




Biodiversity and climate determine the functioning of Neotropical forests

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Abstract

Aim: Tropical forests account for a quarter of the global carbon storage and a third of the terrestrial productivity. Few studies have teased apart the relative importance of environmental factors

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and forest attributes for ecosystem functioning, especially for the tropics. This study aims to relate aboveground biomass (AGB) and biomass dynamics (i.e., net biomass productivity and its underlying demographic drivers: biomass recruitment, growth and mortality) to forest attributes (tree diversity, community-mean traits and stand basal area) and environmental conditions (water availability, soil fertility and disturbance).

Location: Neotropics.

Methods: We used data from 26 sites, 201 1-ha plots and >92,000 trees distributed across the Neotropics. We quantified for each site water availability and soil total exchangeable bases and for each plot three key community-weighted mean functional traits that are important for biomass stocks and productivity. We used structural equation models to test the hypothesis that all drivers have independent, positive effects on biomass stocks and dynamics.

Results: Of the relationships analysed, vegetation attributes were more frequently associated significantly with biomass stocks and dynamics than environmental conditions (in 67 vs. 33% of the relationships). High climatic water availability increased biomass growth and stocks, light disturbance increased biomass growth, and soil bases had no effect. Rarefied tree species richness had consistent positive relationships with biomass stocks and dynamics, probably because of niche complementarity, but was not related to net biomass productivity. Community-mean traits were good predictors of biomass stocks and dynamics.

Main conclusions: Water availability has a strong positive effect on biomass stocks and growth, and a future predicted increase in (atmospheric) drought might, therefore, potentially reduce carbon storage. Forest attributes, including species diversity and community-weighted mean traits, have independent and important relationships with AGB stocks, dynamics and ecosystem functioning, not only in relatively simple temperate systems, but also in structurally complex hyper-diverse tropical forests.

KEYWORDS

biodiversity, biomass, carbon, ecosystem functioning, forest dynamics, productivity, soil fertility, tropical forest, water

1 | INTRODUCTION

Across the globe, environmental conditions have strong effects on the diversity and composition of plant communities and ecosystem functioning. Insights into the underlying mechanisms are crucial to understand and predict how ecosystems will respond to climate change. Additionally, ecosystems are also under the control of attributes of the biotic communities, as both biodiversity (Tilman et al., 2001) and biogeography (Horn et al., 2010) can have a strong and direct impact on ecosystem functioning.

To facilitate comparison of disparate ecosystems and improve understanding of ecosystem functioning, functional traits have emerged as a promising tool, because they allow for quantitative expression of plant form and function using the same yardstick (Westoby, 1998). Functional traits are any characteristics that affect the growth, survival and reproduction of organisms, hence the functioning of communities and ecosystems (Garnier et al., 2004). Here we evaluate the relative importance of environmental drivers and forest attributes on ecosystem functioning of 26 Neotropical forests occurring along large-scale environmental gradients. We focus on (a) biomass stocks and dynamics as key ecosystem functions, because biomass to a large extent drives local and global biogeochemical cycles in carbon, nutrients and water (Chapin, Matson, & Mooney, 2011; Lohbeck, Poorter, Martínez-Ramos,

& Bongers, 2015), and on (b) tropical forests because they play a large role in the global carbon cycle (Beer et al., 2010), but we know little about the role of forest attributes on carbon stocks and dynamics in such diverse systems. We analyse biomass dynamics in terms of biomass growth of surviving trees, biomass increase from recruitment of new stems, biomass loss attributable to mortality, and net biomass change.

To understand ecosystem functioning, we use the conceptual framework of Poorter et al. (2015; Figure 1) and expand it to include the effects of community-weighted mean (CWM) functional traits and biomass dynamics. Biomass stocks and dynamics depend on environmental conditions, in terms of resource availability (water, nutrients and light), and on forest attributes, in terms of vegetation quantity and quality (Lohbeck et al., 2015). Vegetation quantity refers to the amount of tissue, such as the photosynthetically active leaf area, present (as indicated by stand basal area) and vegetation quality refers to species diversity and to the 'average' functional traits of the community (the CWM). Disturbances may modify the vegetation quantity, by removing biomass and opening up the forest canopy, leading to an increased light availability, hence enhanced rates of carbon gain in the remaining forest stand (Toledo et al., 2012; Figure 1).

Most of our knowledge on biomass dynamics of tropical forests comes from a network of forest plots in the wider Amazon region (Johnson et al., 2016). In these Amazonian forests, biomass dynamics

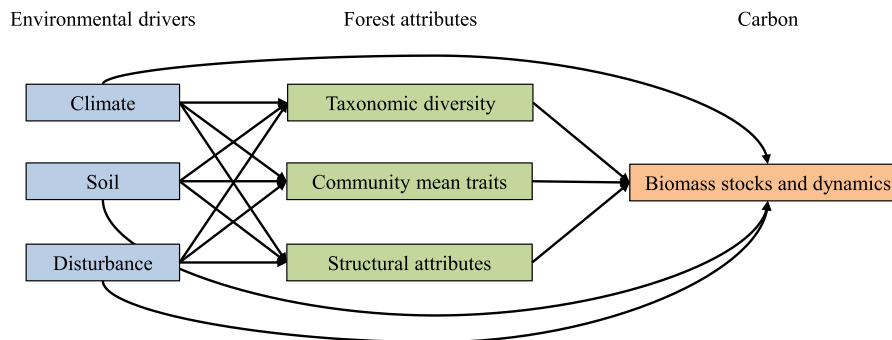


FIGURE 1 Conceptual framework linking environmental conditions and forest attributes to biomass stocks and dynamics

are mainly driven by soil fertility (i.e., phosphorus; Quesada et al., 2012) and associated variation in CWM wood density (WD), with forests on low-fertility soils being dominated by well-defended, long-lived tree species (Galbraith et al., 2013) with high WD (ter Steege et al., 2006), leading to a high standing aboveground biomass (AGB; Baker et al., 2004; Malhi et al., 2006; Quesada et al., 2012). Forests on highly fertile soils, however, show faster biomass dynamics, which seems to be driven more by resource availability than by species traits (Baker et al., 2009). The Amazon is a relatively homogeneous climatic region, and the question is, therefore, whether different relationships emerge when a wider environmental and biogeographical range of lowland Neotropical forests is considered. Along larger gradients, water availability, species richness and different traits (e.g., specific leaf area rather than wood density) may become major drivers of biomass stocks and dynamics.

