Research article

Tree community, vegetation structure and aboveground carbon storage in Atlantic tropical forests of Cameroon

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ABSTRACT

Understanding Atlantic tropical forests' ecological dynamics and carbon storage potential in Cameroon is crucial for guiding sustainable management and conservation strategies. These forests play a significant role in carbon sequestration and biodiversity conservation. This study aimed to fill existing knowledge gaps by characterising plant communities, assessing the vegetation structure, and quantifying the potential of carbon stocks. Twelve 1-ha permanent plots were established within the Atlantic forests of Okoroba and Yingui to achieve these objectives. All the trees with diameters at breast height (DBH) ≥ 10 cm were inventoried, and various environmental data, including soil texture and climate information, were collected. The Multivariate Regression Trees (MRT) technique was employed to analyse species composition and identify different plant communities (PCs). Additionally, multiple regression models were used to examine the effects of environmental variables and stand size structure on non-destructive carbon stock assessments. The MRT analysis was conducted on 6425 trees spanning 317 species, 212 genera and 60 families, and it identified three distinct PCs with unique species compositions and environmental preferences. The study revealed variations in tree density, ranging from 425 to 645 N ha^{-1}, and basal area, from 32 to 38 m^{2}ha^{-1} among PCs and forest types. Although carbon stocks did not differ significantly between the PCs, they varied in distribution, ranging from 195 to 203 Mg C.ha^{-1}. A single-factor model indicated a significant correlation between tree density with DBH ≥ 50 cm and aboveground biomass variability ($R^2 = 0.86$). A multi-factor model, considering DBH ranges of 10–30 cm and 30–50 cm, explained 93 % and 94 % of biomass variability, respectively, incorporating elevation and other tree density factors. These findings enhance our understanding of carbon dynamics in Atlantic forests and support conservation and sustainable management practices. They highlight the importance of biodiversity protection in mitigating climate change and maintaining ecosystem health.

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1. Introduction

The Lower Guinea centre of endemism, located in Central and West Africa, particularly around the Gulf of Guinea harbours unique biodiversity hotspots. This region encompasses the Guinea-Congolian, evergreen rainforest, and Atlantic or Nigero-Camerouno-Gabonese domains, each contributing to the area's rich endemic flora [1]. The Atlantic forests of Cameroon are particularly notable for their high plant taxa richness and endemism, highlighting their importance for conservation and biodiversity management [2,3]. These forests consist of two main types: (i) the Biafran Atlantic forest, characterised by a wealth of gregarious Caesalpinioideae species, and (ii) the coastal Atlantic forest, which is comparatively less rich in Caesalpinioideae [4]. Despite differences in species composition, both forest types provide essential goods and ecosystem services to local communities, including energy, arable land, and non-timber forest products [4]. However, anthropogenic pressures, such as deforestation and forest degradation, threaten their integrity, leading to habitat loss, a decline in species population, and disruption of ecosystem functions [5–9].

Beyond their economic value, the ecological significance of Atlantic forests cannot be overstated. These forests are vital carbon sinks contributing to climate change mitigation [10,11]. Research has shown that they store substantial amounts of aboveground carbon, with carbon stocks positively correlated with species richness [12]. Studies emphasise that forests with high diversity often demonstrate high carbon stocks, indicating a strong relationship between carbon storage and conservation potential [12]. Species diversity is crucial for enhancing the resilience of these ecosystems against disturbances [13] and preserving ecosystem productivity amidst environmental change [14]. Biodiversity conservation should thus be considered an integral element of REDD + initiatives and similar frameworks, as it directly influences forest functioning and ecosystem health [15]. Implementing such mechanisms requires comprehensive data on these forests.

Despite their importance, comprehensive studies on the vegetation structure and species distribution of Atlantic forests remain limited, especially concerning the influence of environmental factors [1,3]. Previous research has highlighted the floristic richness and endemism in various forests across Cameroon [1,3,6,9,11,16–23]. However, there remains a gap in understanding the specific relationships between vegetation structure and environmental variables within Atlantic forests. Furthermore, apart from the preliminary phytogeographical studies conducted by Letouzey [1], there has been a lack of in-depth research linking flora to environmental factors in the Atlantic phytochoria of Cameroon.

Research indicates that habitats are crucial in shaping forest species distribution across various spatial scales, driven by the non-random associations observed between species distributions and environmental variables [24–29]. At a local scale, the clustering of seedling and adult populations reflects the restricted dispersal capabilities of species, which also significantly influence their distribution patterns [30–32]. This makes it difficult to determine the relative importance of niche differentiation and dispersal mechanisms in shaping local community structures. Dispersal processes lead to the clustering of species distributions, thereby contributing to the spatial organisation of communities [33]. The distribution of habitats further influences the spatial structure of communities due to the strong spatial correlation among environmental variables.

Despite substantial evidence highlighting the role of niche partitioning in shaping communities, understanding the relative impact of various environmental factors, particularly in tropical Atlantic forests, remains limited. At the local level, topographic variation primarily influence the niche distribution [34–37], which affects factors such as water availability and biogeochemical processes [38]. However, integrating soil-related characteristics with topographic variables may reveal additional environmental variations. This notion is supported by Baldeck et al. [39], who found that including soil conditions alongside environmental variables significantly increased the proportion of community composition explained by the environment.

Understanding the relationship between habitat and plant distribution is crucial for reinforcing sustainable management and conservation strategies. Zekeng et al. [29] demonstrated the essential role of habitat conditions in tree species distributing at the local scale, highlighting the factors influencing species coexistence. Despite this, the spatial distribution of plant communities in the Atlantic forest is still poorly studied, especially given the high anthropogenic disturbance contributing to vegetation structure and aboveground biomass heterogeneity. Knowledge of plant community distribution is vital for assessing the consequences of anthropogenic disturbance on ecosystems [27] and reinforcing conservation strategies.

Tree communities are integral to carbon storage within forest ecosystems, as the composition and structure of these communities directly affect carbon sequestration. Different tree species have varying growth rates, biomass allocation patterns, and turnover rates, influencing carbon accumulation in aboveground biomass, including stems, branches, and foliage [40]. Moreover, diverse tree species within a community can enhance carbon storage through niche complementarity and facilitation [12,41,42], where species with different resource requirements coexist and utilise resources more efficiently. Tree communities also impact belowground carbon storage by affecting soil organic matter dynamics, root biomass, and microbial activity [43]. Understanding tree communities, their vegetation structure, and carbon storage in Tropical Atlantic forests is essential for developing effective management and conservation strategies to preserve biodiversity and mitigate climate change impacts.

