, forest structural attributes and environmental drivers have independent, positive effects on AGB.

Results Across sites, AGB was most strongly driven by rainfall, followed by average tree stem diameter and rarefied species richness, which all had positive effects on AGB. Our indicator of soil fertility (cation exchange capacity) had a negligible effect on AGB, perhaps because we used a global soil database. Taxonomic forest attributes (i.e. species richness, rarefied richness and Shannon diversity) had the strongest relationships with AGB at small spatial scales, where an additional species can still make a difference in terms of niche complementarity, while structural forest attributes (i.e. tree density and tree size) had strong relationships with AGB at all spatial scales.

Main conclusions Biodiversity has an independent, positive effect on AGB and ecosystem functioning, not only in relatively simple temperate systems but also in structurally complex hyperdiverse tropical forests. Biodiversity conservation should therefore be a key component of the UN Reducing Emissions from Deforestation and Degradation strategy.

Keywords

Biodiversity, biomass, ecosystem functioning, Neotropics, rainfall, REDD+, scale, soil, tropical forest.

INTRODUCTION

Tropical forests are hotspots for carbon and biodiversity; they only cover 7–10% of the Earth's land surface but they store 25% of the terrestrial above- and belowground carbon (Bonan, 2008), are responsible for 34% of terrestrial primary productivity (Beer *et al.*, 2010) and harbour 96% of the world's estimated 45,000 tree species (Fine *et al.*, 2008). From a practical point of view, this provides a win–win situation for the UN Reducing Emissions from Deforestation and Degradation (REDD+) initiative, which aims to conserve carbon storage of tropical forest while safeguarding biodiversity. Importantly, biodiversity conservation can be much more than a side benefit alone, if a higher biodiversity enhances carbon sequestration and storage (Diaz *et al.*, 2009). Forest functioning may be determined not only by taxonomic attributes (i.e. measures of species identity) of the vegetation but also by structural attributes, and by the direct and indirect effects of environmental drivers (see the conceptual model in Fig. 1a). Surprisingly few studies have teased apart the relative importance of these environmental drivers and forest attributes for ecosystem properties and processes (but see Paquette & Messier, 2011; Vilà *et al.*, 2013).

Over the past two decades there has been a strong emphasis on the role of biodiversity in ecosystem properties, processes and services (Naeem *et al.*, 2009, and references therein). Species richness is thought to enhance productivity through: (1) niche complementarity, where species have different niches and are therefore able to access more of the available resources or facilitate each other, thus enhancing overall productivity (Tilman *et al.*, 2001); (2) the selection effect, as by chance a very productive species is included in the community (Loreau & Hector, 2001); and (3) the insurance effect, as one species contributes more to ecosystem productivity in one year and another species in another year (Yachi & Loreau, 1999; Isbell *et al.*, 2011). These hypotheses about the relationship between species richness and productivity could also apply to standing biomass, as higher productivity may lead to faster accumulation of biomass, and productivity and biomass are therefore positively correlated in forests (Chisholm *et al.*, 2013).

Not only taxonomic attributes (i.e. species identity) but also structural attributes, such as stem diameter, tree density and leaf area index, determine biomass, resource capture and productivity. Vegetation structure contributes directly to biomass, but variations in structure, such as leaf layering, may also enhance light capture and carbon gain. Structural attributes may vary more strongly than taxonomic attributes within communities (due to disturbances) and across communities (due to environmental gradients), and may have a larger direct impact on

biomass and ecosystem processes. A recent study found, for example, that vegetation quantity (biomass) rather than vegetation quality (i.e. species functional traits and variation therein) was the main driver of productivity in tropical secondary forests (Lohbeck *et al.*, 2015). The question is therefore whether taxonomic attributes may explain any additional variation in aboveground biomass (AGB) once the role of structural attributes has explicitly been taken into account (Fig. 1a).

A recent meta-analysis showed that in experimental studies species richness increased primary productivity and standing biomass and that biodiversity loss therefore has a negative effect on ecosystem functioning (Cardinale *et al.*, 2011). However, most studies included in the meta-analysis were carried out at small spatial scales and involved grasslands and aquatic systems, and most experiments used a small number of species (fewer than 10; Cardinale *et al.*, 2011); thus the effect of high species richness could not be assessed. It is not clear therefore whether the relationship between biodiversity and biomass will also hold for: (1) larger spatial scales where there may be a saturating effect as the number of species rises without a further increase in carbon storage; (2) areas under different environmental controls; and (3) hyperdiverse communities in the tropics where many species might be functionally redundant.

The relationships between species richness, AGB and productivity may vary with spatial scale. Experimental grassland studies and many forest surveys have typically used small plots, and found that the positive effect of species richness on biomass or biomass productivity saturates with only three to eight species (Tilman *et al.*, 2001; Zhang *et al.*, 2012; Gamfeldt *et al.*, 2013; Vilà *et al.*, 2013). Chisholm *et al.* (2013) found for temperate and tropical forests that species richness and biomass were positively related within forest sites at small spatial scales (20 m × 20 m), probably because in a small area with relatively few species any additional species still matter for productivity and AGB. At larger spatial scales (100 m × 100 m) there was no consistent relationship between species richness and biomass, probably as a result of such a saturation effect.

The relationship between species richness and productivity may also vary with systems under different environmental conditions. In a study using small survey plots in Canada, Paquette & Messier (2011) found that in boreal forests facing harsh environmental conditions, functional tree diversity affected productivity strongly and positively, whereas in benign and productive temperate forests diversity had a weaker effect on productivity. Paquette & Messier hypothesized that in stressful (e.g. cold or dry) environments diversity contributes to facilitation processes and, hence, to productivity, whereas in benign environments diversity results in more competition. It cannot be ruled out,