Species diversity may enhance biomass stocks and dynamics through a variety of mechanisms. For example, niche complementarity or facilitation among species could lead to more efficient resource use and greater biomass growth at the community level (Tilman et al., 2001), and dilution of species-specific pathogens could reduce diseases and increase productivity (Schnitzer et al., 2011). This greater biomass growth may increase biomass stocks over time (Chisholm et al., 2013). A large number of experiments has shown that species diversity indeed enhances productivity (reviewed by Cardinale et al., 2011), but the question is whether the effect is strong enough to be observed in natural ecosystems. It is difficult, however, to assess empirically the independent effect of species diversity on biomass stocks and dynamics in the field, because these variables may respond in a similar way to other drivers, such as environmental conditions. Few studies have simultaneously looked at the independent effects of environmental conditions and diversity on biomass stocks and dynamics. Functional tree diversity increased productivity in climatically harsh boreal forest, but had a weaker effect in climatically more benign temperate forests (Paquette & Messier, 2011), and tree diversity increased biomass growth for four out of 11 European forest types (Vilà et al., 2013). In hyper-diverse tropical forests, diversity might be less relevant because of a saturating effect of diversity, but similar studies have been done only at the local scale (Barrufol et al., 2013; Prado-Junior et al., 2016; van der Sande, Arets et al., 2017; van der Sande, Peña-Claros et al., 2017), only for biomass stocks (Poorter et al., 2015), or have considered only some of the drivers of biomass dynamics (Finegan et al., 2015). Insights into the

mechanisms underlying the effects of climate, diversity and other forest attributes on ecosystem functioning in tropical forests are important to evaluate how ecosystems will respond to climate change, species loss and shifts in species composition.

Here we use dynamic data from >92,000 trees, 201 1-ha plots and 26 sites across the main forest biomes in lowland Neotropics. For each site, we quantified water availability (annual rainfall and climatic water availability), and soil fertility (total exchangeable bases), and for each plot we quantified the CWM of three functional key traits (specific leaf area, wood density and maximal diameter) that are thought to be important for biomass stocks and dynamics (Conti & Díaz, 2013).

The aim of this study is to analyse how environmental conditions and forest attributes drive biomass stocks and dynamics of Neotropical forests (Figure 1). We address two questions. First, how do environmental conditions drive biomass stocks and dynamics? We hypothesize that biomass stocks and dynamics increase with water availability and soil fertility, that biomass dynamics increase but stocks decrease with disturbance, and that biomass stocks and dynamics are more strongly affected by water availability (because this is the main driver of spatial variation in biomass and diversity in the lowlands; Poorter et al., 2015; ter Steege et al., 2003) than by soil fertility. Second, how do vegetation quality (e.g., species richness and functional composition) and vegetation quantity (e.g., basal area) affect biomass stocks and dynamics independent from environmental conditions? We hypothesize that high species diversity enhances biomass stocks and dynamics because of mechanisms such as niche complementarity, facilitation, and dilution of pathogens, and that communities with high values of productivity-related traits (e.g., high CWM specific leaf area) have faster biomass dynamics, whereas communities with conservative trait values (e.g., high CWM wood density) have longer-lived tissues and trees, hence larger biomass stocks.

2 | METHODS

2.1 | Study sites and plots

We used data from 201 1-ha plots in 26 sites distributed across the Neotropics, from Mexico to Brazil (Supporting Information Appendices S1 and S2; for details on plot measurements see Supporting Information Appendix S3). Precipitation ranged from 784 to 3991 mm year⁻¹, and the soil total exchangeable bases from 0.2 to 36.3 cmol+ kg⁻¹. All

plots were located in mature forests, of which 47% had been subjected to timber extraction between 14 and 32 years ago as part of long-term experiments on the effect of logging. We used data coming from two censuses to calculate biomass dynamics. The census period ranged between 4 and 11 years, with an average of 7.9 years. For each plot, a list of variables was calculated representing the different boxes in the conceptual framework in Figure 1.

2.2 | Biomass stocks and dynamics

For each individual tree ≥ 10 cm stem diameter at breast height (DBH, measured at 1.3 m from the ground or above the buttresses) present in the plots in one or two censuses, we calculated AGB using the allometric formula of Chave et al. (2014). The formula needs as input parameter an E value, which is a measure of environmental stress and for each site retrieved from http://chave.ups-tlse.fr/pantropical_allometry/readlayers.r, stem diameter and WD (in grams per cubic centimetre) that was measured at most of the local sites or came from a global WD database (<http://datadryad.org/handle/10255/dryad.235>; Supporting Information Appendix S4). Other life-forms (lianas and palms) were not considered in biomass calculations because they were not consistently measured in all plots. With the AGB at individual stem level, we calculated five variables of biomass stocks and dynamics at the plot level (all in megagrams per hectare per year):

1. Aboveground biomass growth of survivors ($\Delta\text{AGB}_{\text{surv}}$) is the annual increase in biomass of all stems in a plot that survived until the last census. Biomass growth of each stem was calculated as the difference in biomass between the first and last census, divided by the time interval between the two censuses.
2. Aboveground biomass growth of recruits ($\Delta\text{AGB}_{\text{recr}}$) is the annual increment of biomass obtained from trees that were recruited between the first and last census. Biomass of each new stem ≥ 10 cm DBH was calculated as the difference between the biomass when first measured in the last census and the biomass as if the stem had a 10 cm DBH in the first census, divided by the average time between the censuses for that specific plot. This assumes that the tree was recruited immediately after the first census (Talbot et al., 2014).
3. Aboveground biomass loss attributable to mortality ($\Delta\text{AGB}_{\text{mort}}$) is the annual loss of biomass attributable to stems dying between the first and last census. To be consistent with the calculations done for the recruits, the biomass of each dead stem was calculated as the difference between the biomass in the first census (when it was still alive) and the biomass of this stem as if it had a 10 cm DBH, divided by the average time between the first and last census for that specific plot. Note that by calculating mortality from a stem of 10 cm DBH, we allow comparison with recruitment, and in this way the sum of recruitment plus growth minus mortality represents values for net biomass change (cf. Talbot et al., 2014). Mortality was based only on natural tree death, not death because of logging activities or the consequences of these activities.