This study aimed to enhance the sustainable management and conservation of Atlantic tropical forests in Cameroon by investigating their ecological dynamics and carbon storage potential. Specifically, the research sought to: (1) characterise plant communities and their indicator species across various forest sites; (2) assess the vegetation structure within these communities; and (3) quantify and compare their carbon sequestration potential. The guiding research questions were: (i) What are the distinct plant communities and their indicator species in these forests? It was hypothesised that distinct plant communities would be identified, each with specific indicator species reflecting environmental variations. (ii) How does vegetation structure vary across different sites and plant communities? It was hypothesised that significant differences in vegetation structure would exist among communities and sites. (iii) What are the differences in carbon sequestration potential among these communities and sites? It was hypothesised that variability in carbon

sequestration potential would be observed, with some communities and sites demonstrating higher storage capacities due to species composition and structure differences.

2. Material and methods

2.1. Study site

The study was conducted in the Atlantic forests of Okoroba and Yingui, located in the Southwest and Coastal regions of Cameroon, respectively (Fig. 1). The permanent sample plots were established in Forest Management Units (FMU) 00 004 and 11 001 within the Okoroba (5°18′N, 9°05′E) and Yingui (10°20′N, 4°30′E) forests, managed by the Transformation Reef Cameroon (TRC) society. The Okoroba (FMU 00–004) and Yingui (FMU 11-001) forests, situated in the Biafran and coastal forests regions, have altitudes ranging from 100 to 1400 m. FMU 00–004 is located on the seaward slope of the highlands in the South-West and West regions, featuring both high elevations and relatively flat, low-lying terrain, with altitudes ranging from 300 to 1300 m within the FMU. The entire FMU 00 004 is situated on Precambrian formations, notably the Lower Precambrian [44]. Within FMU 11-001, the relief is relatively flat, corresponding to the bottom of the basin, with rocky outcrops in some areas. The altitude varies from 100 to 1400 m between Eyumojock and Akwaya, with soils predominantly ferralitic and sandy, particularly in lowlands areas, where intense erosion contributes to sandy-clay soil formation [45]. Both zones experience an equatorial climate with two distinct seasons: a long rainy season from mid-March to mid-November and a short dry season from mid-November to mid-March. The maximum rainfall occurs in August (445.69 mm), while the lowest rainfall is recorded in January (17.46 mm).

The vegetation in the study areas belongs to the Atlantic Green Forest or Nigero-Cameroon-Gabonese sector [1]. Atlantic forests exhibit varying richness in Caesalpinioideae, with four districts, two of which are characteristic of our study area. The so-called northwestern Atlantic forests (northwestern Atlantic district) are relatively poor in Caesalpinioideae but contain many indisputably Atlantic elements and few or no semi-deciduous forest elements. Moreover, some aspects of neighboring forests penetrate with intrusion from the southern Biafran forests north of Mamfé. Conversely, the Atlantic coastal forests (Atlantic Coastal district) are relatively poor in Caesalpinioideae and geographically occupy the coastal plain area (c. 0–200 m altitude).
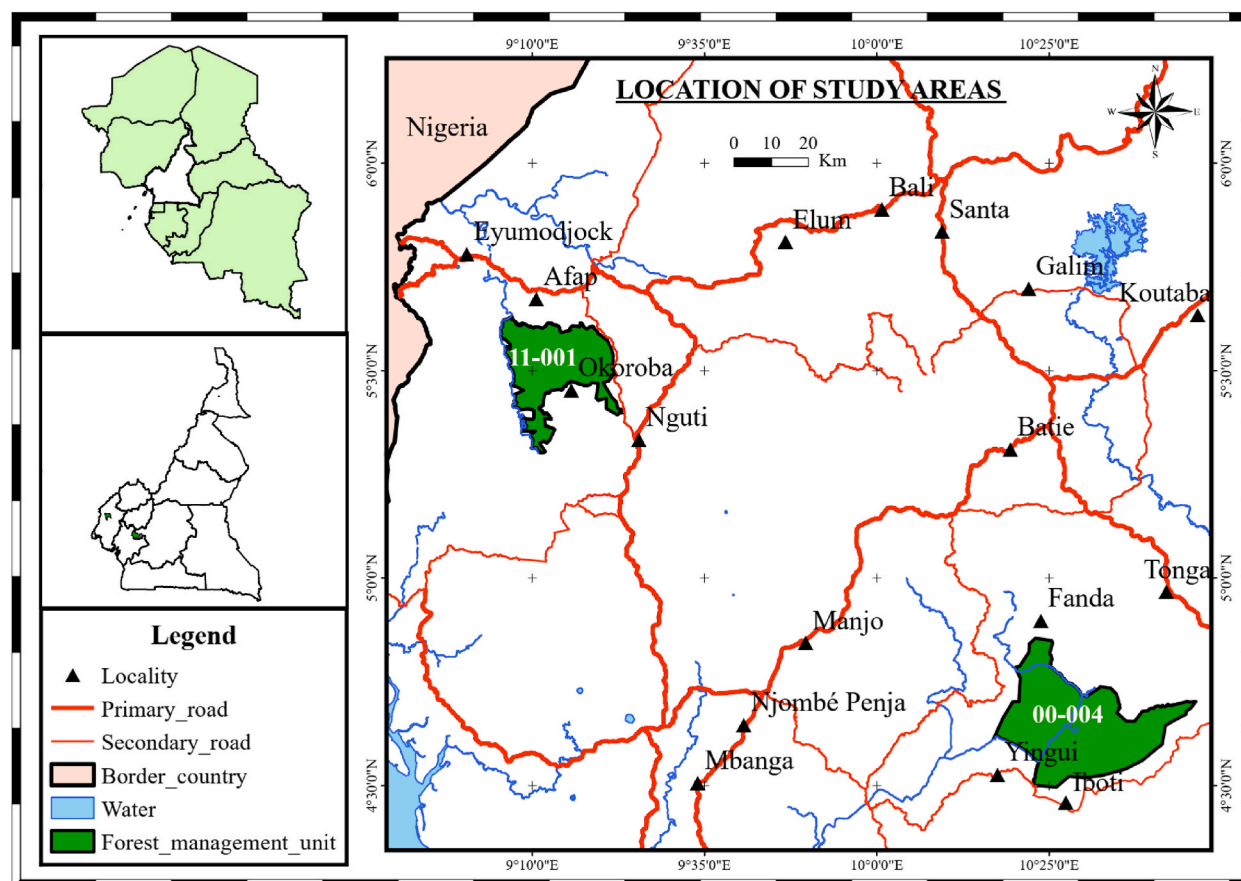

Fig. 1. Location of Okoroba (FMU 00 004) and Yingui (FMU 11 001) forests.

