

## RESEARCH ARTICLE

# Environmental, structural, and taxonomic diversity factors drive aboveground carbon stocks in semi-deciduous tropical rainforest strata in Cameroon

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## Abstract

Forest stratification plays a crucial role in the interception of light and plants' photosynthetic activities. However, there is still a lack of information on the contribution of tropical forest stratification to its functioning, despite the increasing number of studies. Here, we analysed from a perspective of the whole tree community (WTC) and forest strata (i.e., large trees, understory trees, and small stems), the relationship between abiotic, biotic factors and aboveground Carbon (AGC). The abiotic factors-AGC relationships were positive for all strata and WTC. However, soil factors-AGC relationship was stronger for small stems and understory, while topography factor-AGC relationship was stronger for large trees and WTC. Tree size inequality-AGC relationship was positive and much stronger for WTC, large trees and small stems. In addition, a species diversity-AGC relationship was found positive only for large trees and WTC. These results highlight the niche complementarity effect for driving positive relationships of species diversity and individual tree size variation with aboveground biomass at large tree strata and WTC. The lack of positive effect of species diversity on AGC for understory and small stems strata might be attributable to the selection effect or resource complementarity among species.

## KEYWORDS

biodiversity, ecosystem functioning, forest strata, soil fertility/texture, topography, tree size inequality

## Résumé

La stratification des forêts joue un rôle très important dans l'interception de la lumière et les activités photosynthétiques des plantes. Mais les informations sur la contribution de la stratification de la forêt tropicale à son fonctionnement font encore défaut, malgré le nombre croissant d'études. Ici, nous avons analysé la relation entre les facteurs abiotiques et biotiques et le carbone aérien (CBA) du point de vue de la communauté entière des arbres (WTC) et des strates de la forêt (c'est-à-dire les

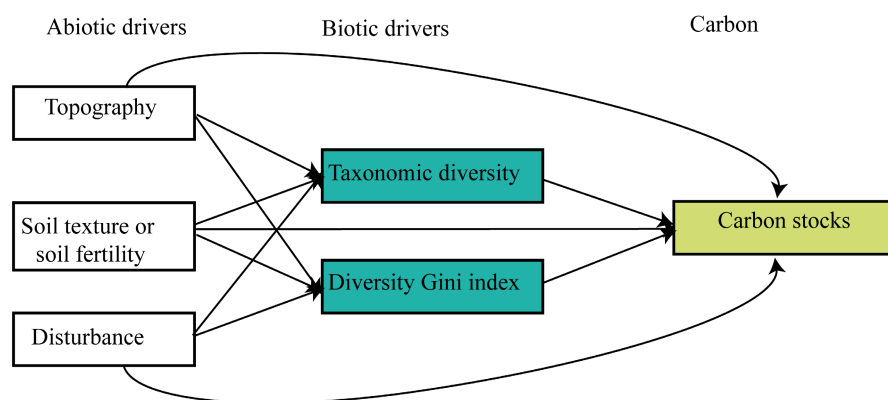
grands arbres, les arbres du sous-étage et les petites tiges). Les relations facteurs abiotiques-AGC étaient positives pour toutes les strates et le WTC. Cependant, la relation facteurs pédologiques-AGC était plus forte pour les petites tiges et le sous-étage, tandis que la relation facteur topographique-AGC était plus forte pour les grands arbres et le WTC. La relation entre l'inégalité de taille des arbres et l'AGC était positive et beaucoup plus forte pour le WTC, les grands arbres et les petites tiges. En outre, une relation entre la diversité des espèces et l'AGC s'est avérée positive uniquement pour les grands arbres et le WTC. Tous ces résultats mettent en évidence l'effet de complémentarité des niches, qui est à l'origine des relations positives entre la diversité des espèces et la variation de la taille des arbres individuels, d'une part, et la biomasse aérienne, d'autre part, au niveau des grandes strates d'arbres et du WTC. Cependant, l'absence d'effet positif de la diversité des espèces sur l'AGC pour les strates de sous-bois et de petites tiges pourrait être attribuée à l'effet de sélection ou à la complémentarité des ressources entre les espèces.

## 1 | INTRODUCTION

Tropical forests are at the center of any current debate on climate change and sustainable forest management because of their dual roles in climate change mitigation and biodiversity conservation (Arasa-Gisbert et al., 2018; Bele et al., 2015; Bodegom et al., 2009; Poorter et al., 2016). It has been shown that biodiversity can enhance forest productivity and carbon storage (Poorter et al., 2017), suggesting that climate change mitigation and biodiversity conservation go hand in hand. Moreover, the forest ecosystem's aboveground carbon pool is critical as it can directly affect carbon fluxes between the atmosphere and the forest ecosystem. Therefore, the accurate estimation of aboveground carbon storage and its drivers would allow the development of effective mitigation strategies against the impact of climate change. The potential for protecting highly diverse and carbon-rich areas of the Congo Basin forest requires a clear understanding of the relationships between carbon storage and biotic and abiotic factors.