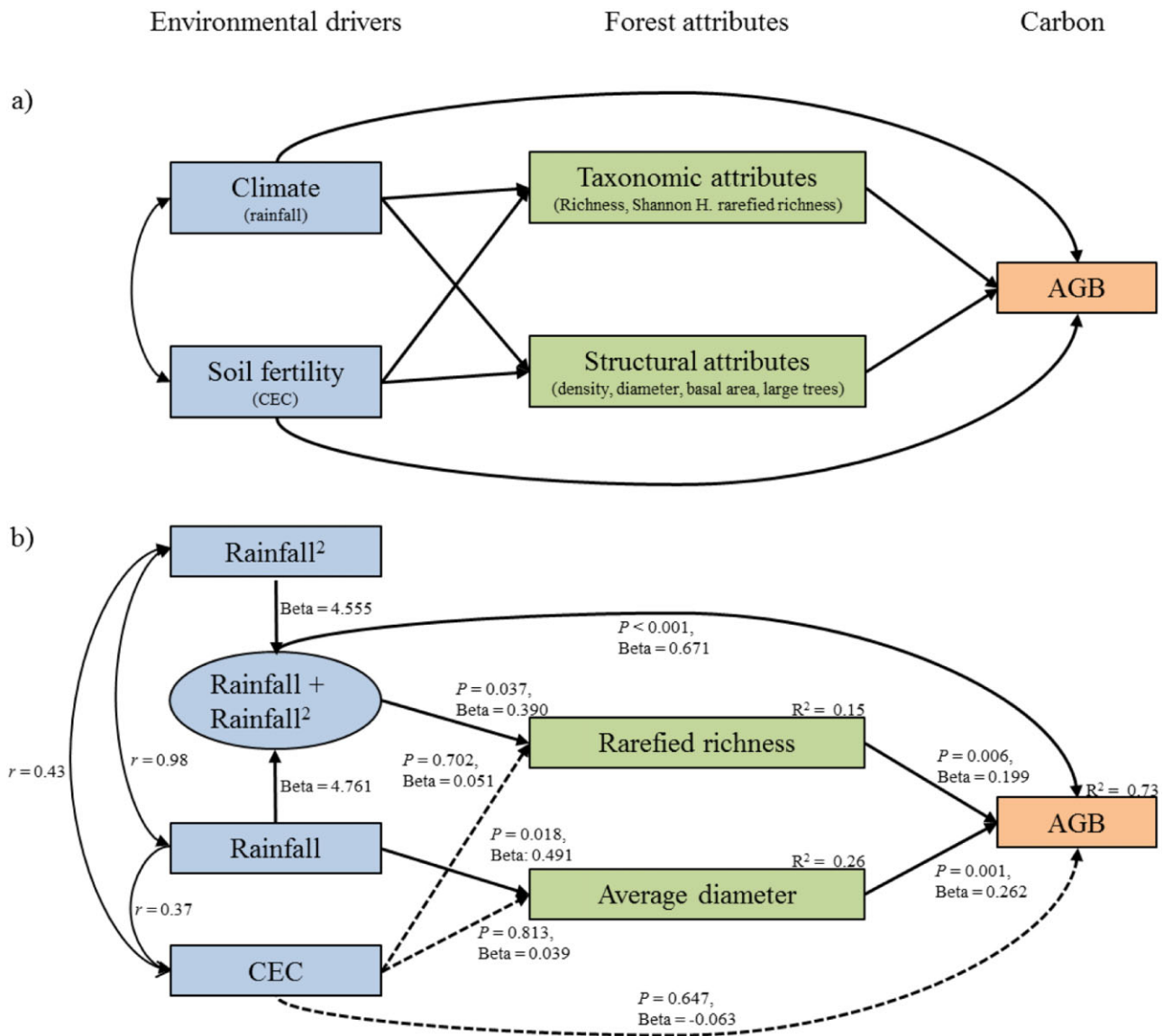


Figure 1 (a) Conceptual diagram showing how environmental drivers (rainfall, soil fertility) affect forest attributes (taxonomic and structural attributes), and how environmental drivers and forest attributes together affect carbon storage in aboveground biomass (AGB). The two types of forest attributes are characterized by their magnitude (e.g. species richness, basal area) and their variation (e.g. species diversity, density of large trees). (b) The final structural equation model relating AGB to biotic drivers (rarefied richness and average tree diameter) and abiotic drivers (rainfall and cation exchange capacity, CEC). Biomass and rarefied richness show a hump-shaped relationship with rainfall (see also Fig. 6a,c), and are therefore modelled as a function of rainfall and rainfall squared (rainfall²). Significant paths (continuous arrows), non-significant paths (broken arrows) and correlations (double-sided arrows) are shown. For each path the significance level (P) and standardized regression coefficient are shown. R^2 indicates the total variation in a dependent variable that is explained by the combined independent variables.

however, that the stronger diversity effect in boreal forests is simply a result of the lower species richness there.

Both taxonomic and structural attributes and ecosystem properties and processes may vary along environmental gradients (Fig. 1a). Species richness of tropical lowland forests tends to increase with rainfall and reduced seasonality (ter Steege *et al.*, 2003). The density of large trees, forest AGB and net primary productivity all increase with resource availability (annual rainfall and soil fertility) and decrease with temperature

(Malhi *et al.*, 2004; Baraloto *et al.*, 2011; Quesada *et al.*, 2012; Slik *et al.*, 2013). Hence, environmental drivers are likely to affect AGB either directly or indirectly (via their effect on taxonomic and structural forest attributes) (Fig. 1a).

Here we relate AGB to taxonomic and structural forest attributes, as well as to rainfall and soil fertility. We use data from 144,000 trees that were sampled in 2050 forest plots established in 59 forest sites. This dataset spans the complete latitudinal and climatic gradient in the lowland Neotropics (ranging from 750

to 4350 mm of rainfall per year) and covers all major forest types (from dry deciduous to wet forests; see Appendix S1 in Supporting Information). Relationships were analysed at a local scale under relatively homogeneous environmental conditions within forest sites (0.1 and 1 ha plots) and at a regional scale along large-scale environmental and biogeographical gradients across forest sites.

We address two major questions. First, what are the effects of taxonomic and structural attributes on AGB and what is their relative importance? We hypothesize that species diversity has a positive effect on biomass (through niche complementarity, the selection effect or the insurance effect) and that this effect can be observed at small (0.1 ha) spatial scales (where richness is low, so an additional species still makes a difference) but not at larger (1 ha) spatial scales (because of species redundancy). We predict that as stem density and average stem diameter increase there will be greater AGB, and that they have stronger effects on AGB than taxonomic forest attributes. The second is what are the direct effects of environmental drivers on AGB, and on the taxonomic and structural attributes of the forest? We hypothesize that with an increase in resource availability (water and nutrients) there will be an increase in AGB, forest structure (i.e. tree size) and taxonomic diversity, and that annual rainfall will have a stronger effect than soil fertility given the large climatic gradient considered.

METHODS

Study sites

We compiled information on species diversity, structure and biomass from 294 1-ha plots and 1975 0.1-ha plots established in 59 mature forest sites that covered nearly the full latitudinal range of Neotropical forests from Mexico to Bolivia (Fig. 2, Appendix S1). Rainfall ranged from 750 to 4350 mm year⁻¹, and soil cation exchange capacity (CEC) ranged from 1 to 83 cmol kg⁻¹. For all analyses we just focus on trees because there was no consistent inventory data for lianas and palms, and in most forests lianas and palms make only a small contribution to AGB. For an extensive description of the methods see Appendix S2.

Biomass calculations

We took advantage of available plot data in mature, fully developed 'old-growth' forests, without visible effects of past human disturbance. The size, shape, spatial distribution and contiguity of plots varied across sites (Appendix S1). For this study, we calculated forest attributes at two spatial scales (0.1 and 1 ha).

In many plots only trees with a stem diameter at breast height (d.b.h.; the diameter of the tree at 1.3 m from the ground) of 10 cm or more were measured, but in other plots data for trees with d.b.h. \geq 5 cm were also included as these small stems can contribute a significant part of AGB in drier forests. AGB was calculated for plots of 0.1 and 1 ha, as the relationship

between AGB and diversity is scale dependent (Chisholm *et al.*, 2013). For each plot, AGB was calculated for each tree using six different allometric equations. The allometric equations were based on stem diameter only (Pearson *et al.*, 2005; henceforth referred to as the 'Brown' equations) or a combination of stem diameter and wood density (Chave *et al.*, 2005; henceforth referred to as the 'Chave' equations). Brown and Chave both present three different equations for different forest types: dry forest, moist forest and wet forest. For use in the Chave calculations wood density (WD, g cm⁻³) data came from local sites or from the Neotropical data of a global WD database (Zanne *et al.*, 2009; <http://datadryad.org/handle/10255/dryad.235>). Biomass was then summed across all trees to obtain AGB (in Mg ha⁻¹). We first checked to what extent AGB varied with the type of allometric equation used for biomass, and with both diameter cut-off limits (Appendix S3). The Chave and Brown estimates of plot AGB for trees with d.b.h. \geq 10 cm were tightly related ($r^2 = 0.81$). The estimated plot AGB using the Chave equations was on average 1.15 times the estimated AGB using the Brown equations (paired *t*-test, $t = 16.1$, $P < 0.001$, $n = 480$). Using the Chave equations, the estimated plot AGB for trees with d.b.h. \geq 5 cm was on average 1.04 times the AGB of trees with d.b.h. \geq 10 cm, and this ratio was especially large for dry forests (on average 1.178) but close to 1 for moist forests (1.033) and wet forests (1.020; Appendix S3). In dry forests, small trees (5–10 cm d.b.h.) therefore make a relatively large contribution to AGB, although their *absolute* contribution is small. For further analysis we then used the Chave equations that corresponded to the forest type (dry, moist or wet) to which the plot belonged, and we used trees with d.b.h. \geq 10 cm, as these data were available for all plots. We used the Chave equations because they include wood density, which is an important source of large-scale variation in AGB (Mitchard *et al.*, 2014).