2.2. Sampling design and plot installation

Twelve permanent plots measuring 1 ha (100 m × 100 m), were installed within the two FMUs. A 1-ha plot size is widely adopted in tropical studies [46] due to its effectiveness in capturing a comprehensive range of plant species and community dynamics while maintaining a manageable area for detailed data collection. Furthermore, it allows for standardized assessment of results per unit area, enhancing comparability with findings from other studies. Its use also reduce the uncertainty associated with extrapolating carbon stocks at the hectare level [47]. Implementing 12 plots allows for robust sampling across different environmental conditions and plant communities within the FMUs. This ensures an accurate representation of variability in vegetation structure and carbon storage potential and provides statistically significant results. Six plots were established in each FMU.

Each 1 ha plot was further divided into 25 subplots measuring 20 m × 20 m to enhance data collection and analysis precision. This approach facilitates targeted sampling and more efficient data collection, thereby improving the overall quality and representativeness of the findings.

Forest companies committed to forest management typically establish a systematic network of linear transects spaced 1–3 km apart to estimate the forest resources within their concessions. In the case of these landscapes, 60 transects were installed in each FMU. These transects, subdivided into geo-referenced plots, effectively covered the forest massif and were utilized for flora inventory. Within each FMU, a 1-ha plot was installed along a transect, resulting in 12 1-ha plots along 12 transects. Using a GARMIN GPSMAP 62S device with accuracy varying between 3 and 10 m, the geographical coordinates of each plot were recorded, allowing for precise geo-referencing of the study sites and accurate location identification within the national territory.

2.3. Botanical inventory and measurements

A field inventory of all vascular plants with a diameter at breast height (DBH) ≥ 10 cm was measured, recorded, and identified within each 1-ha plot. Trees were identified and measured 50 cm above the top of the buttresses or 2 cm above the deformities, if applicable [48]. Aluminium labels inscribed with numbers were affixed to each identified tree, approximately 30 cm above the measurement point for regular trees and 40 cm above trees with buttresses or stilt roots.

Field identification of trees relied on typical botanical traits such as bark characteristics, exudate colour and exudate flow rate, leaf morphology, flowers, and fruits. For species that could not be confidently identified by the field botanical team, fertile and non-fertile samples were collected both within and outside the plots, for further identification at the Cameroon National Herbarium. Herbarium identification was carried by comparing the collected specimens with those available at the herbarium and consulting various plant identification resources, including the Cameroon floras, in particular, the volume on Leguminosae-Caesalpinioideae [49], and the manuals of forest botany of tropical Africa [50]. Species names identified during the fieldwork were corrected and homogenized for synonymies and orthographic problems using several plant databases, including The Plant List database [51]. The botanical nomenclature of families followed the Angiosperm Phylogeny Group IV (APG) [52]. Additionally, for direct comparison with prior studies and considering the specificities of the Fabaceae *sensu* subfamilies APG III [53](Caesalpinioideae, Mimosoideae, Faboideae) and the ecological importance of Caesalpinioideae in Central African forests were considered for each of them separately [1,9,54].

2.4. Environmental data

Four types of environmental data (i.e., soil texture, precipitation data, altitude, and distance to the sea of forests; Table 1) were collected and analysed to determine plant communities. In addition, elevation data were used to assess their effect on carbon stock. The precipitation and distance from the sea data were obtained from the meteorological stations of Yabassi and Mamfe for the Atlantic forests of Yingui and Okoroba, respectively. Soil samples were collected from five 20 m × 20 m subplots, the four corners and the centre [12,29], of each 1-ha plot at 0–10 cm depths. From each sample, 200 g were extracted, mixed, and homogenized to form composite samples for each 1-ha plot, which were then analysed for pH and texture. The soil texture was determined by estimating the percentage of sand (particle size 0.05–2.0 mm), silt (0.002–0.05 mm), and clay (<0.002 mm) obtained by using a Malvern Mastersizer 3000E laser particle size analyzer with a Hydro 3000MU pump accessory for more details please see supplemental materials S1 [55]. pH was determined on a 10 g soil sample, using 50 ml of distilled water and equilibrating for 150 min.

Table 1
Descriptive statistics for all environmental variables (Elevation, precipitation, distance from the sea and soil texture) across the 1-ha plots. Mean, standard deviation (SD), minimum (Min) and maximum (Max) are given.

Variables	Biafran forest				Coastal Forest			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Elevation (m)	294.00	33.30	0.27	375.00	556.67	133.67	0.59	963.00
Precipitation (mm)	2396.67	10.54	2375	2430.00	2490.67	127.97	2086.00	2693.00
Distance from the sea (m)	118.81	7.95	95.79	136.29	141.53	0.38	140.03	142.48
pH	4.21	0.06	3.96	4.43	4.38	0.06	4.22	4.64
Sand (%)	66.55	4.38	45.12	74.00	55.37	4.12	44.37	64.69
Clay (%)	22.38	3.41	15.03	38.60	33.32	2.77	26.81	43.60
Silt (%)	10.82	1.23	8.14	16.28	9.81	1.23	6.72	13.55

Altitude was recorded at the four corners and the centre of each 1-ha plot and used to calculate topographic variables at the 1-ha scale. Mean elevation was calculated as the mean of the measurements at the four corners and the centre of a 1-ha plot.

2.5. Descriptive and statistical analyses

2.5.1. Forest tree community classification

The Multivariate Regression Trees (MRT) technique [56,57] was used to identify different plant communities (PCs). The MRT utilized sample plots with similar species composition (i.e., species assemblages) and environmental variables (Table 1) to distinguish the PCs. Each split was based on a specific value of an environmental factor, dividing the sample into two parts such that the difference within the nodes was minimised and the difference between the nodes was maximised. This splitting process was applied recursively to the resulting groups. Finally, as the MRT score included both dependent and independent variables, the classification results were pruned using cross-validation to produce a regression tree of the appropriate size. In this study, tree size was determined by minimizing the Cross-Validated Relative Error (CVRE) with 1 standard error (SE) rule in all cases, thereby avoiding overfitting [58]. The indicator value is defined as the product of the frequency and fidelity for each habitat type, ranging from 0 (species does not occur in a habitat) to 1 (species occurs in all plots of one habitat type and none in other habitat types). Species with high indicator values for specific habitat types are considered indicator species [29]. The MRT analysis was conducted using 'mvpart' package and the indicator species analysis was performed using 'labdsv' package in R4.2.2 statistical software [59].