Previous studies investigated the simultaneous effects of abiotic (e.g., soil fertility) and biotic (e.g., biodiversity and stand structure) factors on forest functioning based on trees with diameter  $\geq 10$  cm (Borges Silva et al., 2022; Fotis et al., 2018; Poorter et al., 2017; van der Sande et al., 2018; van der Sande, Poorter, et al., 2017), but few have focused on smaller trees and understory

vegetation. Moreover, most of these studies have been realised in Neotropical forests (Chisholm et al., 2013; Poorter et al., 2017; van der Sande, 2016; van der Sande et al., 2018) and subtropical Asiatic forests (Ali et al., 2019; Ali & Yan, 2017). Tropical forests are always structurally complex and composed of plant species with different functional strategies that usually assemble in different vertical layers or forest strata (Rüger et al., 2012; Wright, 2002). The understorey stratum contributes much to most biodiversity and has a higher turnover rate than the overstorey stratum (Ali et al., 2019; Ali & Yan, 2017; Nilsson & Wardle, 2005). Overstorey stratum stores a large amount of aboveground biomass due to their large wood volumes and uneven contribution of large trees to the whole tree community level aboveground biomass (Bastin et al., 2018; Slik et al., 2013). However, understory vegetation grows in lower light levels and may consist of different species compositions. For that reason, processes determining carbon stocks of large trees may not be the same as processes determining carbon stocks of small trees and understory vegetation. Here, we evaluate how abiotic and biotic factors, directly and indirectly, affect independently aboveground carbon stocks of different tree size groups (large trees, understory trees, and small stems) and the whole tree community in a Cameroonian semi-deciduous forest (See conceptual model Figure 1).



**FIGURE 1** Conceptual framework linking abiotic drivers (topography, soil texture/fertility and disturbance) and biotic drivers (taxonomic diversity and diversity Gini index) to aboveground carbon. Disturbance is included as abiotic driver because it affects forest density and light availability.

To understand ecosystem functioning, we follow the conceptual framework (Figure 1) from Poorter et al. (2015) and expand it to include the effect of disturbance. Taxonomic diversity and richness can affect carbon stocks through a variety of mechanisms: (1) niche complementary or facilitation among species is thought to be a key mechanism by which biodiversity affects the rates of resource use that govern the efficiency and productivity of ecosystems (Tilman et al., 2001); (2) the selection effect hypothesis suggesting that diversity effects are caused by a greater chance of one or a few dominant, high biomass species being present in the community (Loreau & Hector, 2001); and (3) insurance effect, where more diverse communities have been shown to have higher and more temporally stable ecosystem functioning than less diverse ones, suggesting they should also have a consistently higher level of functioning over time (Allan et al., 2011).

Besides taxonomic attributes, forest structure, such as stem diameter, tree density, and structural diversity, can determine biomass storage (Ali et al., 2019; Fotis et al., 2018; Poorter et al., 2015). Previous studies have shown that carbon storage in tree aboveground biomass is positively related to stand density (Dimobe et al., 2019; Poorter et al., 2015), basal area (Poorter et al., 2017; van der Sande, Peña-Claros, et al., 2017), and other structural parameters (Dayamba et al., 2016; Mensah, Veldtman, Du Toit, et al., 2016; Michel et al., 2022; van der Sande, Poorter, et al., 2017). In addition, forest structure influences plant light capture and usage (Laurans et al., 2014), thereby shaping aboveground biomass between overstorey and understorey strata. In natural forests, habitat heterogeneity or microsite availability due to different forest layers creates opportunities for infiltration and interception of light, an essential resource for growth (Morin et al., 2011), as it determines the photosynthetic activities of plants at each forest stratum. It has been shown that size inequality conditions or size hierarchy among individual trees greatly influence competition processes in a forest stand. However, other significant components of structural diversity influence, such as spatial heterogeneity or tree size inequality (De Boeck et al., 2006; McElhinny et al., 2005; Pommerening, 2002) on aboveground carbon, have not been studied explicitly (Figure 1).

Local abiotic factors (e.g., climate, soils, and topography) can both directly and indirectly (via biotic factors) affect aboveground biomass (Poorter et al., 2017; van der Sande et al., 2018). For example, steep slopes decrease, and increasing elevation decreases biomass stocks (Gonmadje et al., 2017). Earlier studies in the Congo basin have shown that altitude (Gonmadje et al., 2017), soil nutrients (Doetterl et al., 2015; Fayolle et al., 2012; Lewis et al., 2013), and biotic factors (Bastin et al., 2018; Fayolle et al., 2016; Zekeng et al., 2020) are essential drivers of aboveground biomass. In addition, the spatial heterogeneity and topography at small spatial scales influence soil conditions which also affect aboveground carbon stock. Soil fertility has been shown to positively affect aboveground biomass stocks in tropical forests, such as on the old and leached nutrient-poor soils of the Guiana shield forest

(van der Sande et al., 2018) and the Doume Communal Forest in Cameroon (Zekeng et al., 2020).

Disturbances may modify the vegetation by removing biomass and opening up the forest canopy, leading to the increased availability of light and other resources (Toledo et al., 2012), thereby promoting the growth of understorey vegetation/trees and hence in the long term, overcompensating for the loss in growth from removed trees (van der Sande et al., 2018). Depending on the frequency, intensity, and type, disturbances bring modification in habitat heterogeneity, shifts in competitive balances among species, and the creation of rare habitats, thereby improving species diversity (Chaudhury et al., 2022; Denslow, 1995; Dornelas, 2010; Mouillot et al., 2013). Older and larger trees should dominate where disturbance is occasional, reducing small trees' growth rates and survival probability and leading to more biomass allocated to fewer stems (Holm et al., 2014; Lewis et al., 2013).