Structural attributes

Variation in AGB across forest plots is, amongst other things, a function of the tree density, mean stem diameter and wood density of trees. It is therefore not a question of whether these variables are related to AGB, but what their relative strength is in determining AGB plot biomass. For each plot, five structural attributes were calculated for which data were available and that are relevant to the biomass model used: overall tree density, density of large trees (d.b.h. \geq 60 cm), mean tree diameter and stand basal area. Note that biomass of individual trees is calculated based on tree diameter, and hence tree biomass scales closely with the basal area of the individual tree. This is somewhat different from stand basal area. A high stand basal area can be caused by many small trees (each containing little biomass) or a few trees with a large basal area (each containing a disproportionately large biomass).

Taxonomic attributes

For each plot, three taxonomic attributes were calculated: species richness per area, rarefied species richness per 50 indi-

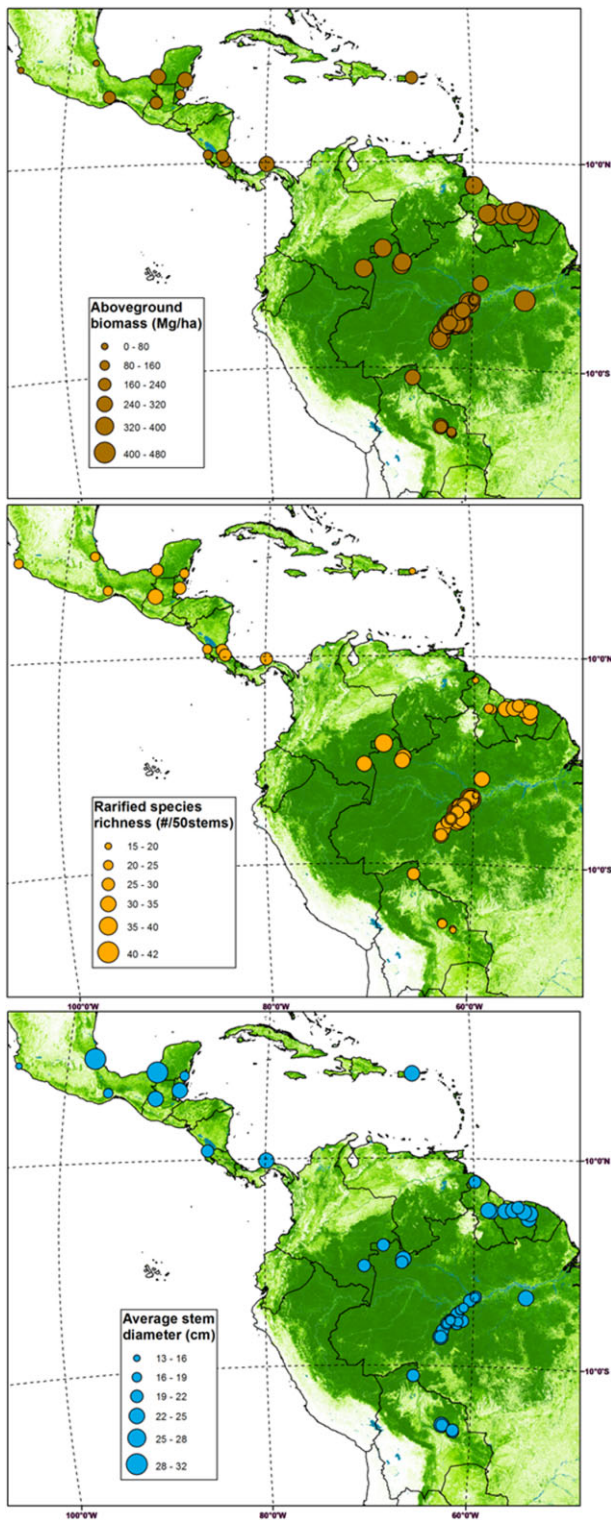


Figure 2 Map of vegetation cover in Latin America, with the location of the 60 study sites: (a) aboveground biomass (AGB, Mg ha^{-1}), (b) rarefied species richness (number of species/50 stems), and (c) average stem diameter (cm). The size of the symbol scales with the value of the attribute. The intensity of the green colour (or shading) indicates the amount of forest cover. The background layer is derived from a Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation continuous fields (VCF) product (Hansen *et al.*, 2003).

viduals and Shannon diversity. Rarefied species richness is the number of species observed when a certain number of trees are randomly drawn from a plot. Such rarefaction removes the confounding effect of tree density on species richness. For rarefied richness we used 50 individuals as a reference, as this number of individuals is found in both the 0.1-ha plots and the 1-ha plots. Calculations were made using either ESTIMATES 9.1.0 (Colwell, 2011) or the R package Vegan (Oksanen *et al.*, 2014).

Environmental factors

For each site, six climatic variables were obtained from the nearest climatological station, or from interpolated climatic maps from WorldClim (Hijmans *et al.*, 2005). We used mean annual rainfall as the main climatic variable for subsequent analyses because it was closely related to all other climate variables, and to AGB and forest attributes. For each site six soil variables were obtained using site coordinates and maps from the Harmonized World Soil Database (Nachtergaele *et al.*, 2012). Data on soil N and P were not available from this database. We used CEC (in cmol kg^{-1}) as our main soil variable because it was strongly correlated with the other fertility measures and provides a straightforward measure of soil fertility.

Statistical analyses

Pearson correlations were used to evaluate whether there was an association between AGB and each of the measures of taxonomic and structural attributes *within sites* for 0.1- and 1-ha plots. For the 1-ha level, one correlation was made per site, using all 1-ha plots (with a minimum of four plots). For the 0.1-ha level, several correlations were made per site if these small plots were nested within a 1-ha plot and if several 1-ha plots were available. In that case a correlation was made per 1-ha plot using all 0.1-ha subplots nested within the larger 1-ha plot, and this was repeated for all the 1-ha plots. Alternatively, a single correlation was made across all plots at a site if these small plots were not nested within a single 1-ha plot. To evaluate how general these within-site correlations were, we then calculated at the 0.1- and 1-ha levels the average and 95% confidence interval of all of these correlation coefficients combined, pooling all sites. If the 95% confidence interval does not overlap with zero, it means that, in general, there is a significant correlation between AGB and the variable concerned. We checked the consistency of the results by repeating this analysis with a mixed linear model in which site was included as a random factor in order to account for the nestedness of the data (Appendix S4). For the 0.1-ha plots, the 1-ha plot to which they belonged was also included as a random factor in the model.

We also analysed whether there was a relationship between AGB, taxonomic attributes and structural attributes *across sites*, and therefore across large-scale environmental gradients. Where data from multiple plots were available at each site we averaged the data per site to avoid problems with nestedness. For the sites

that had both 0.1- and 1-ha plots, we only used the average of the 1-ha plots, as they provide more accurate estimates of biomass and diversity. In total, data were available for 59 sites (26 site averages based on 1-ha plots and 33 site averages based on 0.1-ha plots). One outlying site with a small plot with an exceptionally high AGB was removed from subsequent regression and structural equation modelling (SEM) analyses.