2.5.2. Characterization of the vegetation structure attributes in forest plots

The vegetation structure in each plot was assessed based on density, Basal Area (BA), and mean tree diameter. Species density represented the total number of individuals per ha, while BA was calculated as the sum of the cross-sectional area of tree trunks within 1 ha at breast height aboveground level [60]. BA was expressed in $m^2 ha^{-1}$ and calculated using the formula: $BA = \pi \frac{DBH^2}{4}$, where DBH is the diameter at breast height of individual trees. DBH and basal area were categorised into three classes: $10 \leq DBH < 30$ cm, $30 \leq DBH < 50$ cm, and $50 \geq DBH$, to capture general vegetation patterns and dominant-size classes of trees.

Appropriate statistical tests were employed to compare the various structural parameters between Atlantic forests and identified PCs. The Welch two-sample t-test and the two-sample Wilcoxon test were applied to test for differences in parameters among different types of Atlantic forests when the data did not meet the assumptions of normality. The Kruskal-Wallis was applied to compare different parameters among PCs. The normality assumption was tested using the Shapiro–Wilk test [61]. All p-values <0.05 are reported as significant. All analyses were performed using the R 4.2.2 statistical software [59].

2.5.3. Aboveground biomass and carbon estimation

Aboveground biomass (AGB) for large trees was obtained by converting DBH into AGB using Eq. (1) from Chave et al. [62] with further refinement based on Réjou-Méchain et al. [63]. This equation was refined from an earlier model by Chave et al. [64] developed for humid forests using multiple site data, although it did not include data from African sites. Nevertheless, this allometric equation was used to compare our results with those of other studies.

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

Where E is a measure of environmental stress at the site, depending on temperature seasonality and water deficit, extracted from the raster package of R based on the geographical coordinate of each plot. DBH is the diameter at breast height (cm), and WD is the wood density (g cm^{-3}). WD was determined using local data; otherwise, it was sourced from the Global Wood Density Database [65,66]. For species lacking wood density information, 74 % of the mean wood density of another species within the same genus, as documented in the database of Zanne et al. [66] and through literature review, were used, as genus level gives reliable approximations values of species, except for a few hyper-variable genera [67]. This approach accounted for a further 33 % of species. For species without any genus-level data available, a default wood density value of 0.60 g cm^{-3} was applied, according to Henry et al. [68]. A widely used conversion factor of 0.47, common in tropical African studies [8,69–71], was applied to convert AGB to carbon values,. The AGB for each tree within the twenty-five 20 m × 20 m subplots was aggregated to obtain the AGB in Mg ha^{-1}.

The same appropriate statistical tests applied for structural variables attributes were also employed to compare carbon stocks between Atlantic forests and identified PCs. As stem density and local topography can vary widely among plots even within the same elevation, multiple-regression models were applied to examine the combined effects of site elevation (average elevation in meters asl at 1-ha plot scale) and stand size structure (i.e., tree density by size class) on total stand live aboveground biomass variation. The models were evaluated by comparing the Root Mean Squared Error (RMSE) and coefficient of determination (R2) for model-predicted AGB versus independent variables. All the analyses were performed using the R 4.2.2 statistical software [59].

3. Results

3.1. Tree community in Atlantic forests

A total of 6425 trees representing 317 species, 212 genera, and 60 families were identified. The MRT analysis classified the surveyed plots into three distinct PCs, defined by their distance from the sea and the soil texture (Fig. 2). The first PC (PC1) encompasse plots 1 and 2, located in coastal forests in Yingui, at least 138.2 km from the sea, with soils characterised by low silt content. PC1 is

predominantly characterised by four indicator species: *Allophyllus africanus* (Sapindaceae), *Garcinia lucida* (Clusiaceae), *Olax sub-scorpioides* (Olacaceae), and *Trichoscypha arborea* (Anarcadiaceae), along with 14 associated species (Table 2). The second PC (PC2) consists of plots 3–6, within coastal forests and sharing similar geographical characteristics with PC1 (Fig. 2). However, the soils in PC2 plots are rich in silt. PC2 is characterised by 10 indicator species. Lastly, PC3 comprise plots 7–12 located in the Biafran forests near the sea (Fig. 2). This community is dominated by *Calpocalyx dinklagei*, *Pentaclethra macrophylla*, and 10 associated species (Table 2).

3.2. Vegetation structure of the tree communities and Atlantic forests

On average, each hectare of the twelve Atlantic Forest plots sampled contained 535 trees with a DBH $\geq$10 cm, consisting predominantly of trees (99 %) and a minor proportion of Arecaceae (1 %). There was a noticeable decrease in the number of trees from the Atlantic Biafran forest (493–761 trees ha^{-1}) to the Atlantic Coastal forest (358–645 trees ha^{-1}) (Table 3). However, this variation in tree density between the two forest types was insignificant (Kruskal-Wallis test, *p-value* > 0.05). Nevertheless, significant differences in tree density were observed when considering the identified PCs (Kruskal-Wallis chi-squared = 8.2339, *p-value* = 0.016). PC3, corresponding to the Biafran Atlantic Forest, exhibit the lowest tree density compared to PC1 and PC2 (Table 3).

The average number of trees inventoried occupied a mean basal area of 32.02 ± 5.53 m^{2}ha^{-1}, with a mean DBH of 22.88 ± 01.68 cm across the sampled Atlantic forests. Interestingly, while the Atlantic Biafran forest displayed a lower average diameter, it exhibited a comparatively higher basal area than the Atlantic Coastal forest. However, this trend was reversed when analysing the different PCs, with PC1 showing a low average diameter but a high basal area, followed by PC3 and PC2, respectively (Table 4).

The inventoried plots within the Atlantic forests exhibited an average of 535 trees per hectare, occupying a mean basal area of 32.02 ± 05.53 m^2 ha^{-1}, and were categorised into three diameter classes. The distribution of tree by diameter class in both the overall Atlantic forests (Fig. 3d) and specifically within the Atlantic coastal (Fig. 3b) and Biafran forests (Fig. 3e), as well as within the identified PCs (Fig. 3a,b, and c) revealed an inverted J-shape, indicative of stable and less disturbed forests with good natural regeneration potential.

In the Atlantic forests, tree density declined with increasing diameter class (Fig. 3d). Notably, the first diameter class accounted for approximately 80 % of the total density, followed by 14 % for the second and 6 % for the third diameter classes. On the contrary, an irregular distribution was observed for tree basal area distribution. Trees in the third diameter class occupied 13.27 ± 4.60 m^{2}ha^{-1}, followed by those in the first diameter class with 10.20 ± 2.53 m^{2}ha^{-1}, and finally, trees in the second diameter class cm with 8.56 ± 1.99 m^{2}ha^{-1} (Fig. 3d).