4. Net AGB change (ΔAGB) is the annual net change in biomass between census 1 and 2. The ΔAGB was calculated as the biomass stock in census 2 minus the biomass stock in census 1, divided by time, because for one site (San Emilio) there were no data on biomass dynamics. For the other sites, we also calculated ΔAGB as the difference between biomass growth ($\Delta\text{AGB}_{\text{surv}} + \Delta\text{AGB}_{\text{recr}}$) and biomass loss ($\Delta\text{AGB}_{\text{mort}}$). Both ways of calculating ΔAGB were highly correlated (Pearson's $r = .96$, $p < .001$, d.f. = 187).
5. Aboveground biomass stock (AGB) is the sum of biomass of all live trees in census 1. In the case of plots that received logging disturbance, we used the pre-logging census to calculate biomass stocks.

For each of these five biomass variables, we developed a separate structural equation model based upon the model shown in Figure 1 (see Table 1 for sample size used for each biomass variable). For several factors in the model, we had multiple possible variables (e.g., multiple traits) that could be used, as described below.

2.3 | Vegetation attributes

For each plot and census, species diversity, CWM traits and vegetation structure were calculated (for an extended description of measurements and calculations, see Supporting Information Appendix S4). For each of these vegetation attributes, the values obtained for the first and second census were averaged to obtain one value per plot that better represents the vegetation attributes during the census period. Vegetation structure was quantified in terms of stand basal area (in square metres per hectare) because this indicates the stand closure, and thus the competition within the forest, and it was an important predictor in other single-site studies (van der Sande, Peña-Claros et al., 2017).

Species diversity was quantified as rarefied species richness because it corrects for the potential for encountering more species in forests with high tree density and because it is related to biomass stocks across Neotropical forests (Poorter et al., 2015). We calculated rarefied species richness as the number of species at a random draw of 200 stems, because this number of individuals was found in all plots.

Regarding CWM traits, the biomass ratio hypothesis of Grime (1998) predicts that ecosystem functions are determined by the trait values of the most dominant species in the community. We focused on three traits, namely specific leaf area (SLA), WD and maximal stem diameter (DBH_{max}), that have been found to affect productivity at the species level (Supporting Information Appendix S5). The central tendency of the trait values can be described with the CWM (the 'average' trait value of individuals in the community). The CWM was calculated by weighting for each species in the plot its functional trait value by its basal area (in square metres per hectare). We weighted by basal area because this scales well with the photosynthetically active leaf area of trees (Shinozaki, Yoda, Hozumi, & Kira, 1964). For a description of trait measurements and the calculation of CWM, see Supporting Information Appendix S4.

2.4 | Environmental variables and disturbance

For climate, we used annual rainfall because this variable was available for all sites and is often important for biomass stocks and dynamics (e.g., Poorter et al., 2015), and climatic water availability (CWA) because this represents potential drought stress. For each site, mean annual rainfall was obtained from the nearest climatological station, based on the coordinates of each plot. The CWA was obtained from http://chave.ups-tlse.fr/pantropical_allometry/readlayers.r (where it is referred to as 'climatic water deficit'). The CWA is the amount of water lost during the dry months (when evapotranspiration exceeds rainfall) and may more accurately reflect drought conditions than total annual rainfall, which can be high because of a few months with excessive rain. The CWA is calculated as the total rainfall minus evapotranspiration during the dry months (when evapotranspiration exceeds rainfall). This number is by definition negative, and water stress increases as CWA becomes more negative; sites with values close to zero are not water stressed.

We used total exchangeable bases (TEB; the sum of base cations Ca^{2+} , Mg^{2+} , K^+ and Na^+ , in centimoles of positive charge per kilogram of soil) as an indicator of soil fertility because it was in part locally available and could otherwise be obtained from the Harmonized World Soil Database (HWSD version 1.2; FAO, IIASA, ISRIC, ISSCAS, & JRC, 2012). Soil data were collected at the plot level in the first 20–30 cm of soil. We used locally available data for 73 of the 201 plots and 12 of the 26 sites, whereas data for the other plots were obtained from the HWSD. We acknowledge that other soil nutrients (e.g., phosphorus, nitrogen) may also be important for biomass dynamics, but unfortunately these data were not collected in a consistent way across sites, nor were they available in global databases.

For the experimental plots that had been logged before the censuses used in these analyses (47% of all plots), we estimated logging disturbance by calculating the percentage of stem basal area removed during the logging plus what was lost through subsequent mortality that occurred as a direct result of the logging disturbance or other silvicultural treatments. Disturbance was thus calculated as the basal area that was removed or died as a percentage of the total pre-logging basal area of the plot.

2.5 | Statistical analyses

To evaluate direct and indirect causal effects of environmental conditions and forest attributes on each of the ecosystem functions presented in Figure 1, we developed structural equation models (SEMs), with plots nested within sites. Biomass growth by recruiting trees and biomass loss attributable to mortality were \log_{10} -transformed to result in normally distributed residuals and equal variances. The number of plots and sites in each SEM varied depending on data availability (see Supporting Information Appendix S6 for sample size).