This study aims to analyse the relative independent effects of abiotic and biotic factors on aboveground carbon stocks across tree strata: small stems (<5 cm DBH), understorey trees (10 > cm DBH < 5), large trees (>10 cm DBH), and the whole tree community. We address two questions. Question 1: how do species diversity and tree size inequality (Diversity Gini Index) influence the carbon stocks of each stratum and the whole tree community? We hypothesize that high species diversity positively affects carbon stocks (through niche complementarity, the selection effect, or the insurance effect) carbon stocks. We also hypothesize that AGC decreases with tree size inequality. Question 2: how do abiotic conditions influence AGC directly and indirectly via species diversity and tree size inequality? We hypothesize that AGC increases with soil fertility/texture and that the AGC of each stratum or the whole tree community is most strongly and positively affected by topographic factors. We also hypothesize that long-time disturbance will decrease AGC trees' with DBH ≥ 5 cm while increasing carbon stocks of small stems.

## 2 | MATERIAL AND METHODS

### 2.1 | Research site

The research was carried out in the moist, semi-deciduous forest of Doume Communal, eastern Cameroon (4°31'0" S, 13°47'5" W). The mean annual temperature is 25°C, and annual rainfall varies between 1300 and 1800 mm, with a dry season from November until March. The forest is located on ferralitic red, loose, and permeable soils. These soils are poor in nutrients, acidity, and fragile. In the shallows, the soils are hydromorphic to gley. Topographically, the forest is uneven, with low hills interspersed with small well-marked streams or swampy, sometimes vast depressions (several hundred meters) without a specific watercourse (Anonymous, 2015). The altitude varies from 605 to 760 m, with some marked summits culminating at less than 700 m.

## 2.2 | Sampling plots and sample design

Previous studies using remote sensing and geographical information systems defined the land use and land cover type in the study site (Zekeng et al., 2019). As a result, it allowed us to choose to work only on the terra-firme forest while avoiding rivers and swampy vegetation types. Thirty 1-ha (100×100m) plots were set up in the Doume Communal forest across four villages. The 1-ha plots were subdivided into 25 20×20m subplots. In the whole 1-ha plot, trees ≥10 cm diameters at breast height (DBH) (hereafter 'large trees'), and in 13 subplots, trees with DBH between 5.0 and 9.9 cm (hereafter 'understorey trees') were identified and measured. In addition, in the subplots situated in the four corners and the center of each 1-ha plot, a quadrat of 5×5 m was installed to inventory trees between 1.0 and 4.9 cm diameter at 30cm aboveground (hereafter 'small stems'). Hence, in total per 1-ha plot, we sampled all trees ≥10 cm DBH, while understorey trees were sampled in 13 subplots of 20×20m representing 5200m<sup>2</sup>, and small stems were sampled in 5 subplots of 5×5 m representing 125m<sup>2</sup>. More information on forest inventory and environmental factors in this forest are already published (Zekeng et al., 2020, 2021, 2022).

## 2.3 | Carbon stock estimation

We calculated carbon stocks of the whole tree community (all trees ≥1 cm diameter) and the different tree size groups (i.e., small stems, understorey trees, and large trees). Their biomass was converted to carbon using conversion factors according to the recommendation of IPCC (2006): a conversion factor of 0.47 (Thomas & Martin, 2012), widely used in the literature review.

Large and understorey trees were measured at 1.3 m breast height or, if applicable, 50cm above the top of the buttresses or 2 cm above the deformity (Condit, 1998), while small stems were measured at 0.30m aboveground level. We calculated aboveground biomass (AGB) for large and understorey trees using Equation (1) of Chave et al. (2014) but see Réjou-Méchain et al. (2017). The aboveground biomass of small stems was computed using Equation (2) developed by Djomo and Chimi (2017).

$$AGB = \exp \left[ -2.024 - 0.896E + 0.920 \ln(WD) + 2.795 \ln(DBH) - 0.0461 [\ln(DBH)]^2 \right] \quad (1)$$

$$AGB_{\text{small stems}} = \exp \left[ -2.026 + 2.101 \times \ln(D) + 0.635 \times \ln(WD) \right] \quad (2)$$

where E is a measure of environmental stress of the site, which depends on temperature seasonality and water deficit and is extracted from [http://chave.ups-tlse.fr/pantropical\\_allometry/readlayers.r](http://chave.ups-tlse.fr/pantropical_allometry/readlayers.r) with the retrieve\_raster function in R. DBH is the diameter at breast height (cm), and WD is the wood density (gcm<sup>-3</sup>). WD was based on local wood density if available and otherwise on wood density obtained from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009).

Species-level WD was used for 61.5% of plots species, while genus or family-average per plot was used for 31.9% of species. We used WD averaged per plot for the few cases (46 species) without genus- or family-level WD (5.6%).

## 2.4 | Taxonomic diversity

For the whole tree community and each tree's size groups per 1-ha plot, three species diversity measures were computed (Appendix S1–S7): species richness (number of species per plot), rarefied species richness, and Shannon-Weaver index (Shannon & Weaver, 1949). Rarefied species richness is the number of species observed when a fixed number of trees are randomly drawn from a plot, therefore removing the confounding influence of tree density on species richness (Poorter et al., 2017). We calculated rarefied species richness here as the number of species at a random draw of 469 stems for the whole tree community, 458 stems for large trees, 62 stems for understorey trees and 10 for small stems, as these numbers of individuals were found in all 1-ha plots according to the sampling design. The Shannon-Weaver index required species abundance and was calculated as follows:

$$H = - \sum_{i=1}^S p_i \ln(p_i), \quad (3)$$

where  $p_i$  is the proportion of individuals belonging to the  $i^{\text{th}}$  species found in a sample. The calculations were done using the R package vegan (Oksanen et al., 2018).