The Atlantic coastal and Biafran forests exhibited similar distributions to the overall Atlantic forests in tree densities and basal areas (Fig. 3b–e). In the Atlantic coastal forests, there were 393 ± 107 trees per ha with a basal area of 9.52 ± 2.70 m^{2}ha^{-1} for the first diameter class, 74 ± 22 trees per ha with a basal area of 8.37 ± 2.33 m^{2}ha^{-1} for the second diameter class, and 31 ± 12 trees per ha with a basal area of 13.80 ± 6.18 m^{2}ha^{-1} for the third (Fig. 3b). Similarly, in the Biafran Atlantic forests, there were 465 ± 91 trees per ha with a basal area of 10.87 ± 2.38 m^{2}ha^{-1} for the first diameter class, 77 ± 17 trees per ha with a basal area of 8.75 ± 1.79 m^{2}ha^{-1} for the second diameter class, and finally, 31 ± 12 individuals per ha with a basal area of 13.80 ± 6.18 m^{2}ha^{-1} for third diameter class (Fig. 3e).

The distribution of individuals across diameter classes for the various plant communities exhibited an inverted J-shape (Fig. 3b,c, and a), similar to the pattern observed in the overall Atlantic forests. Furthermore, except for PC1 (Fig. 3a), the same distribution of basal areas (Fig. 3b and c) described for the Atlantic forests (Fig. 3d,e and b) was observed. Indeed, for PC1, the basal area distribution was proportional to the tree density (Fig. 3a).
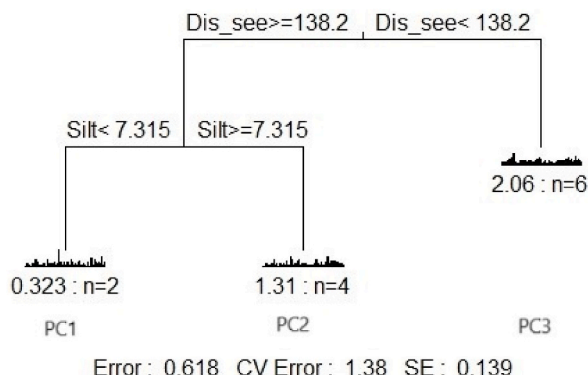
Fig. 2. Multivariate regression tree for plant communities (PC) associations' classification in the Atlantic forests. The values 0.3233, 1.31, and 2.06 represent the mean species importance value for each Plant Community (PC1, PC2, PC3). CV Error, the relative error of cross-validation; Error, relative error; n, the number of 1-ha plots in each community; SE, standard error.

Table 2

Indicators and associated *species* characterise each identified tree community (PC 1,2 and 3). $*p < 0.05$; $**p < 0.01$ $***p < 0.001$.

Families	Species	Indval	Plant community (PC)
Anacardiaceae	*Sorindeia grandifolia*	0.67*	PC1
Anacardiaceae	*Trichoscypha arborea*	1.00**	PC1
Annonaceae	*Xylopia parviflora*	0.83*	PC3
Annonaceae	*Xylopia staudtii*	0.78*	PC1
Apocynaceae	*Landolphia* sp.	0.83*	PC3
Apocynaceae	*Tabernaemontana crassa*	0.47*	PC2
Burseraceae	*Dacryodes edulis*	0.59*	PC1
Burseraceae	*Dacryodes macrophylla*	0.57**	PC1
Chrysobalanaceae	*Maranthes glabra*	0.83**	PC1
Chrysobalanaceae	*Maranthes inermis*	0.82*	PC1
Clusiaceae	*Endodesmia calophylloides*	0.83*	PC1
Clusiaceae	*Garcinia lucida*	1.00*	PC1
Dichapetalaceae	*Tapura africana*	0.83**	PC3
Dilleniaceae	*Tetracera alnifolia*	0.80*	PC1
Ebenaceae	*Diospyros simulans*	0.73***	PC2
Euphorbiaceae	*Uapaca guineensis*	0.57*	PC1
Euphorbiaceae	*Usteria guineensis*	0.83*	PC3
Fabaceae-Caesalpinioideae	*Anthonotha fragrans*	0.82**	PC3
Fabaceae-Caesalpinioideae	*Erythrophleum ivorense*	0.85**	PC2
Fabaceae-Caesalpinioideae	*Hylodendron gabunense*	0.68*	PC3
Fabaceae-Mimosoideae	*Pentaclethra macrophylla*	1.00***	PC3
Fabaceae-Papilionoideae	*Baphia nitida*	0.83*	PC3
Fabaceae-Papilionoideae	*Calpocalyx dinklagei*	1.00***	PC3
Fabaceae-Papilionoideae	*Pterocarpus soyauxii*	0.61**	PC2
Irvingiaceae	*Klainedoxa gabonensis*	0.61*	PC1
Malvaceae	*Sterculia rhinopetala*	0.75*	PC2
Meliaceae	*Santiria trimera*	0.61*	PC1
Myristicaceae	*Staudtia kamerunensis*	0.47*	PC2
Myrtaceae	*Syzygium rowlandii*	0.82*	PC1
Olacaceae	*Olax subscorpioides*	1.00**	PC1
Olacaceae	*Oncoba gilgiana*	0.69*	PC2
Olacaceae	*Oncoba glauca*	0.71*	PC2
Phyllanthaceae	*Antidesma laciniatum*	0.87**	PC3
Putranjivaceae	*Drypetes preussii*	0.69*	PC1
Rubiaceae	*Pausinystalia macroceras*	0.70**	PC3
Sapindaceae	*Allophyllus africanus*	1.00**	PC1
Sapotaceae	*Gambeya boukokoensis*	0.80*	PC1
Strombosiaceae	*Strombosia pustulata*	0.51*	PC2
Ulmaceae	*Celtis tessmannii*	0.83**	PC3
Violaceae	*Rinorea* sp.	0.69**	PC2

Table 3

Variation of structural parameters (density, mean diameter at breast height $(DBH)_2$ basal area) in Atlantic forests.

| Forest type	Density (Trees/ha)			Mean DBH (cm)	Basal area (m2/ha)
	Trees	Palms	Total		
Biafran forest	564	09	573 ± 102	22.19 ± 00.86	32.35 ± 05.13
Coastal forest	497	01	498 ± 126	23.56 ± 02.08	31.69 ± 06.37
Atlantic forest	531	05	535 ± 115	22.88 ± 01.68	32.02 ± 05.53

Table 4

Variation in structural parameters (density, mean DBH, basal area) Plant Community (PC).