We considered six possible structural equation models per biomass variable, which resulted from combining three CWM traits (WD, SLA and DBHmax) with two climate variables (rainfall and CWA). Rarefied species richness, basal area, TEB and basal area removed were included

in all models. In some cases, climate has a hump-shaped relationship with vegetation attributes or ecosystem processes. We tested a priori whether hump-shaped relationships needed to be included in the SEMs by relating the forest attributes and biomass variables to rainfall and rainfall squared or to CWA and CWA^2 (Supporting Information Appendix S7). In only one case, we found a significant relationship (between CWA^2 and rarefied species richness), and therefore we did not include the quadratic terms in further SEM analyses. The six models per biomass variable were compared based on the χ^2 statistic for model fit. If the p -value of the χ^2 was $> .05$, then the model was not rejected. If several of the six models were not rejected, then we selected the one with the highest R^2 for the biomass variable because this was our main response variable of interest. To test whether the relationships between rarefied species richness, CWM traits and biomass stocks and dynamics also hold within floristically and environmentally more homogeneous zones, we repeated the same SEMs for (a) old-growth forests versus logged forest, (b) dry forests (precipitation $< 1,700 \text{ mm year}^{-1}$) versus wet forests ($> 1,700 \text{ mm year}^{-1}$), (c) central America versus South America, and (d) within each of seven sites that had > 15 plots, which allowed us to test these relationships.

We evaluated the contributions of biomass recruitment, growth and mortality to ΔAGB using a linear mixed restricted maximum likelihood model, with site as a random variable. The relative contributions of these demographic processes change with the time scale considered. For example, recruitment may contribute little to net biomass change over a time scale of a few years, but more over a time scale of a few decades. Here we assess the contribution of these demographic processes over nearly a decade, thus averaging out the stochastic effects of extreme years. In addition to the SEMs, we evaluated simple bivariate relationships between forest attributes, environmental variables and the biomass variables, using Spearman correlations.

All analyses were performed in R 3.1.2. Correlations were evaluated using the *rcorr* function of the *Hmisc* package, linear mixed models with the *lme* function of the *nlme* package, and structural equation models with the *sem* function of the *lavaan* package (Rosseel, 2012). We corrected for nesting of plots within sites in the SEMs by using the *svydesign* function of the *survey* package (Lumley, 2015) and the *lavaan.survey* function of the *lavaan.survey* package.

3 | RESULTS

To evaluate our conceptual model (Figure 1), we used SEM. We selected one model for biomass stocks and each of the components of biomass dynamics (Figure 2; see Supporting Information Appendix S8 for the results on model selection). The variation explained in biomass dynamics ranged from 13% for net biomass change to 87% for biomass stocks (Figure 2).

Environmental conditions had direct and indirect effects on biomass stocks and dynamics (Figures 2 and 3; Supporting Information Appendix S6). Water availability (as indicated by rainfall or CWA) increased biomass growth (standardized regression coefficient $\beta = 0.36$; Figures 2a and 4a) and AGB ($\beta = 0.48$; Figures 2e and 5b).

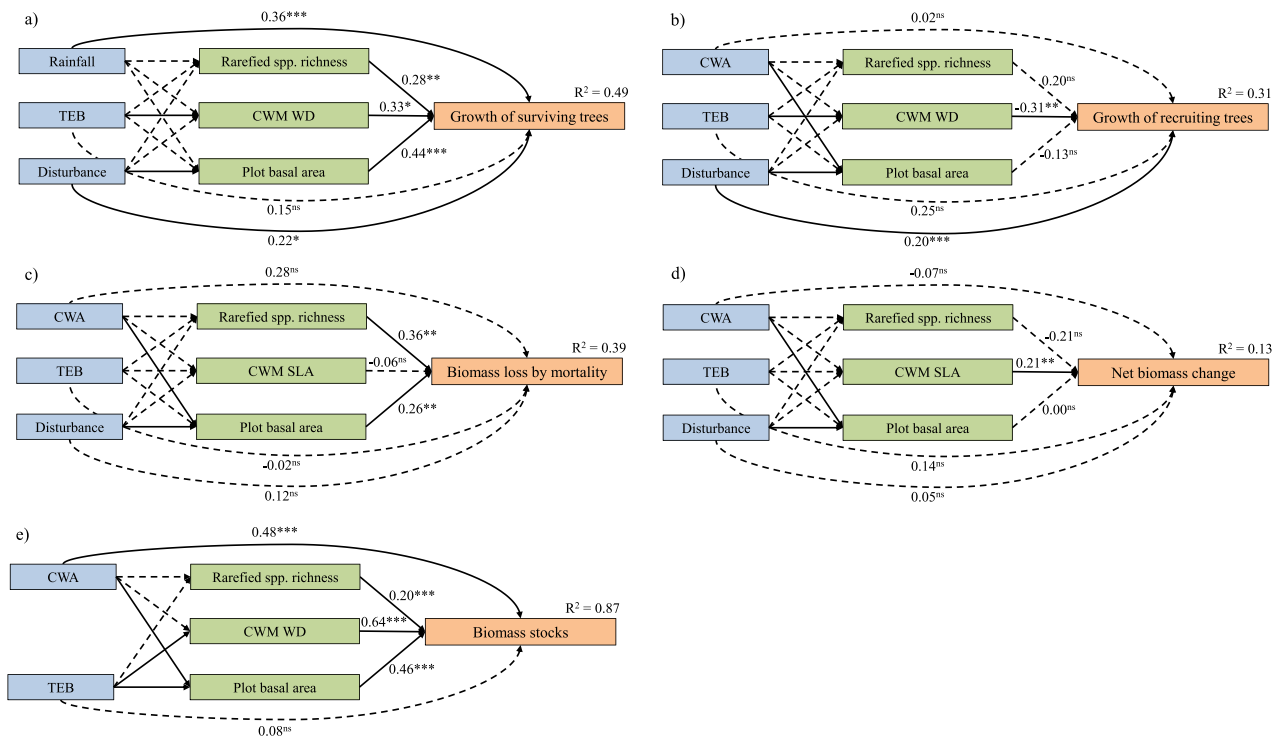


FIGURE 2 Structural equation models for the effects of the environmental variables (climate, soil and disturbance) and vegetation attributes [taxonomic richness, community-weighted mean (CWM) traits and plot basal area] on each of the five ecosystem processes: (a) biomass growth by surviving trees ($\Delta\text{AGB}_{\text{surv}}$), (b) biomass growth by recruiting trees ($\Delta\text{AGB}_{\text{recr}}$), (c) biomass loss attributable to mortality ($\Delta\text{AGB}_{\text{mort}}$), (d) net biomass change (ΔAGB), and (e) aboveground biomass stocks (AGB). Standardized coefficients with significance level (ns = not significant; * $p < .05$; ** $p < .01$; *** $p < .001$) are given for all relationships with the ecosystem process. The standardized coefficients and significance for all other relationships can be found in Supporting Information Appendix S6. Black lines indicate significant effects, whereas dotted lines indicate non-significant effects. Per ecosystem process, the explained variation (R^2) is provided. For statistics of model fit, see Supporting Information Appendix S8. CWA = climatic water availability; SLA = specific leaf area; TEB = total exchangeable bases; WD = wood density