## 2.5 | Structural diversity

This study aimed to determine the relative strength of structural diversity (Gini index) in determining carbon stocks. Previous studies have highlighted that forest structure as tree density (e.g., Lewis et al., 2013; Poorter et al., 2015; Zekeng et al., 2020) and basal area (van der Sande, Peña-Claros, et al., 2017; van der Sande, Poorter, et al., 2017) drive biomass, and hence in this study, we decided to test the effect of tree size inequality in carbon stocks using the Gini index. Indeed, several authors recently advocated that the Gini index is continuous and more directly related to size hierarchy and thus better linked to asymmetric competition between trees (Cordonnier & Kunstler, 2015). In addition, several studies indicated that it performs better in discriminating stands of different diameter distributions (Lexerød & Eid, 2006; Valbuena et al., 2012). It is, therefore, a good parameter to address the effects of stand inequality on stand productivity. The Gini measures the inequality among values of tree size distribution. A Gini of zero expresses perfect equality, while a Gini of 1 expresses maximal inequality (i.e., high structural diversity) among the tree size distribution (Weiner & Solbrig, 1984). In practice, the values of Gini index observed for the distribution of individual tree basal areas in forest stand of more than 0.25 ha are

often between 0.2 and 0.7 (Duduman, 2011). The Gini index was quantified using equation (4) below (Cordonnier & Kunstler, 2015; Damgaard & Weiner, 2000; Duduman, 2011):

$$\text{Gini} = 2 \frac{\sum_{i=1}^n ig_i}{nG} - \frac{n+1}{n} \quad (4)$$

where  $g_i$  is the basal area of tree  $i$  (trees are sorted in ascending order),  $G$  is the total basal area, and  $n$  is the number of trees.

## 2.6 | Soil properties, topography, and logging disturbance

The plots are situated in the region where the topography is slightly uneven with a succession of low hills with generally gentle slopes (0.00%–14.91%) interspersed with small well-marked streams and fine-scale variation in soil conditions. Therefore, per the 1-ha plot, five sampling points were used: one towards the four corners and one towards the center of the plot. More details about the collection and analyses of soil variables can be found in supporting information S1. Per sampling point, soil samples were taken between 0 and 20 cm for bulk density, texture, moisture content (MC), cations exchange capacity (CEC), and concentrations of carbon, total nitrogen ( $N_{\text{soil}}$ ), available phosphorus ( $P_{\text{soil}}$ ), and the ratios between carbon and nitrogen ( $C:N_{\text{soil}}$ ) and nitrogen and phosphorus ( $N:P_{\text{soil}}$ , Appendix S2).

This study used four topographic variables: elevation, slope, curvature, and aspect. Elevation was recorded throughout each 1-ha plot, at the four corners and the center and used to calculate topographic variables at the 1-ha scale. Mean elevation was calculated as the mean of the elevation measurements at the four corners and the center of a one ha plot. The slope was calculated as the average angular deviation from the horizontal of each of the four triangular planes formed by connecting three of its four corners. Aspect is the direction of the slope faces, and  $\cos(\text{aspect})$  and  $\sin(\text{aspect})$  were calculated to make aspect data usable in linear models (Baldeck et al., 2013; Wang et al., 2017). Elevation and slope variables were obtained during forest inventory using GPS and clinometer, respectively, while the two other topographical variables were derived using ArcMap 10.1.

We found that some plots had been disturbed by logging during field inventory, which occurred 20 years ago, and hence we could not directly account for the tree damage due to logging. Therefore, to take into account the entire disturbance (i.e., logging + damage), we measured the stumps of trees logged which were still present in the field and quantified it basal area using the empirical relationship equation:  $\alpha_B = 0.01439 \times \exp^{(0.1829 \times N_{\text{log}})}$  (Durrieu de Madron et al., 1998 but see Picard et al., 2012), where  $\alpha_B$  is the proportion of damaged basal area and  $N_{\text{log}}$  the number of trees logged. Logging disturbance was computed as a continuous disturbance variable because logging disturbance depends on the distribution and density of commercial species and is therefore not evenly distributed in space and not varies strongly within the plot and between plots (Appendix S3). The relative logging disturbance (in %) was computed

per ha, based on the basal area of all the stumps trees that were logged + damaged basal area divided by the total pre-logging basal area of the plot.

## 2.7 | Statistical analyses

Structural equation modelling (SEM) offers the possibility to test multivariate and hierarchical direct and indirect relationships among the measured variables (Shipley, 2016). Because we could also have many interactions among the predictive variables (e.g., the topographic variables can influence soil texture or soil fertility), we limited the number of possible models and the number of explanatory variables per model by evaluating only the framework corresponding to our a priori, as simple as a possible hypothesis (see Figure 1).