Plant community	Tree density (trees/ha)	Mean DBH (cm)	Basal area (m^2/ha)
PC1	645±0[b]	21.94 ± 1.21	33.34 ± 4.92
PC2	425 ± 69[a]	24.37 ± 2.03	30.87 ± 7.54
PC3	573 ± 102[ab]	22.19 ± 0.86	32.35 ± 5.13
Average	535.42 ± 115.85	22.88 ± 1.68	32.02 ± 5.53

The column with different letters(a,b) showed a difference significant between tree density.
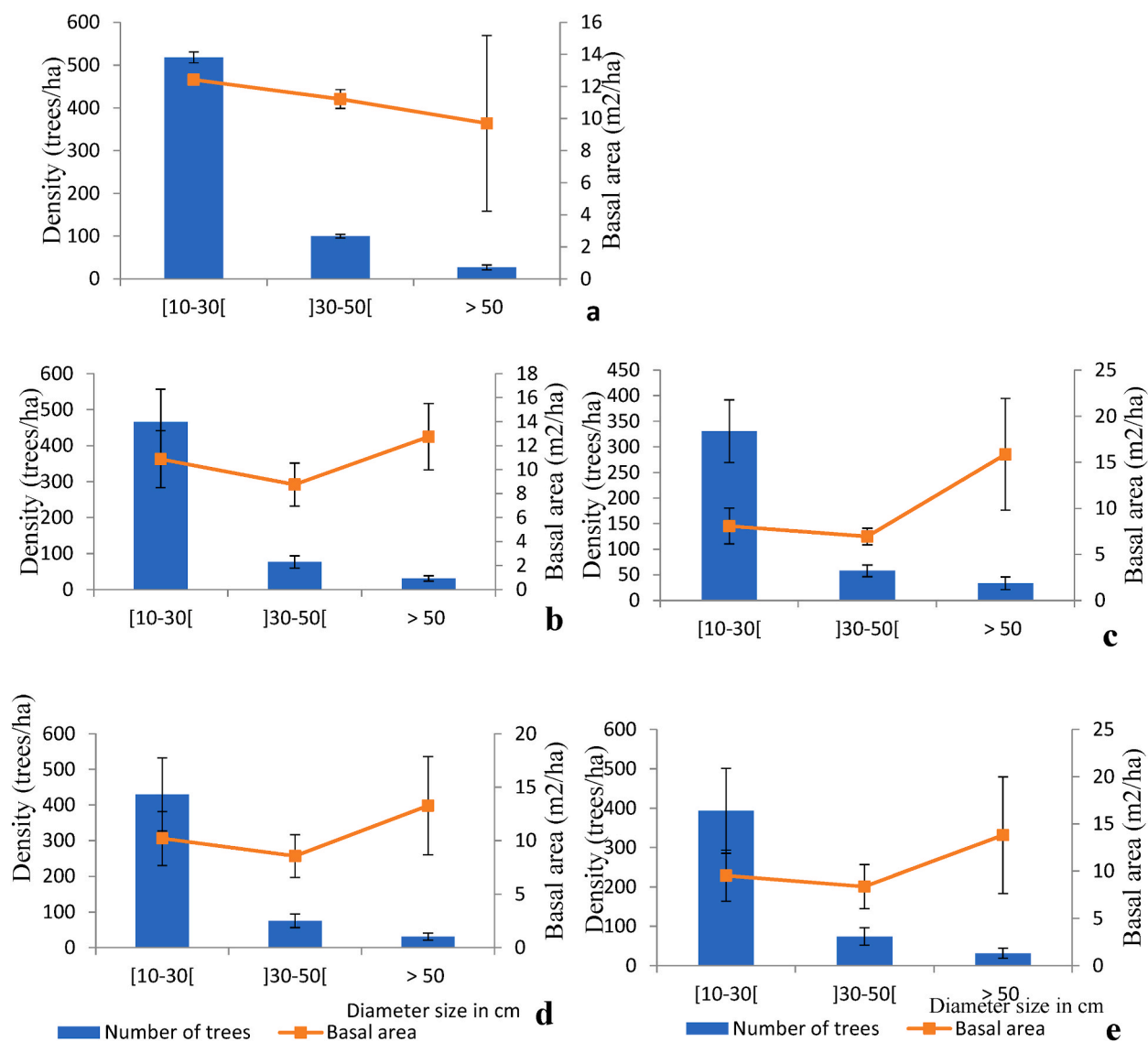
Fig. 3. Densities and basal areas distribution per diameter size in: (a) Plant Community 1; (b) Coastal Atlantic forest or Plant Community 3; (c) Plant Community 2; (d) Atlantic forests; (e) Biafran Atlantic forest.
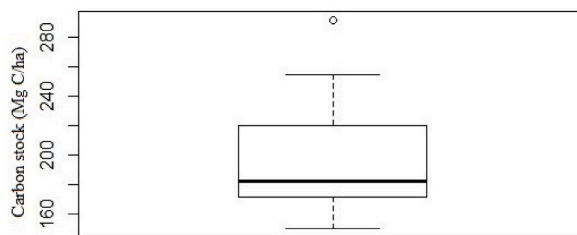
Fig. 4. Distribution of carbon stock in the sample plots of Atlantic forests.

3.3. Carbon stock

3.3.1. Carbon distribution within Atlantic forests and tree communities

The Atlantic forests store 198.66 ± 39.69 Mg C ha^{-1} with variations ranging between 149.82 and 291.73 Mg C ha^{-1}. Notably, one plot exhibit a significantly high value of 291.73 Mg C ha^{-1}, standing out from the others due to its asymmetric distribution of carbon stocks (Fig. 4).

Although there is no significant difference ($p > 0.05$) in the carbon stored by the Atlantic Biafran and Coastal forests when considered separately (Fig. 5), the Atlantic Coastal forests, on average, store slightly more carbon than the Biafran forests, with 202.37 $\pm$ 50.51 Mg C ha^{-1}, compared to 194.95 ± 34.59 Mg C ha^{-1}, respectively. Despite this lack of significant difference, there is a skewed distribution of carbon stocks among the plots within each forest studied. This skewed distribution is particularly evident in the Atlantic Coastal forest, which serves as a notable example (Fig. 5).

Moreover, Fig. 6a shows a distinct dispersion in the distribution of carbon stocks within the three identified plant communities. Despite the close average carbon stock values among the three PCs, PC2 and PC3 exhibit greater dispersion than PC1. However, despite these differences in dispersions, Fig. 6b does not indicate any significant difference in the distribution of carbon stocks among the three PCs. This assertion is confirmed by the Kruskal-Wallis test (chi-squared = 0.23077, p-value = 0.891).