Structural equation modelling

We used SEM to test for the direct and indirect effects of climate, soil fertility and taxonomic and structural attributes on AGB (Fig. 1a). To avoid complexity with nestedness of plots within sites, we based the SEM on average values for 58 sites. Average site values were estimated with a different accuracy. To account for this, sites in the SEM were weighted by the square root of the total plot area per site.

To test the conceptual model of Fig. 1(a), we selected only one variable per 'box' (climate, soil, taxonomic attributes or structural attributes) as we had a limited number of replicates (sites). We used annual rainfall as the climate variable and CEC as the soil variable. Because bivariate scatterplots indicated that AGB and rarefied richness showed a hump-shaped relationship with rainfall, we included for these two response variables both rainfall and rainfall squared as predictor variables in the analysis (Fig. 1b), allowing us to model such a hump-shaped relationship. The combined effect of rainfall and rainfall squared was evaluated by including a composite variable (the oval box in Fig. 1b).

Of the three taxonomic attributes considered, we only included rarefied species richness in the SEM, because it is less dependent on plot size and multiple regressions indicated that it was the best predictor of AGB (data not shown). Of the four structural attributes considered (stand basal area, average tree diameter, number of trees larger than 60 cm d.b.h. and stem density), we did a series of SEMs using the same model structure as in Fig. 1(a) but a different structural variable each time. The models included: square root-transformed AGB as the dependent variable; rarefied species richness as an endogenous variable (i.e. a variable that is affected by other variables); annual rainfall, rainfall squared and CEC as exogenous variables (i.e. independent variables that have only an effect on other variables); and a composite variable combining rainfall and rainfall squared. The only model that significantly fitted the data (i.e., it had a *P*-value greater than 0.05) was the model that included average tree diameter as a structural attribute.

The indirect effects of the exogenous variables (rainfall and CEC) on AGB were calculated by multiplying the standardized coefficients of all paths on one route between one of the exogenous variables and AGB. All SEM analyses were performed in R 3.0.2. The models were specified with variables and paths (the 'arrows' between variables) using the *sem* function of the *lavaan* package (Rosseel, 2012). The replicate weights were defined using the *svydesign* function of the *survey* package, and the *lavaan.survey* function was used to evaluate the models when taking replicate weights into account.

RESULTS

Within-site relations

Within each study site, the AGB of the plots was regressed against the forest attributes. Within most study sites, AGB tended to increase (non-significantly) with species richness, Shannon diversity and rarefied richness for the 0.1-ha plots, whereas there were no clear relationships for the 1-ha plots (Fig. 3). Within each study site, AGB increased consistently with average tree diameter, stand basal area and large tree density of the plots, for both 0.1- and 1-ha spatial scales, whereas tree density was only significant at the 0.1-ha scale (Fig. 4). The relationship was especially strong between AGB and stand basal area.

To test the generality of these relationships, we conducted a meta-analysis on the value of the correlation coefficient between AGB and each of the predictor variables within each site (Fig. 5; $n = 103$ – 196 correlations for 0.1-ha plots and $n = 16$ – 17 correlations for 1-ha plots) and calculated the mean correlation and 95% confidence intervals. This meta-analysis confirmed that, overall, there was a consistent significant positive relationship between AGB and taxonomic attributes at the 0.1-ha scale (i.e. the 95% confidence interval of the average correlation coefficient did not overlap with zero), whereas this relationship disappeared at the 1-ha scale. Not surprisingly, structural variables such as stand basal area, average tree diameter and the density of large trees are significantly and strongly positively related to AGB at both 0.1- and 1-ha spatial scales (Fig. 5). Similar results were found with a mixed linear model in which site was included as a random factor, to account for the nestedness of the data (Appendix S4). The strength of this within-site correlation between AGB and taxonomic diversity/stem density declined with the amount of annual rainfall at the site (Appendix S5).

Cross-site relationships between AGB and forest attributes

In addition to testing within sites, we also analysed whether there were bivariate relationships between AGB and taxonomic attributes and structural attributes across our 58 Neotropical forest sites, and thus across large-scale environmental gradients. For this analysis we selected the best scalable measure of diversity (rarefied richness) and one of the best structural predictors of AGB (average tree diameter). Rarefied richness varied 2.7-fold across sites (from 15 to 42 species per 50 stems; Fig. 2b), average tree diameter varied 2.4-fold (from 13 to 32 cm; Fig. 2c) and AGB varied 8.1-fold (from 59 to 479 Mg ha⁻¹; Fig. 2a).

Rarefied richness (Fig. 6a) and AGB (Fig. 6c) showed a hump-backed relationship with annual rainfall and peaked halfway along the rainfall gradient, between 2000 and 3000 mm year⁻¹. Average tree diameter increased continuously with rainfall (Fig. 6b). All three variables tended to decrease with the CEC of the soil (Appendix 6), although the relationships were non-significant. AGB was not only related to environmen-

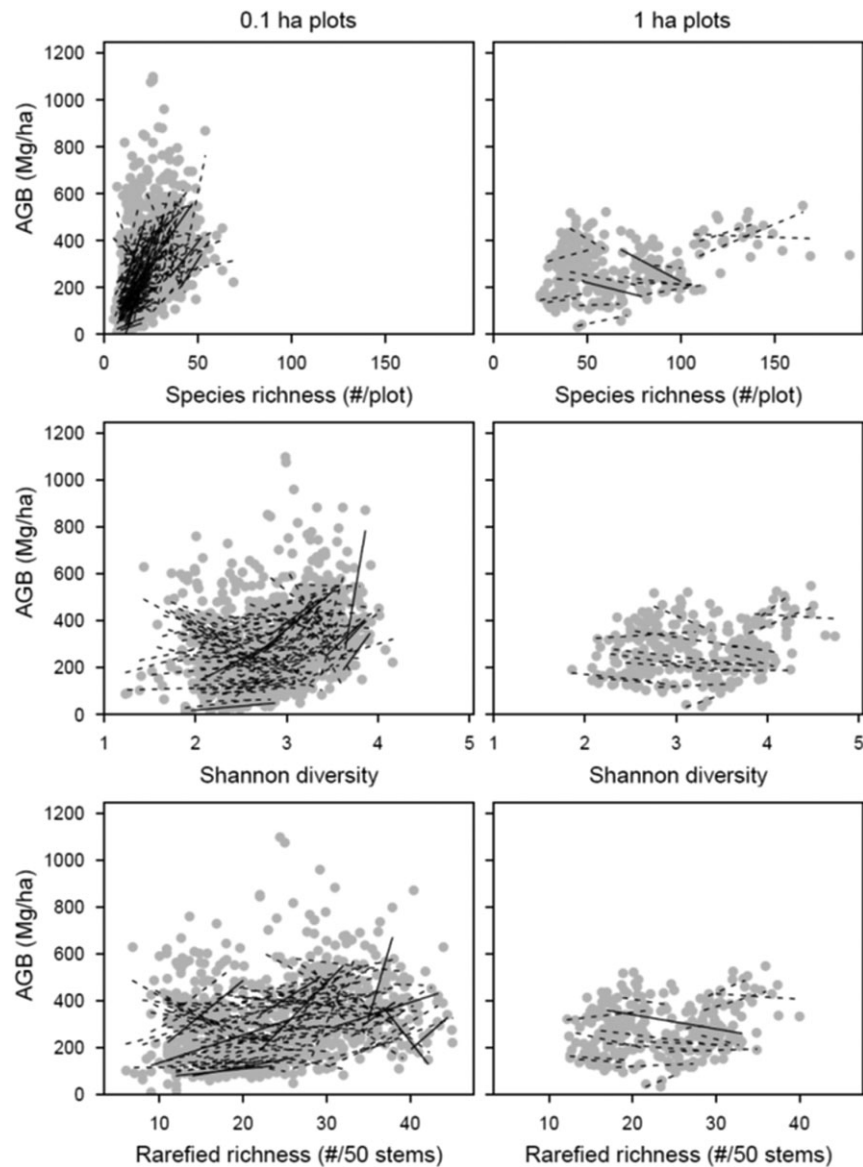


Figure 3 Relationship between aboveground biomass (AGB) and three taxonomic attributes: species richness per unit area (top panels), Shannon diversity (middle panels) and rarefied species richness per 50 stems (bottom panels). Relationships are shown for 0.1-ha plots (left panels, $n = 47$ – 53 sites and 916 – 1837 plots) and 1-ha plots (right panels, $n = 25$ sites and 294 plots). All data are based on trees with d.b.h. ≥ 10 cm. Dots indicate the observed values. Regression lines are shown for each site (for the 1-ha plots), or several regression lines are shown per site (0.1-ha plots within a 1-ha plot). Continuous regression lines are significant, broken regression lines are not significant ($P > 0.05$).