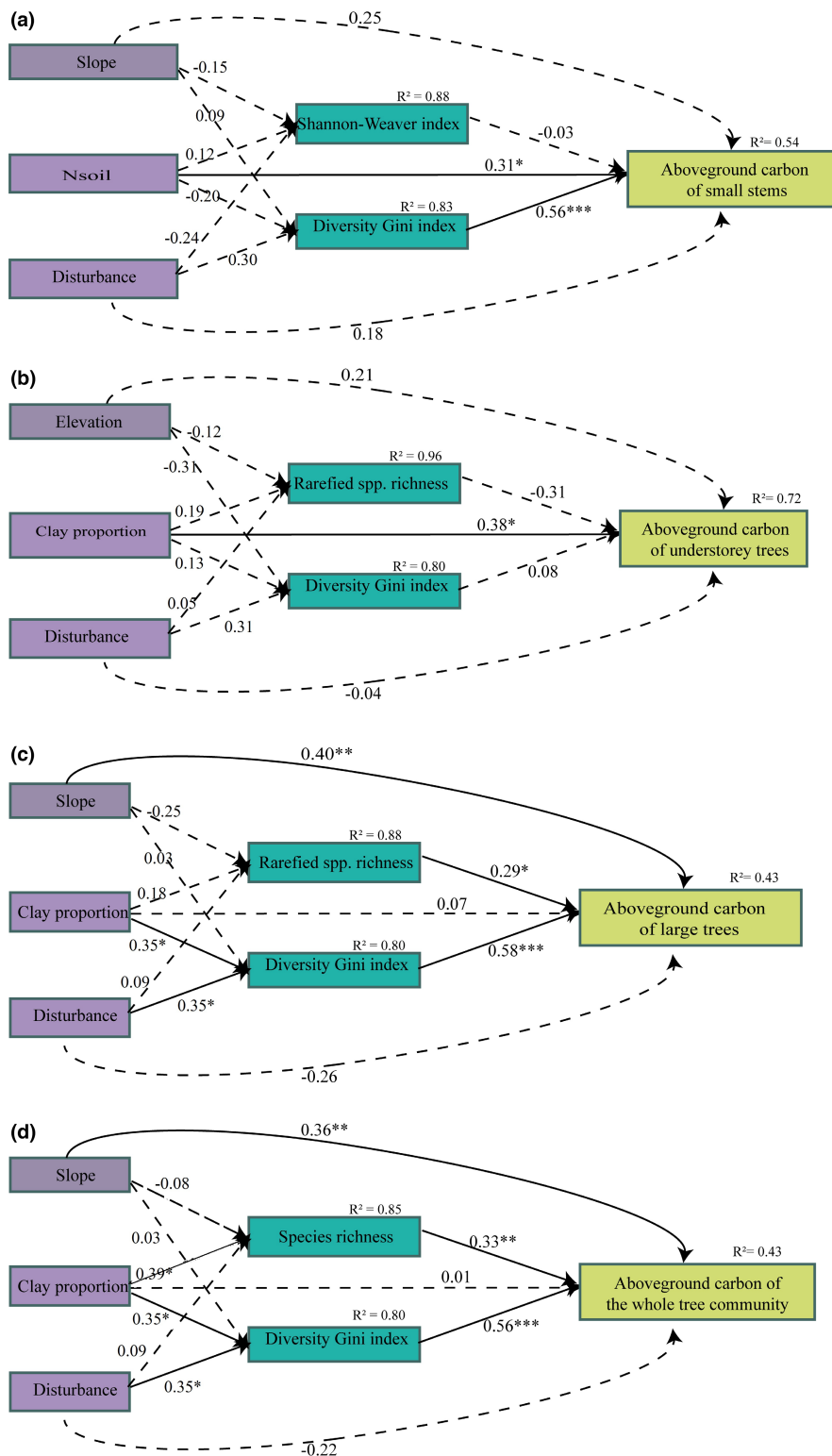
Because we had multiple indicator variables for abiotic conditions (i.e., soil and topographic variables; Appendix S2) and taxonomic diversity, we first performed subsets regression analyses (Supporting information S2), including all topographic, soil fertility/texture, and taxonomic as the predictor variable and aboveground carbon stocks as a response variable. However, we also included disturbance and diversity Gini index in subsetting analyses to have their relative importance. From these results, we selected one for topographic and taxonomic variables or two variables for soil (i.e., one textural and one fertility variable) with the highest relative importance value (see Appendix S4). Soil variables were represented by soil texture (i.e., the proportion of clay, silt, and sand) and soil fertility (i.e., CEC,  $C:N_{\text{soil}}$ , EC, MC,  $N:P_{\text{soil}}$ ,  $N_{\text{soil}}$ ,  $P_{\text{soil}}$ , pH), topography was represented by five variables (sine and cosine of aspect, elevation, terrain curvature, and terrain slope), and taxonomic diversity was represented by three variables (richness, rarefied species richness, and Shannon-Weaver index). Disturbance and structural diversity were included in all SEMs. Then per carbon stock variable, several SEMs were tested, from which we selected the SEM with the highest explained variation ( $R^2$ ) of the carbon stocks. The overall fit of the SEMs was assessed using  $\chi^2$ -test (a  $p$ -value  $> 0.05$  would indicate an absence of significant deviations between data and model, and means that the model is not rejected). In addition to the SEMs, simple bivariate relationships between biotic, abiotic factors, and the carbon stocks variables using Spearman correlations showed no collinearity between each group of factors (Appendix S5 and S6).

All analyses were performed in R 3.5.1. 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).

## 3 | RESULTS

Only one model per carbon stocks variable was selected that was accepted by the Chi-square test and had the highest  $R^2$  for aboveground carbon stock (Figure 2; Table 1; see Appendix S7). The





**FIGURE 2** Structural equation models for the effects of the abiotic (i.e., topographic variables, soil fertility/texture and disturbance) and biotic variables (i.e., taxonomic richness and diversity Gini index) on aboveground carbon stocks of the small stems (a), of the understory trees (b), of the large trees (c) and of the whole tree community (d). All four SEMs models selected were accepted (Appendix S7). For all significant relationships (continuous black lines), the standardised regression coefficients and significance level are given only for direct relationships (\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ), and for all non-significant relations (black, dashed lines), no statistics are shown.  $R^2$  values show the explained variance of the biotic factor and carbon stocks. More statistics of the structural equation model can be found in Table 1.

variation explained in carbon stocks ranged from 43% for the whole tree community to 72% for understory trees (Figure 2).