Despite the non-significant difference in carbon stocks among the three PCs, each exhibits a unique distribution of carbon stocks. For instance, PC2, consisting of four plots, holds the highest quantity of stored carbon, with a mean value of 203.67 ± 58.96 Mg C ha^{-1}. However, this PC has a skewed distribution of carbon stocks. Conversely, PC1, with two plots, serves as the second largest carbon reservoir, with an average stored carbon quantity of 200.07 ± 48.05 Mg C ha^{-1}, demonstrating a symmetrical distribution between these two plots. Finally, PC3, still representing the Biafran forests, ranks lowest in carbon storage, with an average of 194.95 ± 34.59 Mg C ha^{-1}, and also exhibits a skewed distribution with plots having varying carbon stock values (Fig. 6).

3.3.2. Effect of forest structure and altitude on aboveground biomass

No multi-factor model with several significant factors was identified (Table 5). However, a simple one-factor model explained 86 % of the variability in total aboveground biomass across the elevation gradient. The main factor was the density of individuals with DBH ≥50 cm at the plot level, showing a strong correlation with aboveground biomass ($R^2 = 0.86$). This factor also explained the variation in biomass of trees with DBH ≥50 cm, along with the cumulative negative effect of elevation and the density of individuals within the DBH ranges of 10–30 cm and 30–50 cm. Furthermore, a multi-factor model integrating the density of individuals within the DBH range of $10 \leq$ DBH <30 cm and $30 \leq$ DBH <50 cm explained 93 % of the variation in aboveground biomass for individuals within the $10 \leq$ DBH <30 cm range. Similarly, the model explaining 94 % of the variation in individuals within the $30 \leq$ DBH <50 cm range included a positive effect of elevation and density of individuals within the DBH ranges of $10 \leq$ DBH>30 cm and DBH <50 cm.

4. Discussion

4.1. Influence of environmental gradients on tree species distribution in Atlantic forest

This study highlights the crucial role of environmental gradients, particularly soil texture and proximity to the ocean, in shaping tree species distribution. These findings align with previous studies by Gonmadje et al. [27] and Zekeng et al. [29], reinforcing that microclimatic variations and spatial environmental factors drive vegetation patterns. Specifically, it was observed that variations in distance from the sea correlate with shifts in tree species composition, suggesting a significant decline in marine climatic influence, a concept corroborated by Senterre [72] and Sevegnani et al. [73].

Moreover, Mack and Bever [74] argue that the coexistence of tree species within each PC could be influenced by seedling and adult population aggregation, which limits large-scale dispersal. These study findings provide further support to this theory; the presence of indicator species within each PC reflects localised ecological conditions, echoing previous work by Fobane et al. [3].

The strong spatial correlation of environmental variables with species composition at a small scale, as found by Zekeng et al. [29], emphasizes the importance of microhabitat differentiation. Gonmadje et al. [27] also highlighted that those microclimatic differences, such as those between two slopes, can drive species composition gradients. Multivariate regression trees revealed progressive changes in species distribution with increasing distance from the sea, further affirming the impact of oceanic influence on forest structure.
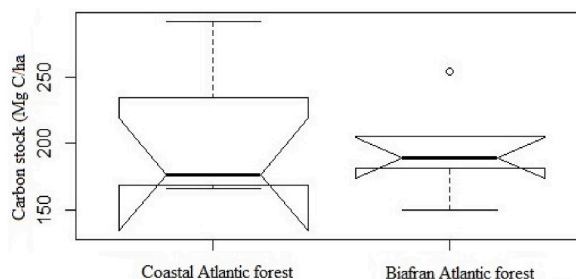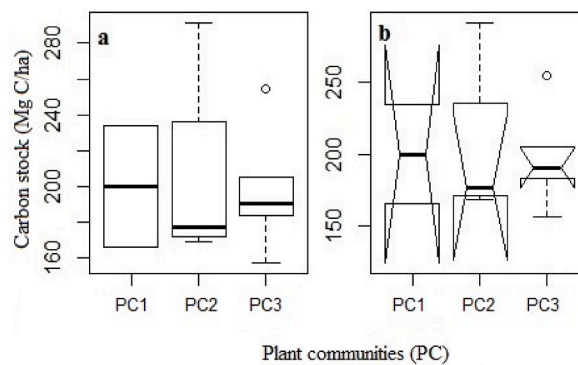

Fig. 5. Distribution of carbon stocks within sample plots of coastal and Biafran forests.

Fig. 6. Distribution of carbon stocks of different plant communities: a) Notched box showing distribution; b) Notched box showing no significant difference. PC1, 2 and 3 are related to Plant Communities 1, 2 and 3.

Table 5
Summary of multiple regression models with variable selection to examine the combined effects of elevation and stand structure (tree density per class) on the total change in aboveground biomass and biomass of different diameter classes. ABG = aboveground biomass; R^2 = coefficient of determination; RRMSE = relative root mean square error.

Biomass components	Predictive variables				F.value	RRMSE	R^2	P.value
	Elevation	Tree density						
		DBH 10–30 cm	DBH30-50 cm	DBH >50 cm				
Total AGB	0.006	0.218	0.314	3.950***	18.59	1.06	0.86	<0.001
AGB trees of DBH 10–30 cm	0.004	0.082***	0.0624	0.203*	40.08	0.19	0.93	<0.0001
AGB trees of DBH 30–50 cm	0.007	0.018	0.496***	0.070 ns	40.67	0.16	0.94	<0.0001
AGB trees DBH >50 cm	−0.005	−0.078	−0.245	3.677***	17.14	0.65	0.85	<0.01

Note: Statistical analyses are significant at 95 % confidence interval. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; and ns (non-significant) $p > 0.05$.

Notably, in the Ngovayang Massif of Southern Cameroon, Gonmadje et al. [27] observed distinct species diversity gradients from the coast to the interior, a pattern mirrored in our study. This suggests that coastal proximity and related environmental factors play a critical role in shaping the ecological landscape, with broader implications for biodiversity conservation and forest management strategies.

4.2. Spatial variation and factors driving carbon stock within Atlantic forests of Cameroon

This research provides critical insights into the carbon stocks of the aboveground biomass in the Atlantic forests of Cameroon, estimated at 198.66 ± 39.69 Mg C/ha for trees with DBH ≥10 cm. These values fall within the range of 195 and 396 Mg C/ha reported in various studies conducted across the Congo Basin [17,28,46,75–77]. This consistency with previous research confirms the importance of Atlantic forests as carbon reservoirs in Central Africa Still, this study also highlights the spatial variability in carbon stocks within these forests.

One of the key findings is the strong association between carbon stocks and DBH and wood density, rather than the sheer number of trees, as reported by Kabelong Banoho et al. [11]. This challenges the traditional assumption that higher tree density automatically results in greater carbon storage. Instead, the increase in carbon content with larger diameter sizes underscores the crucial role of large-diameter trees in carbon sequestration. Similar observations have been reported in the Atlantic forests of Brazil [78–80], reinforcing the importance of preserving these large, hyper-dominant tree species for carbon conservation.