tal variables but also to forest attributes; AGB showed a positive relationship with rarefied richness (Fig. 7a) and average stem diameter (Fig. 7b) across sites.

Structural equation modelling; what are the main drivers of AGB variation?

We used SEM to evaluate our conceptual model (Fig. 1a). Our SEM included six variables: annual rainfall, annual rainfall squared, CEC, rarefied species richness, average stem diameter and AGB. Average stem diameter was selected as the structural attribute because this was the only accepted model (i.e. it described the data with sufficient accuracy) with a P -value for the overall model fit larger than 0.05 (Fig. 1b; $\chi^2 = 4.95$, $P = 0.176$, d.f. = 3), whereas the models including basal area ($\chi^2 = 23.10$, $P < 0.001$) or stem density ($\chi^2 = 11.80$, $P = 0.008$) were rejected. The accepted model explained 73% of the vari-

ation in AGB, 15% of the variation in rarefied richness and 26% of the variation in average stem diameter.

The composite variable 'rainfall + rainfall squared' had the strongest direct effect on AGB ($\beta = 0.67$, $P < 0.001$), followed by average stem diameter ($\beta = 0.26$, $P = 0.001$), rarefied richness ($\beta = 0.20$, $P = 0.006$) and CEC ($\beta = -0.06$, $P = 0.647$) (Table 1, Fig. 1b). Rarefied richness was most strongly affected by rainfall + rainfall squared ($\beta = 0.39$, $P = 0.037$) and average diameter was most strongly affected by the linear effect of rainfall ($\beta = 0.49$, $P = 0.018$). The linear effect of rainfall had, via average diameter, the strongest indirect effect on AGB ($\beta = 0.129$; Appendix S7).

DISCUSSION

Tropical forests store a significant part of global carbon and biodiversity, and the question is whether this biodiversity

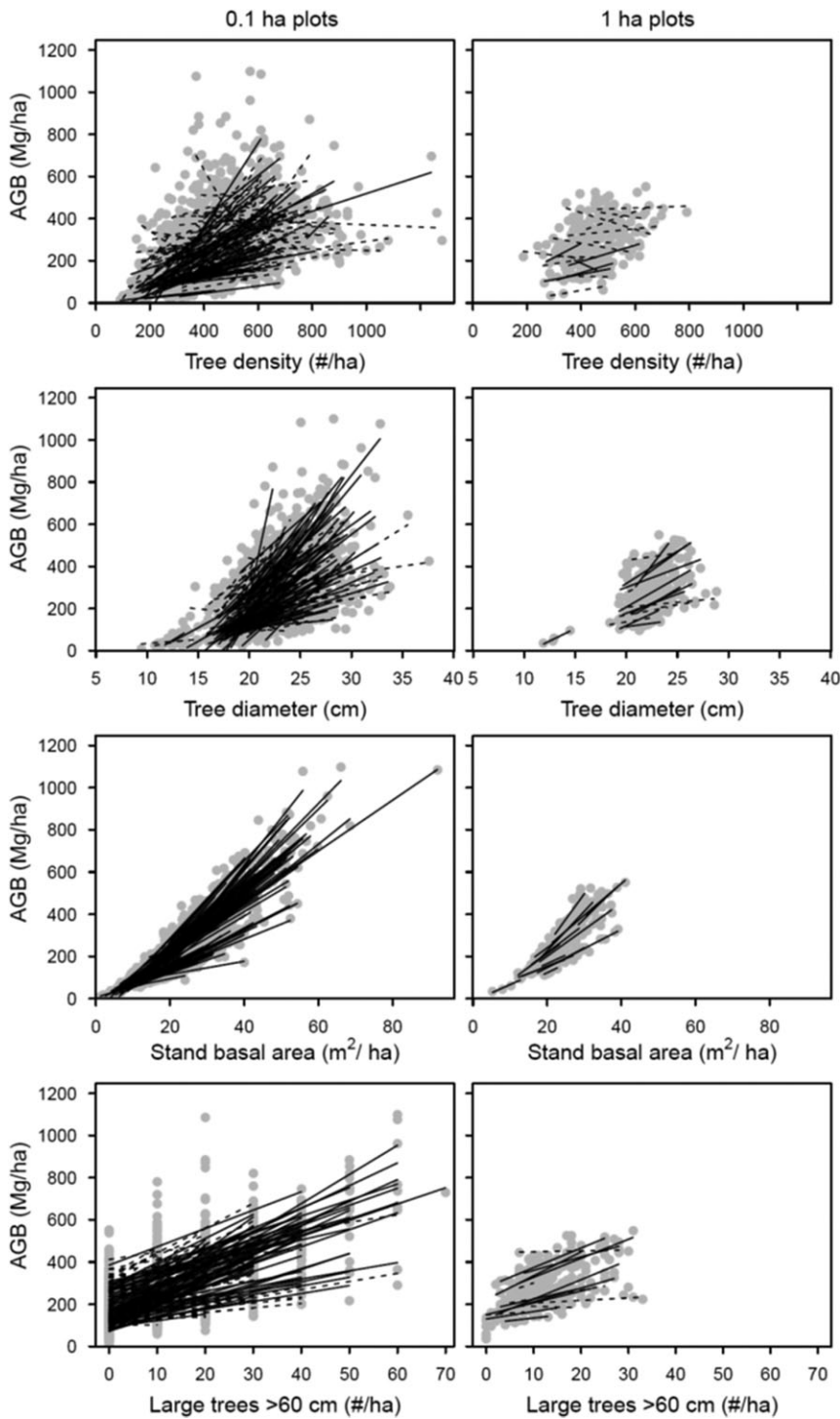


Figure 4 Relationship between aboveground biomass (AGB) and four structural attributes: tree density (top panels), average tree diameter (upper middle panels), stand basal area (lower middle panels) and density of large trees (d.b.h. ≥ 60 cm) (bottom panels). Relationships are shown for 0.1-ha plots (left panels, $n = 53$ sites and 1837 plots) and 1-ha plots (right panels, $n = 25$ sites and 294 plots). All data are based on trees with d.b.h. ≥ 10 cm, with the exception of the density of large trees. Dots indicate the observed values. Regression lines are shown for each site (for the 1-ha plots), or several regression lines are shown per site (0.1-ha plots within a 1-ha plot). Continuous regression lines are significant, broken regression lines are not significant ($P > 0.05$).

