Diversity and Distributions

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Tree Diversity and Carbon Stocks in Seasonally Flooded and *Terra Firme* Forests in the Inner Congo Basin

Modestine Kompanyi[1,2] | Wannes Hubau[3,4] | Jean-Remy Makana[2] | John Hart[5] | Terese Hart[5] | Adeline Fayolle[1,6,7]

[1]Terra Teaching and Research Centre, Forest is Life, Université de Liège – Gembloux Agro-BioTech, Gembloux, Belgium | [2]Faculté des Sciences, Laboratory of Ecology and Forest Management, Université de Kisangani, Kisangani, Democratic Republic of Congo | [3]Royal Museum for Central Africa, Service of Wood Biology, Tervuren, Belgium | [4]Department of Environment, UGent-Woodlab, Laboratory of Wood Technology, Ghent University, Gent, Belgium | [5]Lukuru Wildlife Research Foundation, Kinshasa, Democratic Republic of Congo | [6]CIRAD, UPR Forêts et Sociétés, Campus International de Baillarguet, Montpellier Cedex 5, France | [7]Forêts et Sociétés, CIRAD, Univ Montpellier, Montpellier, France

Correspondence: Modestine Kompanyi (modestine.kompanyiamisi@uliege.be)

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ABSTRACT

Aim: Forest plots are a benchmark tool to quantify aboveground carbon (AGC) stocks and biodiversity in tropical forests. However, atypical edaphic forest types such as seasonally flooded forests or forests on sandy soil are scarce in the plot networks, despite their widespread occurrence. This study assessed how edaphic conditions shape tropical forests, in terms of forest structure, tree diversity and composition.

Location: Lomami National Park in the Democratic Republic of Congo.

Methods: We installed 89 plots of 0.25 ha each in the understudied southeastern Congo basin. Plots are spread over eight different combinations of flooding regime (seasonally flooded vs. *terra firme*), soil texture (clay vs. sand) and region (north vs. south). We tested the influence of flooding regime, soil texture and region on structural attributes, tree diversity, and tree species composition. We also assessed relationships between structural attributes, diversity indices, and compositional gradients.

Results: We inventoried 9156 trees and identified a total of 416 tree species, with 93 species (22.4%) belonging to the Fabaceae family. Species diversity is much higher in *terra firme* than in seasonally flooded forests. The latter also shows a different species composition but holds similar AGC (163 Mg C ha^{-1} on average). We also found that region influences both species diversity and structural attributes (diversity and AGC highest in the north), while soil texture only influences structural attributes (AGC highest on clay). Finally, we found that structural attributes are independent of diversity indices at different scales.

Main Conclusions: This study describes for the first time the forests in the southeastern Congo basin, which show a high degree of structural variability, high tree biodiversity and important carbon stocks. The region merits further exploration, with specific attention to seasonally flooded forests which harbor a less diverse but different tree flora, and similar carbon stocks as compared to *terra firme* forests.

1 | Introduction

Tropical forests provide numerous ecosystem services, hosting more than two-thirds of terrestrial species (Myers et al. 2000), storing important carbon reservoirs, and mitigating anthropogenic CO_2 emissions (Pan et al. 2011). Unfortunately, deforestation, degradation, and fires threaten the maintenance and functioning of tropical forests (Baccini et al. 2017). In addition, these forests face significant (but less visible) threats from rapid climate change leading to biodiversity loss (Aguirre-Gutiérrez et al. 2020), severe tree mortality (Brienen et al. 2015), and carbon sink saturation (Hubau et al. 2020) with maximum temperatures being the strongest determinant of tropical forest biomass and carbon stocks (Sullivan et al. 2020). Despite their primordial importance for biodiversity, the global carbon cycle, and their status as critically endangered ecosystems (Hansen et al. 2020; Réjou-Méchain et al. 2021), tropical forests remain the least studied terrestrial biomes (White et al. 2021).

One of the remaining uncertainties in tropical forests is the effect of soil type on structural attributes (Poorter et al. 2015). Existing studies yielded mixed or even contradictory results. For example, Paoli et al. (2008) found that aboveground carbon (AGC) in Bornean forests is higher on rich clay than on poor sandy soils. However, under certain conditions clay soils can be a poor substrate for tree growth, yielding low AGC stocks (Malhi and Phillips 2004). In Amazonian forests, some studies have revealed a positive association between AGC and sandy soils, where tree communities are slow-growing and tree species show high wood density (Saatchi et al. 2007). Similarly, in south-western forests of the Central African Republic, Gourlet-Fleury et al. (2011) found comparable aboveground biomass (and thus AGC stocks) between clay and sandy soils because the higher wood density of tree species growing on sandy soils compensates for lower basal area. However, different structural attributes respond differently to soil types, particularly stem density which often shows contrasting patterns (Phillips et al. 1994).