TEB did not have a significant direct effect on any of the biomass variables, but it had a negative indirect effect on biomass growth and stocks through its negative effect on CWM WD (Figure 3; Supporting Information Appendix S6). Additionally, disturbance increased biomass growth ($\beta = 0.22$) and recruitment ($\beta = 0.20$; Figures 2a,b and 4b). All the environmental conditions tested also had indirect effects on all five biomass variables via forest attributes (Figure 2). Bivariate relationships between environmental conditions and biomass stocks and dynamics are shown in Supporting Information Appendix S9.

Forest attributes had generally strong and significant effects on biomass stocks and dynamics, with 10 (67%) from the 15 tested relationships being significant (Figure 2). Species richness was important for three, CWM traits for four, and plot basal area for three biomass variables. Rarefied species richness increased biomass growth, mortality (Figure 4f) and AGB, whereas it tended to increase biomass recruitment and decrease ΔAGB (Figures 2 and 3). Plot basal area increased biomass growth, mortality and AGB. CWM WD had a positive effect on biomass growth and AGB (Figures 2a,e and 5d), whereas it decreased biomass recruitment (Figures 2b and 4e). CWM SLA increased ΔAGB (Figures 2d and 5c). Figures of all bivariate relationships between forest attributes and biomass variables are shown in Supporting Information Appendices S9 and S10.

To test for the generality of the results for smaller geographical areas, we repeated the same SEMs for different subsets of the Neotropical datasets based on biomes, biogeographical zones and logging (analyses shown and discussed in Supporting Information Appendix S11). Sometimes these SEMs confirmed the Neotropical wide pattern; sometimes it was significant for only one of the subsets. When tests were done within each of the seven sites, then the biodiversity and CWM effects were in most cases not significant (Supporting Information Appendix S11).

Across the Neotropical sites, ΔAGB was most strongly predicted by biomass mortality ($\beta = -0.97$, $p < .001$), followed by biomass growth ($\beta = 0.50$, $p < .001$) and not by biomass recruitment ($\beta = 0.06$, $p = .14$).

4 | DISCUSSION

We asked how environmental conditions and forest attributes (vegetation quantity and vegetation quality) drive biomass stocks and dynamics of Neotropical forests, and used structural equation modelling to test for their independent effects. We found the following: (a) biomass stocks and dynamics were more often significantly related to the evaluated forest attributes (significant in 67% of the tested relationships)

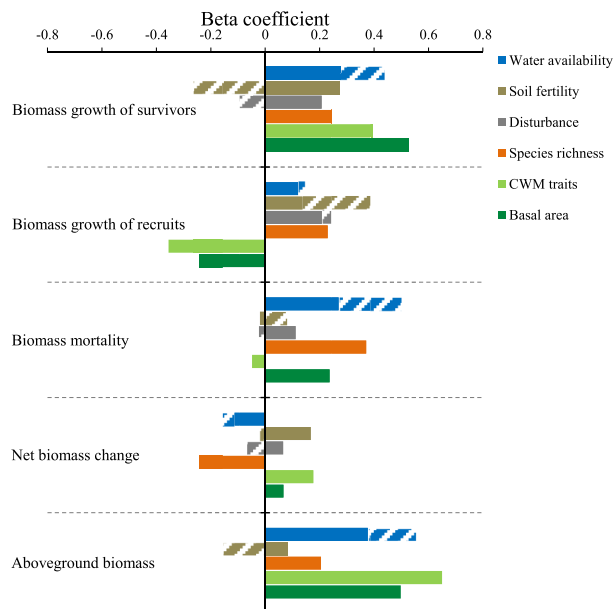


FIGURE 3 Beta coefficients of environmental conditions and forest attributes on biomass stocks and dynamics: growth by surviving trees ($\Delta\text{AGB}_{\text{surv}}$), growth by recruiting trees ($\Delta\text{AGB}_{\text{regr}}$), biomass mortality ($\Delta\text{AGB}_{\text{mort}}$), net biomass change (ΔAGB) and biomass stocks (AGB). The colours represent different environmental conditions or forest attributes: blue = water availability (rainfall or climatic water availability); brown = soil fertility (total exchangeable bases); grey = disturbance; orange = species richness; light green = community-weighted mean (CWM) traits; and dark green = basal area. The filled bars show the direct effects and the hatched bars show the indirect effects of environmental conditions on biomass stocks and dynamics

than to the environmental conditions (significant in 33% of the relationships), although the average standardized effect size of the significant relationships is very similar (0.35 for forest attributes and 0.32 for environmental conditions); (b) water availability and disturbance were the strongest environmental drivers of biomass stocks and dynamics; and (c) rarefied species richness and CWM trait values had consistent significant relationships with biomass stocks and dynamics. These results suggest that large-scale environmental gradients lead to biogeographically and functionally distinct forest communities, with cascading effects on biomass stocks and dynamics. Below we discuss the underlying mechanisms and the implications for the conservation, management and climate change mitigation potential of tropical forests.

4.1 | Abiotic control: rainfall, soil fertility and disturbance

We hypothesized that biomass stocks and dynamics increase with resource availability (water availability, soil fertility and increased irradiance owing to disturbance) and that biomass stocks and dynamics are most strongly affected by water availability (because this is the main driver of spatial variation in biomass and diversity in lowland tropical forests) and to a lesser extent by soil fertility. When significant, water availability indeed increased biomass variables (growth of survivor and

biomass stocks), whereas TEB did not have a significant effect on any of the biomass variables.