Different abiotic and biotic variables were selected per tree size group and the whole tree community in the SEMs. As a taxonomic diversity variable, the Shannon-Weaver index was selected for aboveground carbon (AGC) of small stems, rarefied species richness for AGC of understory and large trees, and species richness for AGC of

the whole tree community. Elevation was selected as a topographic variable influencing carbon stocks of understory trees, and the terrain slope was selected for the two other tree size groups and the whole tree community. For soil variables, clay proportion was selected for AGC of the whole tree community and all tree size groups, except for small stems where Nsoil was selected (see Appendix S4 for results of all subsets regression analyses).

**TABLE 1** The direct and indirect standardised effects of abiotic and biotic factors on aboveground carbon of all tree size classes (i.e., small stems, understorey trees and large trees) and the whole tree community level based on structural equation models (SEM; Figure 2).

SEM response variable	SEM predictor variable	Coeff	Std.Coeff	z-Value	p-Value
Small stems					
Aboveground carbon (AGC)	Slope	0.03	0.25	1.69	0.092
	Nsoil	<b>1.07</b>	<b>0.31</b>	<b>2.02</b>	<b>0.044</b>
	Disturbance	0.03	0.18	1.20	0.232
	Shannon-Weaver index	-0.04	-0.03	-0.22	0.825
	<b>Diversity Gini index</b>	<b>2.56</b>	<b>0.56</b>	<b>3.80</b>	<b>0.000</b>
Shannon-Weaver index	Slope	-0.02	-0.15	-0.80	0.425
	Nsoil	0.35	0.12	0.64	0.520
	Disturbance	-0.03	-0.24	-1.38	0.167
Diversity Gini index	Slope	0.00	0.09	0.49	0.621
	Nsoil	-0.16	-0.20	-1.12	0.263
	Disturbance	0.01	0.30	1.81	0.070
$R^2$ AGC		0.54			
$R^2$ Shannon-Weaver index		0.88			
$R^2$ Diversity Gini index		0.83			
Understorey trees					
Aboveground carbon	Elevation	0.01	0.21	1.09	0.277
	<b>Clay proportion</b>	<b>0.07</b>	<b>0.38</b>	<b>2.30</b>	<b>0.022</b>
	Disturbance	-0.01	-0.04	-0.23	0.821
	Rarefied species richness	-0.06	-0.31	-1.96	0.050
	Diversity Gini index	4.95	0.08	0.42	0.672
Rarefied species richness	Elevation	-0.02	-0.12	-0.67	0.506
	Clay proportion	0.17	0.19	1.05	0.295
	Disturbance	0.09	0.05	0.27	0.784
Diversity Gini index	Elevation	0.00	-0.31	-1.83	0.068
	Clay proportion	0.00	0.13	0.77	0.440
	Disturbance	0.01	0.31	1.87	0.061
$R^2$ AGC		0.72			
$R^2$ Rarefied species richness		0.96			
$R^2$ Diversity Gini index		0.8			
Large trees					
Aboveground carbon	<b>Slope</b>	<b>5.22</b>	<b>0.40</b>	<b>3.20</b>	<b>0.001</b>
	Clay proportion	0.52	0.07	0.53	0.596
	Disturbance	-3.66	-0.26	-1.91	0.056
	<b>Rarefied species richness</b>	<b>1.12</b>	<b>0.29</b>	<b>2.24</b>	<b>0.025</b>
	<b>Diversity Gini index</b>	<b>868.59</b>	<b>0.58</b>	<b>4.27</b>	<b>0.000</b>
Rarefied species richness	Slope	-0.82	-0.25	-1.42	0.155
	Clay proportion	0.34	0.18	1.03	0.305
	Disturbance	0.77	0.21	1.21	0.227
Diversity Gini index	Slope	0.00	0.03	0.19	0.846
	<b>Clay proportion</b>	<b>0.00</b>	<b>0.35</b>	<b>2.12</b>	<b>0.034</b>
	<b>Disturbance</b>	<b>0.00</b>	<b>0.35</b>	<b>2.11</b>	<b>0.035</b>
$R^2$ AGC		0.43			
$R^2$ Rarefied species richness		0.88			

(Continues)

TABLE 1 (Continued)

SEM response variable	SEM predictor variable	Coeff	Std.Coeff	z-Value	p-Value
$R^2$ Diversity Gini index		0.8			
Whole tree community					
Aboveground carbon	<b>Slope</b>	<b>4.67</b>	<b>0.36</b>	<b>3.02</b>	<b>0.003</b>
	Clay proportion	0.06	0.01	0.06	0.951
	Disturbance	-3.12	-0.22	-1.69	0.091
	<b>Species richness</b>	<b>0.91</b>	<b>0.33</b>	<b>2.60</b>	<b>0.009</b>
	<b>Diversity Gini index</b>	<b>838.00</b>	<b>0.56</b>	<b>4.23</b>	<b>0.000</b>
Species richness	Slope	-0.36	-0.08	-0.44	0.657
	<b>Clay proportion</b>	<b>1.05</b>	<b>0.39</b>	<b>2.29</b>	<b>0.022</b>
	Disturbance	0.45	0.09	0.51	0.611
Diversity Gini index	Slope	0.00	0.03	0.19	0.846
	<b>Clay proportion</b>	<b>0.00</b>	<b>0.35</b>	<b>2.12</b>	<b>0.034</b>
	<b>Disturbance</b>	<b>0.00</b>	<b>0.35</b>	<b>2.11</b>	<b>0.035</b>
$R^2$ AGC		0.43			
$R^2$ Species richness		0.85			
$R^2$ Diversity Gini index		0.80			

Note: The path coefficients (Coeff), standardised path coefficients (Std. coeff), Z-values and p-values are given for all regressions (i.e., all arrows in Figure 2). All four models were accepted ( $p = 0.06, 0.14, 0.59, 0.10$  and  $\chi^2 = 3.65, 5.40, 0.29, 2.64$  for aboveground carbon of small stems, understorey trees, large trees and the whole tree community, respectively; Appendix S7). Significant effects are indicated in bold ( $p < 0.05$ ).