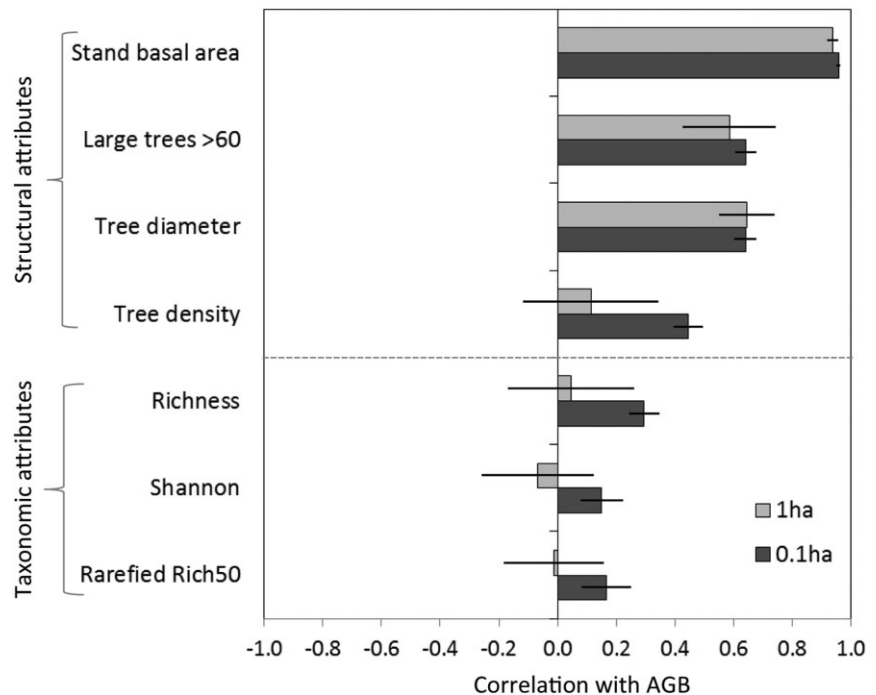
is relevant for carbon storage. We related AGB to forest attributes and environmental drivers, and found that taxonomic attributes had the strongest relationships with AGB at small spatial scales (0.1 ha), whereas structural attributes had strong relationships with AGB at both spatial scales (0.1 and 1 ha). Species richness had an independent, positive effect on AGB at local scales and when sites across the continent were compared. We shall now discuss the

implications of these results for conservation and REDD+ activities.

Taxonomic attributes have the strongest relationships with AGB at small spatial scales

We hypothesized that species richness and diversity would have a positive effect on biomass through niche complementarity, the

Figure 5 Meta-analysis of the within-site correlation between aboveground biomass (AGB) and taxonomic attributes and structural attributes. Correlations are shown at two spatial scales: 0.1-ha plots (black bars) and 1-ha plots (grey bars). Taxonomic attributes (shown below the dashed line) are rarefied species richness at 50 stems (Rarefied Rich50), Shannon diversity (Shannon) and species richness (Richness). Structural attributes (shown above the dashed line) are tree density, average tree diameter, density of large trees (d.b.h. ≥ 60 cm) and stand basal area. Means and 95% confidence intervals are shown. $n = 103$ – 196 correlations for 0.1-ha plots, and $n = 16$ – 17 correlations for 1-ha plots.



selection effect or the insurance effect, and that these effects would be observed especially within sites at a small spatial scale (where the species richness value is low because of the small sample area) but not at larger spatial scale (because of species redundancy). Indeed, within sites we found positive relationships between AGB and taxonomic diversity measures at the 0.1- but not the 1-ha scale (Fig. 5). The relationship was strongest for area-based diversity measures (richness) and the weakest for Shannon diversity and rarefied species richness (Fig. 5), indicating that variation in stem density among plots partly drives the AGB–diversity relation. Similarly, in a global analysis of larger forest plots (> 16 ha), Chisholm *et al.* (2013) also found that diversity–biomass relationships were always strong and positive at very small spatial scales ($20 \text{ m} \times 20 \text{ m}$), whereas at larger spatial scales (0.25 and 1 ha) there was no consistent relationship. Higher species richness enhances the variation in species traits found in the community, leading to niche complementarity, a higher resource capture, more efficient resource use and higher productivity. Higher species richness may also enhance facilitation (where, for example, a nitrogen-fixing species enhances soil fertility, and through this the productivity of the other species). Higher species richness also increases the chance of a selection effect (in which a highly productive or large species that stores a lot of biomass is included in the stand).

It should be acknowledged that 0.1-ha plots are rather small to accurately estimate biomass: in some forests this plot size will include very few trees, or an emergent tree. This may strongly affect the biomass estimate, and partly explain the large scatter in AGB at a given site. Hence, within-site relationships between taxonomic diversity and AGB may be partly affected by gap dynamics and cyclic succession: just after disturbance there may be a low tree species richness and biomass in the gap, whereas

with patch development both the number of species and their biomass increase over time, in line with the intermediate disturbance hypothesis (Connell, 1978). Alternatively, the relationship between diversity and AGB within sites may be driven by more permanent local environmental gradients, where areas with adverse conditions, such as shallow soils (e.g. Emilio *et al.*, 2014), rocky outcrops, waterlogged areas or ridge tops exposed to intense winds, contain fewer stems, fewer species and lower biomass than areas with deep well-developed humid and fertile soils.

Structural attributes are tightly related to AGB at all spatial scales

We expected that greater tree density and basal area of the forest would lead to an increase in AGB, as structure positively influences biomass, but we did not know their relative importance. We found that, within sites, AGB moderately increased with increasing tree density, more strongly with large tree density and most strongly with stand basal area (Fig. 5). Variation in AGB across forest plots is a function of the stem density, and the mean stem diameter, height, crown area and wood density of trees. Biomass increases exponentially with tree diameter, and large trees therefore contribute disproportionately to stand biomass compared with small trees. This explains why average tree diameter, large tree density and stand basal area are better predictors of AGB than overall tree density. A recent Pantropical analysis for 120 lowland tropical forests (Slik *et al.*, 2013) showed that 70% of the site variation in AGB was determined by the density of large trees (d.b.h. > 70 cm). Because of the paucity of large trees, Neotropical forest contained *c.* 30% less biomass than Palaeotropical forests. Large trees play an important role in eco-