High rainfall the year round increases the length of the growing season and the growth of individual trees and stands (Toledo et al., 2012; cf. Figure 2a), resulting in the accumulation of a larger standing biomass over time (Figure 2e; Poorter et al., 2015). Several climate change scenarios predict an increase in the intensity and frequency of droughts, and field studies indicate that such droughts may lead to increased mortality and reduced biomass in the short term (Phillips et al., 2010). Our SEMs indicate that such droughts may also lead to reductions in forest biomass stocks and dynamics in the long term (Figure 2).

Water availability and disturbance affect partly different processes. Water availability is especially important for growth of surviving trees (van der Sande, Zuidema, & Sterck, 2015), because these large trees face higher radiation loads and vapour pressure deficits in the forest canopy, which, in combination with longer hydraulic path lengths, leads to increased drought stress (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015). For recruiting trees, disturbance is important because these small trees are mainly limited by light availability in the lower forest strata. Soil fertility did not increase net biomass change, in contrast to other studies (Quesada et al., 2012). See Supporting Information Appendix S12 for further discussion how water, soil fertility and light disturbance affect biomass dynamics.

4.2 | Biotic control; how does species diversity affect biomass stocks and dynamics?

We hypothesized that high species diversity enhances biomass stocks and dynamics through a variety of mechanisms, such as niche complementarity, facilitation, dilution of pathogens, the selection effect and the insurance effect. Rarefied species richness had a significant, independent and positive relationship with biomass stocks and dynamics, but no significant relationship with net biomass change (Figure 2). Other measures of species diversity, such as species richness or Shannon diversity, had similarly strong correlations with biomass stocks and dynamics (Supporting Information Appendix S13). Clearly, diversity enhances the overall carbon stocks and productivity of the forest, leading to larger biomass dynamics, but also to higher biomass loss attributable to mortality and, for that reason, it does not have a significant effect on net biomass change.

To our knowledge, this is the first large-scale study analysing the relationships between biomass dynamics in tropical forests and its multiple underlying drivers, and the first to demonstrate that species diversity has a strong independent effect on dynamics. Most large-scale studies that looked at diversity effects ignored confounding effects of environment (e.g., Asase, Asitoakor, & Ekpe, 2012; Chisholm et al., 2013) or forest structure (e.g., Baker et al., 2009; Finegan et al., 2015). Poorter et al. (2015) used a similar approach and found a positive effect of tree species diversity on AGB across 59 Neotropical forest sites. A few single-site studies carried out for tropical forests did find a positive and independent effect of species diversity on productivity (Barrufol et al., 2013; van der Sande, Peña-Claros et al., 2017, during succession),