Despite the consistency in tree density across the Atlantic forest elevation gradient (535 trees per ha), no significant differences in carbon stocks were observed. This finding contrasts with other studies showing notable variations across different forest types in Cameroon. The study's lack of observable differences could be attributed to the dominance of large-diameter species, which play a disproportionate role in carbon storage. As demonstrated by Slik et al. [81], the prevalence of trees larger than 70 cm in diameter is strongly associated with higher carbon stocks in African and Asian tropical forests (197 and 185 Mg C/ha, respectively), compared to South American forests, storing 135 Mg C/ha. Similarly, Lewis et al. [46] have documented significant spatial variation in carbon estimates within the African continent, reporting higher values in Central Africa (202 Mg C/ha), where Atlantic forests are located, compared to West Africa (143 Mg C/ha) and East Africa (129 Mg C/ha). Bastin et al. [82] agree with Slik et al. [81] by attributing the higher carbon stocks in Central African forests to the increased presence of hyper-dominant trees, which contribute more than 50 % to carbon storage.

Local-scale variations in carbon stock were evident between the Yingui and Okoroba forests, with the former exhibiting slightly higher average values (202.37 ± 50.51 Mg C/ha) than the latter (194.95 ± 34.59 Mg C/ha). These findings align with the observations

of Day et al. [10], Kuyah et al. [83], who reported spatial variations in aboveground carbon stock across different types of Central African dense rainforest and East African Miombo forest, respectively. These variations may stem from structural differences driven by anthropogenic disturbances and/or edaphic and altitudinal gradients, as highlighted by Alves et al. [78]. In this study, the forests' proximity to riparian villages and their history of selective logging, hunting, and other land use activities have likely contributed to the observed heterogeneity in biomass.

The analysis of species composition and forest structure (e.g., basal area, height-diameter relationships, stem density) revealed significant variation in biomass across the study area. The differences in carbon stocks among the three identified plant communities further support the notion that floristic composition and forest structure explain much of the observed variability. The use of MRT allowed us to differentiate these plant communities based on their specific composition, reinforcing the idea that variations in species composition at plot, species group, or ecosystem levels likely underlie spatial differences in carbon stocks. These results are consistent with the findings of Djuikouo et al. [17], who showed that monodominant stands of *Gilbertiodendron dewevrei* (Fabaceae-Caesalpinioideae) in Cameroon store as much or more aboveground biomass than younger mixed forests.

Several studies have further suggested that forests dominated by trees from specific families, such as Olacaceae, Caesalpiniaceae, and Burseraceae tend to exhibit significantly higher biomass compared to forests dominated by trees from other families, like Burseraceae, Myristicaceae, and Euphorbiaceae [76,77,84]. Fayolle et al. [85] also emphasized the role of species composition and forest structure in driving spatial variations in aboveground biomass between evergreen and semi-deciduous forests in Cameroon. Tropical forests are mosaics of vegetation of varying ages and species compositions, and they are highly sensitive to canopy disturbance regimes and local conditions. Past human disturbance is critical in shaping these forests' structure and biomass accumulation across tropical forests [12,47,86–88].

In this context, the presence of high-density small-diameter individuals (<30 cm DBH) in the Atlantic forests may indicate ongoing recovery processes from past anthropogenic activities, such as logging and land use. However, the influence of altitude should not be overlooked. As Zekeng et al. [21] noted, altitude significantly affects biomass variation by promoting the presence of large-diameter trees, which contribute disproportionately to total biomass. This finding aligns with Paoli et al. [89], who observed similar patterns in Southeast Asian forests, suggesting that fine-scale topo-edaphic gradients may be crucial in shaping forest structure and carbon storage in high-altitude sites.

5. Conclusion and implications

This study offers a comprehensive analysis of tree communities, vegetation structure, carbon stock distribution, and factors influencing aboveground biomass in the Atlantic forests of Cameroon. A total of 6425 trees, representing 317 species, 212 genera, and 60 families, were identified across the study plots. The classification of distinct plant communities (PCs), based on elevation and soil texture, has enhanced our understanding of the dynamics shaping these forest ecosystems. For instance, PC1, situated in coastal forests with low silt content, is primarily characterised by *Allophyllus africanus* and *Garcinia lucida* species. The spatial structure of the vegetation, with a mean tree density of 535 trees per hectare and a basal area of 32.02 ± 5.53 m^2/ha, indicates stable forest conditions with strong natural regeneration potential.

Although no significant difference in carbon stocks was observed between the Atlantic Biafran and Coastal forests, with carbon stocks averaging 198.66 ± 39.69 Mg C/ha, the study reveals uneven carbon distribution. For example, one plot in the Atlantic Coastal forest exhibited a notably high value of 291.73 Mg C/ha, underscoring the importance of site-specific factors. Furthermore, the strong correlation between aboveground biomass and the density of large-diameter trees ($R^2 = 0.86$) highlights the vital role of old-growth forests in carbon storage and ecosystem stability.

These findings emphasise that while overall trends are informative, localised factors significantly influence carbon sequestration potential. The implications of this research extend beyond academic discourse to inform practical conservation efforts and land management decisions. By recognizing the unique characteristics and carbon dynamics of different tree communities, stakeholders can prioritize conservation interventions in areas with high carbon storage potential. Furthermore, identifying key factors influencing aboveground biomass, such as tree density and diameter distribution, provides valuable insights for forest management practices to enhance carbon sequestration and ecosystem resilience. Integrated approaches that consider ecological, socio-economic, and cultural factors are essential for the effective conservation and sustainable management of the Atlantic forests in Cameroon. By exploiting the knowledge generated from this study, policymakers can develop evidence-based policies and initiatives to safeguard these valuable ecosystems for future generations while mitigating the impacts of climate change.

CRediT authorship contribution statement

Jean Louis Fobane: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Jules Christian Zekeng:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Cédric Djomo Chimi:** Writing – review & editing. **Jean Michel Onana:** Writing – review & editing, Writing – original draft, Conceptualization. **André Paul Ebanga:** Writing – review & editing, Writing – original draft. **Léonnel Djoumbi Tchonang:** Writing – review & editing. **Ameline Clarance Talla Makoutsing:** Writing – review & editing. **Marguerite Marie Mbolo:** Writing – review & editing, Writing – original draft, Conceptualization.

Disclosure statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The data supporting this study's findings are available on request from the corresponding author, [J.L.F.].

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e41005.

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