Biotic factors had generally strong and significant effects on AGC stocks, with 5 (63%) from the eight tested relationships being significant (Figure 2; Table 1). In addition, the effects of taxonomic diversity were significant and positive on AGC of both large trees ( $\beta = 0.29$ ;  $p = 0.03$ ; Figure 2c) and of the whole tree community ( $\beta = 0.33$ ;  $p = 0.009$ ; Figure 2d), while effects of tree size inequality (Gini index) was significantly positive for all AGC stocks except AGC of understorey trees (Figure 2b).

Abiotic factors had direct and indirect effects on AGC stocks (Figure 2; Table 1). The terrain slope had a direct and significant positive effect only on AGC of large trees ( $\beta = 0.40$ ;  $p = 0.001$ ) and the whole tree community ( $\beta = 0.36$ ;  $p = 0.003$ ). On the other hand, elevation had a direct and non-significant positive effect on AGC of understorey trees ( $\beta = 0.21$ ). Moreover, via taxonomic diversity, it was found that AGC of the whole tree community, large trees, and small stems decreased with the increase of terrain slope while AGC of understorey trees increased with the increase of elevation. Contrary to taxonomic diversity via the tree size inequality, it was found that AGC of the whole tree community and all tree size classes except for understorey trees increased with the increase of terrain slope while AGC of understorey trees decreased with the increase of elevation (Table 1).

For soil variables, we found that Nsoil had a significant direct and positive effect on AGC for small stems ( $\beta = 0.31$ ;  $p = 0.04$ ; Figure 2a). Soil texture (Clay proportion) had a direct and significant positive effect on AGC of understorey trees ( $\beta = 0.38$ ;  $p = 0.02$ ). Except on AGC for small stems, we found that clay proportion increased AGC stocks via taxonomic diversity. The same patterns were also found for the tree size inequality effect (Figure 2a; Table 1). The results showed that the effects of clay proportion were significant and positive via species richness only on AGC for the whole tree community

(Figure 2d; Table 1) and via tree size inequality on AGC of large trees and the whole tree community (Figure 2c,d; Table 1). Indeed, for the indirect effects of Nsoil on AGC for small stems, opposite patterns were observed as AGC increased when Nsoil increased via the Shannon-Weaver index while it decreased when Nsoil increased via tree size inequality (Figure 2; Table 1).

We did not find any significant direct effect of logging disturbance on the AGC (Figure 2; Table 1). More specifically, when its intensity increased directly, it was found out that AGC stocks for understorey trees ( $\beta = -0.04$ ), large trees ( $\beta = -0.26$ ), and the whole tree community ( $\beta = -0.22$ ) decreased (Figure 2b-d; Table 1). However, it was also found that AGC of small stems increased with increasing disturbance intensity (Figure 2a; Table 1). However, it indirectly increased the AGC of large trees and the whole tree community through tree size inequality and taxonomic diversity (Figure 2c,d; Table 1).

## 4 | DISCUSSION

Our study explores the relationship between disturbance, abiotic factors, species diversity, tree size inequality, and AGC from a perspective of the WTC and forest strata (large trees, understorey trees, and small stems). We found that abiotic factors-AGC relationships were positive for all strata and WTC. Still, soil factors-AGC relationship was stronger for small stems and understorey, while topography factor-AGC relationship was stronger for large trees and WTC. Species diversity-AGC relationship was positive only for large trees and WTC. In addition, tree size inequality factor-AGC relationship was positive for each stratum and the WTC but highly stronger for WTC, large trees and small stems.



#### 4.1 | Species diversity increases carbon stocks

The species diversity-AGC positive relationship for large trees and WTC found in this study supports the idea that increased diversity enhances forest functions (Forrester & Bauhus, 2016; Wang et al., 2011). This can be attributed to the complexity and heterogeneity of tropical forests (structural variation, tree size inequality, and multiple canopy strata), which allow for greater light interception and efficient use of resources by plants, resulting in increased AGC. The benefits of plant-plant interactions such as facilitation may also explain these results. Hence, some species could enhance soil fertility for the productivity of other species. But it might also be well possible that increasing species richness increases the chances of highly productive favoured dominant species (Ruiz-Benito et al., 2014). To our knowledge, this is the first local scale study analysing the relationship between carbon stocks across tree size groups and the whole tree community of Cameroonian tropical rainforest and its multiple underlying drivers. Most empirical studies that have examined the effects of diversity on forest carbon or productivity have ignored the impact of forest structure and the environment (but see Day et al., 2013). The significant positive effects species richness on aboveground carbon stocks of the large trees and the whole tree community found in this study have also been reported in several local and global tropical forest ecosystems (Cavanaugh et al., 2014; Con et al., 2013; Day et al., 2013; Poorter et al., 2017; van der Sande et al., 2018).