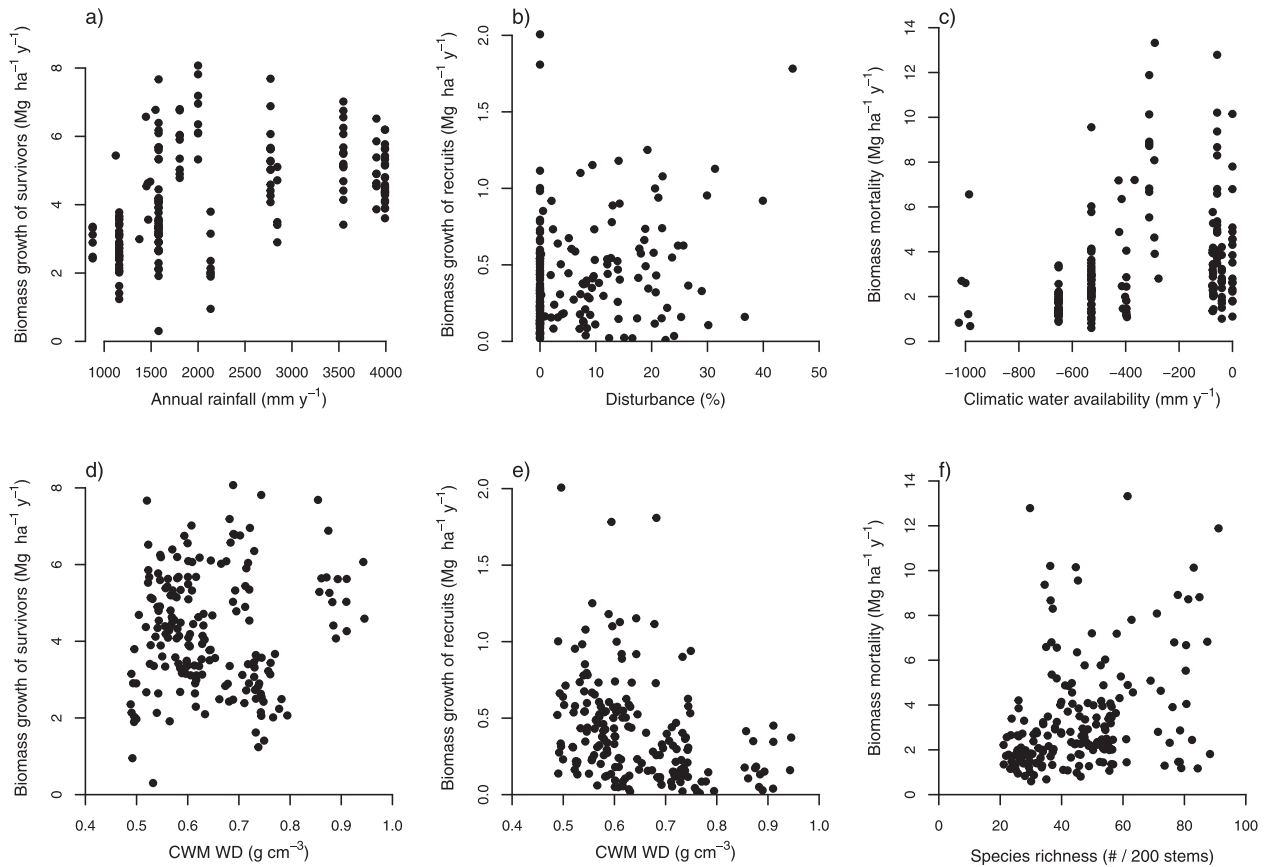


FIGURE 4 Bivariate relationships of one environmental predictor (upper row) and one ‘vegetation quality’ predictor [i.e., species richness or community-weighted mean (CWM) trait values] with biomass growth of surviving trees ($\Delta\text{AGB}_{\text{surv}}$; left column), biomass growth of recruiting trees ($\Delta\text{AGB}_{\text{recr}}$; middle column) and biomass mortality ($\Delta\text{AGB}_{\text{mort}}$; right column). The chosen environmental and vegetation quality variables were the ones that had the strongest effect in the structural equation models (Figure 2a–c). Each dot is a 1-ha plot. WD = wood density. Note that these bivariate relationships are for illustration purposes only and may not necessarily provide the same results as in the structural equation models (Figure 2a–c). For plots of all bivariate relationships tested in Figure 2, see Supporting Information Appendices S9 and S10

whereas other studies did not (Prado-Junior et al., 2016; van der Sande, Arets et al., 2017), perhaps because the range in diversity is smaller within forest sites (van der Sande, Poorter et al., 2017; see also Supporting Information Appendix S14). Our large-scale study shows that the importance of diversity for ecosystem functioning found by experimental studies (van Ruijven & Berendse, 2005) and relatively simple temperate systems (Gamfeldt et al., 2013) can also be extended to hyper-diverse tropical forests.

4.3 | Biotic control; how do CWM traits affect biomass stocks and dynamics?

Most studies assume that relationships between traits and demographic rates observed at the species level should also apply at the community level. We hypothesized, therefore, that communities dominated by productive trait values (e.g., high SLA, low WD) would realize a fast biomass growth, recruitment and ΔAGB , whereas communities dominated by conservative trait values (high WD) would realize large AGB. We indeed found that CWM SLA increased ΔAGB , probably because it increases light capture (Figure 5c; cf. Finegan et al., 2015;

Reich, 2014 for growth of survivors and recruits). We also found that CWM WD increased AGB, either directly because high WD implies more stem biomass per wood volume, or indirectly because WD enhances stem longevity. Other studies also found that regional variation in WD and stem survival have strong positive effects on AGB (Baker et al., 2009; Johnson et al., 2016). Surprisingly, high CWM WD increased the biomass growth of surviving trees (Figures 2a and 4d), which contrasts sharply with studies carried out at the species level, where high WD decreased the stem diameter growth of trees (Poorter et al., 2008; Rüger, Wirth, Wright, & Condit, 2012). Although high WD implies less volumetric growth, this does not mean that it should also lead to less biomass growth, as high WD contributes directly to higher biomass. Also, high stand-level WD indicates that the stand is dominated by shade-tolerant trees, which can be packed at higher densities, leading to higher area-based stand productivity. Finally, an increase in CWM WD decreased the biomass growth of recruits (Figures 2b and 4e), probably because communities dominated by high WD possess trees with longer crowns that cast a deeper shade, leading to less recruitment of small trees into the 10-cm-diameter class (Kunstler et al., 2016).

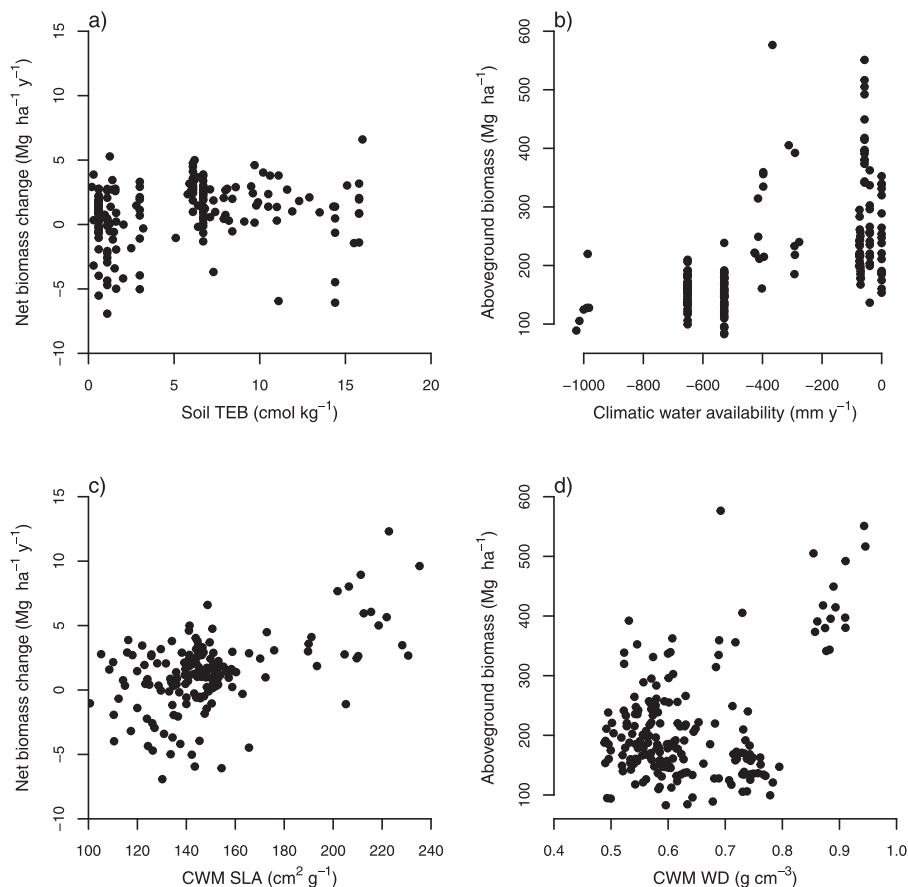


FIGURE 5 Bivariate relationships of one environmental predictor (upper row) and one 'vegetation quality' predictor [i.e., species richness or community-weighted mean (CWM) trait values] with net biomass change (Δ AGB; left column) and biomass stocks (AGB; right column). The chosen environmental and vegetation quality variables were the ones that had the strongest effect in the structural equation models (Figure 2d,e). Each dot is a 1-ha plot. SLA = specific leaf area; TEB = total exchangeable bases; and WD = wood density. Note that these bivariate relationships are for illustration purposes only and may not necessarily provide the same results as in the structural equation models (Figure 2d,e). For plots of all bivariate relationships tested in Figure 2, see Supporting Information Appendices S9 and S10