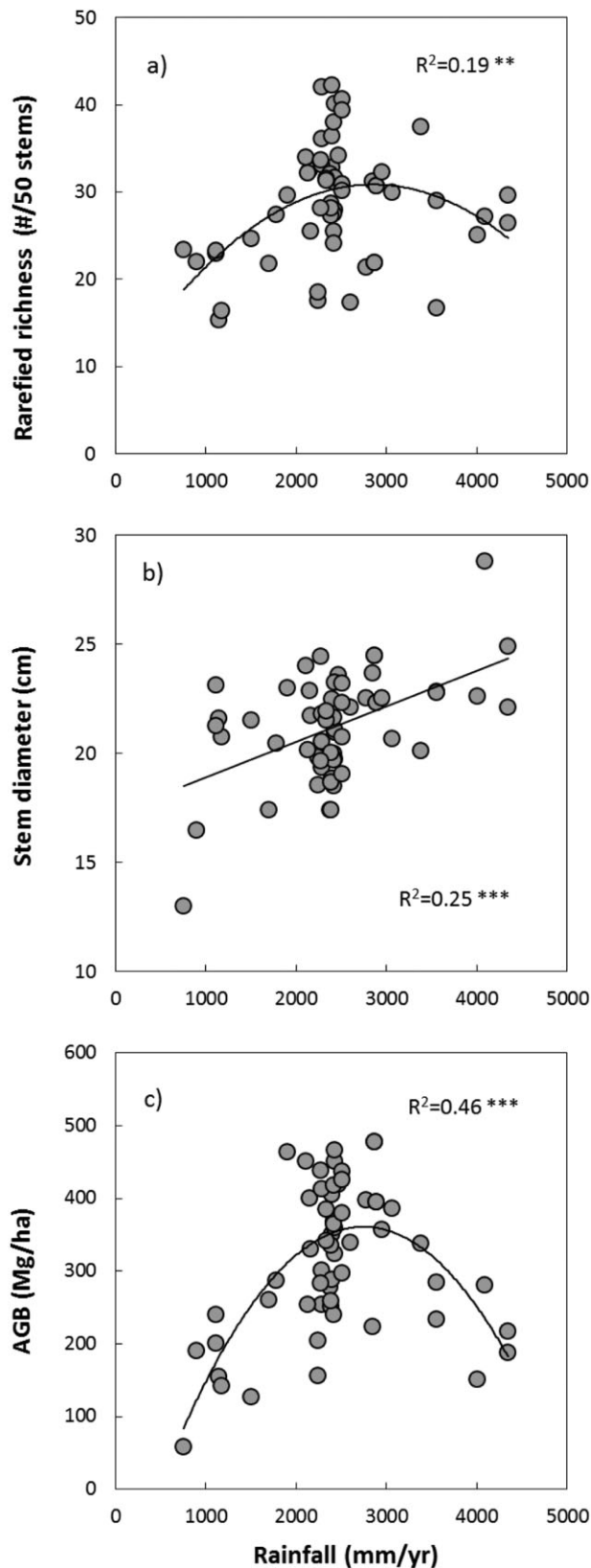


Figure 6 Relationship between annual rainfall and (a) rarefied species richness, (b) average tree diameter, and (c) aboveground biomass (AGB) for 58 Neotropical forest sites. For each site, average values were calculated for the largest plot size available (1- or 0.1-ha plots). All data are based on trees with a d.b.h. ≥ 10 cm. Regression lines and coefficients of determination (R^2) are shown. $^{***}P < 0.001$; $^{**}P < 0.01$.

system functioning, not only because they contribute most AGB but also because they form the forest canopy, where most of the photosynthetic carbon gain is concentrated. These large trees possess large and well-lit crowns, and therefore make the largest contribution to forest primary productivity (Stephenson *et al.*, 2014).

Rainfall is a stronger driver of AGB and biodiversity than is soil fertility

We hypothesized that with an increase in plant water availability (rainfall) and nutrient availability (CEC) there would be an increase in AGB (Fig. 1a), whereas at very high rainfall levels we would expect that soils would be highly weathered and leached (e.g. Swaine, 1996), leading to a decline in AGB. We indeed found that AGB showed a unimodal relationship with the rainfall gradient across sites (Fig. 6c). Our results were not due to the equations used (moist forest equations predict a higher biomass than dry and wet forest equations), because when we tested this effect using the same moist forest equation for all plots then the same unimodal relationship was found (Appendix S8). In our case, the decline in AGB at high rainfall was not due to leaching, as there was no relationship between rainfall and CEC in our dataset (Pearson $r = 0.02$, $n = 60$, $P = 0.866$). A negative relationship between rainfall and soil fertility might be found in relatively geologically homogeneous areas (Swaine, 1996). At the spatial scale of our study across distant Neotropical forest sites, however, there is a large variation in ecological and geological history, and parent rock material (cf. Stropp *et al.*, 2009), which may override more subtle relationships between soils and rainfall.

Reasons for the decline in AGB at high rainfall may be due to reduced insolation because of cloud cover (Graham *et al.*, 2003) or to species composition and forest structural attributes. At intermediate levels of rainfall, forests are more likely to be dominated by tall, large-diameter drought-deciduous canopy trees that contribute a large amount of biomass, whereas at higher levels of rainfall forests are more dominated by shorter-statured slender trees that better compete and persist in dense and shaded closed-canopy forest before they are able to access the canopy (Hall & Swaine, 1981; Fauset *et al.*, 2012). At low rainfall, AGB declined, indicating that low water availability and/or a shorter growing season length may constrain tree stature (probably because of hydraulic limitation) and tree growth (Toledo *et al.*, 2011), and hence AGB stocks. It should be noted that at the same rainfall level there is a large variation in AGB across forest sites (Fig. 6c), indicating that rainfall may set an upper limit to

Figure 7 Relationship between aboveground biomass (AGB) and: (a) rarefied species richness and (b) average tree diameter for 58 Neotropical forest sites. For each site, average values were calculated for the largest plot size available (1- or 0.1-ha plots). All data are based on trees with a d.b.h. ≥ 10 cm. Regression lines and coefficients of determination (R^2) are shown. $***P < 0.001$.

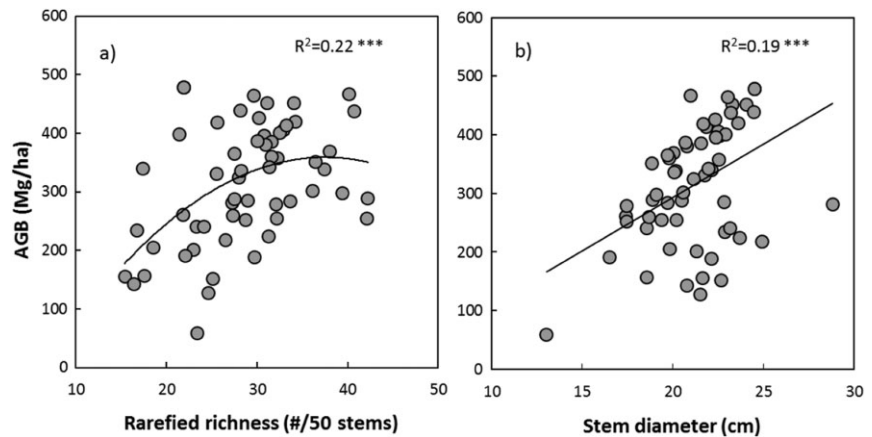


Table 1 The results of the structural equation model shown in Fig. 1(b). Unstandardized coefficient, standard error, Z-value, P-value and standardized coefficient are given for each path (i.e. each arrow in Fig. 1b). These statistics are given for the composite variable, the regressions between the remaining variables and the intercepts and error variances of the three dependent variables (aboveground biomass [AGB], rarefied richness and average diameter). The model was accepted ($\chi^2 = 4.95$, $P = 0.176$) and had three degrees of freedom (note that this is based on the number of 'knowns' minus the number of free parameters in the model, not on the sample size).

Response variable	Predictor variable	Coefficient	SE	Z-value	P-value	Standard coefficient
Composite variable:						
Rainfall + rainfall squared	Rainfall	4.44				4.76
	Rainfall squared	-0.80	0.03	-26.15	<0.001	-4.56
Regressions:						
✓(AGB)	Rainfall + rainfall squared	2.61	0.28	9.24	<0.001	0.67
	ln(CEC)	-0.19	0.41	-0.46	0.647	-0.06
	Rarefied richness	0.09	0.04	2.73	0.006	0.20
	Average diameter	0.39	0.12	3.36	0.001	0.26
Rarefied richness	Rainfall + rainfall squared	3.19	1.53	2.08	0.037	0.39
	ln(CEC)	0.32	0.83	0.38	0.702	0.05
Average diameter	Rainfall	1.21	0.51	2.37	0.018	0.49
	ln(CEC)	0.08	0.33	0.24	0.813	0.04

biomass stocks but that other factors (topography, shallow soils or rocky soils) may constrain biomass from reaching its potential maximum value. Apart from rainfall, other climatic features that determine plant water availability, such as length or severity of the dry season, may explain additional variation in AGB.