We found negative effects of species diversity on AGC in the understorey and small stem strata, which might be attributable to the developmental effect of tree species (Ali & Yan, 2017). Indeed, these strata include shrub species and regeneration of canopy tree species, which are functionally different in coping with biotic interaction and resource competition. Although the regeneration of trees could have a more diverse ecology than developed trees, as trees grow, they may experience varying environmental conditions or pre-programmed ontogenetic switches, which can induce concomitant changes in tree structure and function (Meinzer et al., 2011). Therefore, the mixture effects of development or life stage and a high degree of environment interaction and resource heterogeneity may also explain the negative relationships between species diversity and AGC for these strata. In addition, tree species in large tree strata with high AGC and great tree size may consume a large part of the resource, thus probably reducing resource availability to understorey and small stem species (Mason et al., 2011).

#### 4.2 | Structural diversity increased aboveground carbon stocks

We found a significant positive effect of the tree size inequality on aboveground carbon stocks of the whole tree community, large trees, and small stems. Strong layering within the canopy can more efficiently fit high amounts of biomass in the same area when structural diversity is high. Also, high structural diversity may indicate the presence of some large trees that contribute disproportionately

to forest biomass and carbon. This is confirmed by an earlier study in this forest, which showed that aboveground carbon in the whole tree community and the large tree group is strongly driven by big-diameter trees (Zekeng et al., 2020). Moreover, with dynamic perspectives and integration management actions, some studies have proved that high tree size inequality is not incompatible with wood production and economic returns (Buongiorno et al., 1994; Lafond et al., 2015). Furthermore, it has been shown that tree size inequality benefits several essential components of biodiversity of forest ecosystems, such as understory vegetation cover and composition, bird diversity, and forest regeneration (Buongiorno et al., 1994; Király & Ódor, 2010). Integrating all these components to find an optimal balance between ecosystem services in the long term is still an avenue of research.

#### 4.3 | Topography, soil conditions, and disturbance shape aboveground carbon stocks

The positive effect of slope on AGC of large trees and the whole tree community showed evidence that differences in AGC stocks can result from topological constraints, particularly differences in terrain slope (Chave et al., 2003; de Castilho et al., 2006; Mensah, Veldtman, Assogbadjo, et al., 2016; Salinas-Melgoza et al., 2018). It is important to note that the dominant terrain slopes in our rainforest vary from 3% to 15%, hence considered steep slopes (Zare Chahouki et al., 2012). Aboveground carbon is expected to decrease in steep slopes because they have shallow soils (Gong et al., 2008) and are richer in sand but poorer in silt content (Pachepsky et al., 2001), and hence are more vulnerable to erosion, but surprisingly, we found out that AGC was higher on steeper slopes in our plots.

Soils of the semi-deciduous communal forest of Doume are leached and hence may be nutrient-poor habitats. We, therefore, expected that increasing soil resources would strongly determine carbon storage. Indeed, soil nitrogen significantly increased aboveground carbon stocks of small stems, and higher soil clay content – which is generally correlated with higher fertility – increased AGC of understory trees and structural diversity. It has been recognised as found in this study that soil textural properties are the most important characteristics of the soil, influencing, directly and indirectly, cascades of relations between soil nutrients, ions, and soil drainage (Silver et al., 2000), and hence expected to have strong effects on AGC stocks. These results align with other studies (Lewis et al., 2013; van der Sande et al., 2018; Zarin et al., 2001) and demonstrate the importance of small-scale variation in soil conditions for the forest's capacity to store carbon.

The small variation in disturbance intensity and the time elapsed since the disturbance allowed carbon stocks to recover may explain the contrary results from our expectation. Indeed, in this study, logging as a continuous variable did not reduce the whole tree community's and all tree size groups' carbon stocks. Therefore, carbon stocks can rapidly recover. Contrary, disturbance significantly increases large trees and the whole tree community's carbon stocks

through the tree size inequality. It has been shown in the Amazonian forest that disturbance resulted in a decrease in AGB, but with time, it increases the recruitment of small trees (Holm et al., 2014). Hence, this phenomenon could explain the results observed in our study. In conjunction with recent studies across Neotropical forests (Poorter et al., 2017; van der Sande et al., 2018), our results indicate that disturbance is a necessary process by increasing the availability of light and other resources, hence promoting the recruitment of small trees in the lower forest strata.

## 5 | CONCLUSIONS AND IMPLICATIONS FOR CARBON AND REDD+

This study found that tree size inequality significantly affects the aboveground carbon stocks of the whole tree community, large trees, and small stems, which means that it is important to maintain a layered structure and tall trees in the Cameroonian tropical rainforest. We also found that aboveground carbon increased with increasing species richness, hence conserving biodiversity is not just an objective in itself. This result showed the implication for REDD+ that forests with high diversity also tend to have high carbon stocks, indicating that forests with high carbon storage potential also have high conservation potential. Furthermore, species richness could also help protect ecosystem productivity from environmental change (Isbell et al., 2011) and enhance the resilience of these ecosystems to disturbance (Díaz et al., 2009). Therefore, as diversity co-determines the functioning of the forest, many authors recommended that biodiversity conservation should not be seen as a simple simultaneous benefit of REDD+, but as an integral and crucial component of all its activities (Díaz et al., 2009). Hence, due to his essential role in forest functioning, biodiversity conservation is a win-win strategy for programs such as REDD+ and those under the Convention of Biological Diversity.

### AUTHOR CONTRIBUTIONS

JCZ and MMM designed the research; JCZ and PAE collected the data; JCZ analysed the data; JCZ and MTVS wrote the first paper; all the authors discussed the results and provided comments.

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### CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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