Other studies also found that current paradigms on trait–rate relationships at the species level can play out differently at the community level, especially when resources become limiting. For example, in tropical dry forests in Brazil (Prado-Junior et al., 2016) or on nutrient-poor soils in Guyana (van der Sande, Arets et al., 2017), conservative CWM trait values (i.e., low SLA) rather than acquisitive trait values increase productivity, and acquisitive CWM trait values (i.e., a higher leaf phosphorus concentration) rather than conservative trait values increase biomass stocks in Guyana. The authors argue that communities dominated by trees with conservative trait values (thick, dense and long-lived leaves) reduce transpiration and enhance the residence time of nutrients in plants. As a result, these communities are more efficient in their water and nutrient use, which enhances their productivity in conditions of limited resources.

The CWM trait values are good predictors of biomass stocks and dynamics (Figures 2 and 3) for several reasons. First, these traits have a direct mechanistic impact on forest functioning, (i.e., they are 'effect traits'). Second, the CWM reflects the traits of the dominant species in the community that have the largest impact on ecosystem productivity and fluxes (cf. Fauset et al., 2015). Finally, these traits also reflect how

species are filtered out by the environment (Figure 2), thus accounting for the indirect effects of abiotic conditions on biomass stocks and dynamics (van der Sande, Arets et al., 2017).

4.4 | Biomass mortality is the strongest predictor of net biomass change but relatively unpredictable itself

To understand net biomass change, we need to understand the underlying demographic processes. Interestingly, Δ AGB was the biomass variable that was least explained by our SEM models ($r^2 = 0.13$, compared with 0.31–0.87 for the other variables of carbon dynamics). The Δ AGB was most strongly driven by biomass mortality ($\beta = -0.97$), followed by biomass growth ($\beta = 0.50$), and not significantly by biomass recruitment. The question then becomes: what drives biomass mortality? Recent studies also show that mortality is the main driver of net biomass change in Bolivia (van der Sande, Peña-Claros et al., 2017) and of stand biomass across the Amazon (Johnson et al., 2016). In our study, biomass mortality did not depend on environmental conditions or on CWM trait values (Figure 2c), which makes it more difficult to model mortality in a mechanistic way. Mortality is an absolute flux rate,

and it increased, therefore, with the biomass of the vegetation (i.e., plot basal area), but also with the species richness, as species-rich forests have high AGB. Johnson et al. (2016) showed that aboveground forest biomass is more strongly driven by the mortality rate of individual trees than by the total biomass they contain. Tree mortality rate is likely to be a major determinant of the size class distribution of tropical forests, which in turn dictates how many trees attain large sizes (Johnson et al., 2016), and it is especially those large trees that determine aboveground forest biomass.

4.5 | Demographic processes are shaped by different drivers

Demographic processes are driven by trees of different sizes that experience different limiting resources and environmental hazards. For example, biomass recruitment is determined by small trees that establish in the understorey or treefall gaps, whereas biomass growth and mortality are mainly driven by tall canopy trees. From the understorey to the canopy, irradiance, temperature, wind exposure and atmospheric water stress increase. Hence, biomass recruitment by understorey trees may be more limited by light (in our case reflected by disturbance; Figure 2b), whereas biomass growth of exposed canopy trees may be more limited by water availability (i.e., rainfall; Figure 2a). Biomass mortality by large canopy trees is driven by strong episodic droughts and stochastic wind disturbances (Bennett et al., 2015), hence it cannot be predicted by the average environmental and trait variables that we considered. Overall, our analysis suggests that tree size and size-dependent processes are important factors shaping biomass dynamics of tropical forests.

5 | CONCLUSIONS AND IMPLICATIONS

We demonstrate that biomass stocks and dynamics of Neotropical forests are under strong control of environmental conditions and, especially, forest attributes. Water availability exerts a strong effect on forest biomass and dynamics, which indicates that forest functioning is sensitive to climate change. Increasing (atmospheric) drought may especially reduce biomass growth of large trees and ultimately carbon stocks. We may have underestimated the role of soil fertility on biomass dynamics, because we used TEB rather than phosphorus or nitrogen availability, which are often the main limiting factors for productivity on old and weathered tropical soils.

Tree species diversity had strong positive relationships with biomass stocks, growth and mortality. As a result, there was no relationship between species diversity and net biomass change, although patterns in net biomass change can also be the result of stochastic mortality during the monitoring period. If our results reflect long-term trends, then this implies that diversity enhances carbon storage and components of productivity but that it does not affect the net carbon sequestration potential. We used SEMs to control, as much as possible, for potentially confounding factors, but correlation does not necessarily mean causation. Controlled experiments and modelling studies (e.g., Maréchaux & Chave, 2017; Sakschewski et al., 2016) are needed to

provide further support for a causal relationship between biodiversity and biomass dynamics in the tropics (van der Sande, Poorter et al., 2017). Biodiversity is more than merely species richness, because it encompasses forest attributes in general. We show that also other forest attributes, such as CWM trait values, are very strong drivers of biomass stocks and dynamics, indicating that biodiversity strongly shapes ecosystem functioning. High tree diversity also makes tropical forests more resilient to climate change (Sakschewski et al., 2016). Biodiversity conservation in the broader sense, including functional attributes, should, therefore, be an integral component for global strategies, such as UN REDD+ and Convention of Biological Diversity.

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DATA AVAILABILITY

Environmental site data can be found in Supporting Information Appendix S1. Data on vegetation characteristics and biomass dynamics can be obtained from the first author upon request.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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