We hypothesized that AGB would increase with soil fertility. However, we found that AGB showed a non-significant decrease with increased CEC (our indicator of soil fertility; Appendix S6), and CEC was not significant in the multivariate structural equation model (Fig. 1b). Interestingly, Quesada *et al.* (2012) found that forest AGB in the Amazon decreased with potassium concentration, which is one of the cations that contributes to CEC. However, they also found that total available phosphorus was by far the best predictor of AGB in their study, and that phosphorus had a positive effect on AGB and biomass productivity. This is in line with the widely held idea that phosphorus limits productivity and biomass in the tropics (Vitousek *et al.*, 2010; but see Santiago *et al.*, 2012). It should be stressed that AGB is a state variable that reflects the outcome of various underlying factors that affect biomass production, retention

and loss. Biogeographical patterns in species traits (such as maximum height, tree longevity and wood density) determine biomass retention (Slik *et al.*, 2013; Fauset *et al.*, 2015), whereas recent local disturbance history may determine biomass loss. As a result, the observed bivariate relationship between biomass and any other variable is dependent on location and scale, may be weaker than expected, and may have different ultimate causes. For example, the tendency for the negative relationship between AGB and CEC that we observed is not driven by a higher productivity in areas with poor soils, but probably by species having adaptations to local soil conditions that enhance longevity at the species level (high WD, long life span), and therefore biomass retention and the build-up of a larger biomass pool at the stand level (Baker *et al.*, 2009).

AGB is most strongly driven by rainfall, followed by structural attributes and taxonomic attributes

We used SEM to test the independent effects of taxonomic and structural attributes on AGB, and to evaluate the relative

importance of biotic and environmental drivers of variation in AGB across sites. Standardized path coefficients indicate that AGB is most strongly driven by the direct and indirect effects of rainfall (Table 1, Appendix S7, Fig. 1b), followed by average stem diameter and rarefied richness, whereas CEC had a negligible effect (Fig. 1b).

At this continental scale, rainfall was a much stronger driver of AGB than our indicator of soil fertility (CEC). It should be stressed that this may partly be the result of methodological constraints; we did not use data on soil conditions at each site and for each plot, but instead used a global soil database to infer soil fertility and we did not consider other nutrients, such as phosphorus. Yet, it may also indicate that rainfall constrains productivity and AGB at large spatial scales, whereas soil fertility may become more important at regional (Quesada *et al.*, 2012) and local scales (Laurance *et al.*, 1999).

Rarefied species richness has a clear, independent and positive effect on AGB at this continental scale, once other structural and environmental drivers have been taken into account. To our knowledge, this is the first large-scale study to analyse the multivariate relationships between AGB and its drivers (environment and forest attributes) and to demonstrate that biodiversity has an independent positive effect on the AGB of highly diverse tropical forests. Most empirical studies that have examined the effects of biodiversity on forest AGB or productivity have ignored the effect of forest structure (e.g. Gamfeldt *et al.*, 2013), the environment (Cavanaugh *et al.*, 2014) or both (Chisholm *et al.*, 2013). Baruffol *et al.* (2013) showed for a single subtropical forest site that during succession diversity had an independent, positive effect on plot basal area growth. Our study shows that the findings from experimental studies, temperate grasslands and relatively simple temperate forests that biodiversity matters for ecosystem functioning can therefore also be extended to structurally complex and hyperdiverse tropical forests that contain as many as 15–42 species per 50 stems (Appendix S1).

We used a SEM approach to control as well as possible for other potentially confounding factors, but correlation does not necessarily mean causation. Controlled experiments (e.g. Hector *et al.*, 2011) and modelling studies (e.g. Sakschewski *et al.*, 2015) are needed to provide further support for a causal relationship between biodiversity and carbon storage in the tropics. Our study shows that the biodiversity effect is sufficiently strong to be picked up in the real world, and to be ecologically relevant.

Implications for carbon storage and REDD+

We have shown that AGB is related to the environment as well as to structure and diversity of the forest, and these results have three important implications for carbon storage in tropical forest and the REDD+ programme.

First, our results show that rainfall is the most important driver of AGB, and that AGB peaks in the middle of the rainfall gradient. If AGB also scales closely with belowground biomass then this result implies that, in terms of carbon storage, poten-

tial gains from REDD programmes are highest in tropical moist forests as these forests occur at intermediate rainfall and store the largest amount of biomass (Fig. 2). So for REDD+, forest conservation, restoration or reforestation could best be concentrated in these areas. The hump-backed relationship between AGB and rainfall means that any decrease in rainfall will have different repercussions for long-term carbon storage in wet and dry forests. In currently wet forests, a decline in rainfall may lead in the long term to higher AGB (e.g. Fauset *et al.*, 2012), whereas in currently moist and dry forest it may lead to lower AGB.

Second, structural attributes are amongst the best predictors of AGB, and they are tightly related to AGB at all spatial scales assessed – from small spatial scales (Fig. 4) up to large spatial scales across the continent (Figs 1b & 7). Structural attributes have the advantage that they can easily be measured in the field by local communities or assessed using remote sensing techniques. By using remote sensing techniques one can easily scale up field data and produce spatially continuous AGB information over large areas (Baccini *et al.*, 2012), thus providing a better assessment of global carbon storage, deforestation and forest degradation, and providing benchmark maps for REDD+ monitoring, reporting and verification activities. Although remote sensing maps hold great promise, they may fail to capture regional gradients in biomass that are driven by other forest attributes, such as forest height and wood density (Mitchard *et al.*, 2014). By linking field data to structural indices derived from remote sensing, one may map and detect large-scale patterns in AGB while maintaining local realism.

A third implication for REDD+ is that areas with high diversity also tend to have a high biomass (Fig. 7a), indicating that areas with a high carbon storage potential also have a high conservation potential. Moreover, species richness has an independent and positive effect on AGB (Fig. 1b). Species richness may also buffer ecosystem productivity against environmental change (Isbell *et al.*, 2011), and enhance the ecosystem's resilience to disturbance (Diaz *et al.*, 2009). We found that rarefied species richness had a direct effect on forest biomass, despite the very large number of species found in these hyperdiverse tropical forests. The fact that in this study diversity co-determines forest functioning indicates that the conservation of biodiversity should not be considered as a simple co-benefit of REDD+ (Diaz *et al.*, 2009), but as an integral and crucial component of all REDD activities.

CONCLUDING REMARKS

To our knowledge, this is the first study to show the relative importance of environmental conditions and structural and taxonomic attributes for the amount of AGB of highly diverse tropical forests across large spatial scales. AGB is mainly driven by rainfall, followed by structure and species richness. Species richness has an independent positive effect on AGB. From the perspective of REDD+, biodiversity conservation is therefore not only a goal in itself but will also help to increase carbon storage. Hence, conserving biodiversity is a win-win strategy because biodiversity is crucial for forest functioning.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Overview of sites included in the study.

Appendix S2 Extended methods.

Appendix S3 Aboveground plot biomass estimates using the Chave and Brown equations and using different diameter cut-off limits.

Appendix S4 Mixed linear model results of the relationship between aboveground biomass and taxonomical and structural forest attributes at the 0.1- and 1-ha level.

Appendix S5 Strength of the relation between aboveground biomass, species richness and stem density versus annual rainfall of the sites.

Appendix S6 Relationship between cation exchange capacity and rarefied richness, average stem diameter and aboveground biomass.

Appendix S7 Standardized coefficients of the indirect paths in the structural equation model.

Appendix S8 Relationship between average aboveground biomass at a site and annual rainfall.

BIOSKETCH

This data analysis was carried out as a collaborative research effort amongst people involved in the EU-funded ROBIN project (the ROle of Biodiversity In climate change mitigation) and other forest researchers with an interest in the diversity and dynamics of tropical forests. We hope that such a large-scale comparative approach provides a better insight into the functioning of these forests.

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