Another remaining uncertainty in tropical forests is the effect of soil type on tree species diversity and composition. Recent estimates suggest that tropical forests harbour more than 53,000 tree species (Slik et al. 2015), representing more than 95% of all tree species on Earth. One of the striking characteristics of tropical forests is the significant variation in soil types and habitats which allows for a high tree diversity. In Panama, heterogeneity in tree species composition is clearly linked to heterogeneity in soil types (Condit et al. 2002) and specialist species are clearly affiliated with particular habitats (Comita et al. 2007). Heterogeneity in the composition and structure of tropical forests has been linked to soil heterogeneity in Costa Rica (Jones et al. 2006), in the Amazon (Laurance et al. 1999) and in central Africa (Vleminckx et al. 2015). The spatial configuration of sites in a region is also a factor structuring tree communities, inducing floristic dissimilarity between them (Potts et al. 2002). The decay in similarity of tree communities with distance generally reported across the tropics (Sullivan et al. 2017) may be due to the decrease in environmental similarity or to limited dispersal that may affect gene flow within the landscape (Condit et al. 2002).

In this study, we aim to analyse for the first time the structure, diversity, and composition of tropical forests in the Lomami National Park (NP), a large but unknown area in the Democratic Republic of the Congo (DRC), which hosts 98 million hectares of tropical forest (Vancutsem et al. 2021), and various mammal assemblages (Fonteyn et al. 2024). The region however remains vastly understudied (White et al. 2021) in terms of forest structure, including carbon stocks (Hubau et al. 2020), tree diversity (Parmentier et al. 2011) and tree species composition (Fayolle et al. 2014). We also aim to disentangle the influence of flooding regime and soil texture on these three components because permanently and seasonally flooded forests are often neglected in plot-based studies (Lewis et al. 2013; Sullivan et al. 2017). Studies on primary forest attributes are almost non-existent in flooded forests of central Africa, apart from the recent interest in central peatlands, which are among the largest on the planet (Dargie et al. 2017). We installed the first network of forest plots in the region with a careful design sampling eight different combinations of flooding regime (seasonally flooded vs. *terra firme*), soil texture (clay vs. sandy soils) and region (north vs. south) within Lomami NP. We addressed the following research questions and tested the associated hypotheses.

1. What is the influence of flooding regime, soil texture and region on tree species diversity and composition? We tested the hypothesis that variations in tree diversity and composition are both related to niche processes (flooding regime and soil texture) and neutral processes in tropical forests (Ho et al. 2020).
2. What is the influence of flooding regime, soil texture and region on forest structural attributes including tree density, basal area, wood density, Lorey's height (the basal area-weighted mean height of trees) and aboveground carbon stocks? We tested the hypothesis that soil texture has little influence on carbon stocks in mature tropical forests, due to the offset between structural attributes, notably wood density and basal area (Gourlet-Fleury et al. 2011) and possibly tree height.
3. What is the relationship between forest structural attributes and tree species diversity and composition? We tested the hypothesis that there is no correlation between tree diversity and carbon stocks in mature tropical forests, as demonstrated in South America (Poorter et al. 2015) and across the global tropics (Sullivan et al. 2017) in contrast to what is observed in secondary forests where both the structure and diversity recover quicky after disturbance (Poorter et al. 2016). We tested this hypothesis for the Lomami NP plot data, and in combination with available plot data for the DRC (Makana et al. 2008, 2011; Kearsley et al. 2013; Doetterl et al. 2015) and across the tropics (Sullivan et al. 2017).

2 | Materials and Methods

2.1 | Study Area

The Lomami National Park (NP) is located between 1° and 3° South and between 24.5° and 25.5° East with 8874 km^2 across the Tshopo (6368 km^2) and Maniema (2506 km^2) provinces of the DRC (Figure 1). This forest massif, limited to the west by

the Tshuapa River and to the east by the Congo River (Lualaba), is crossed from the south to the north by the Lomami River (Figure 1b). Lomami NP was established in 2016, after the discovery of a new monkey species (Hart et al. 2012), which highlighted the need to describe and monitor, the forest structure and biodiversity in this area. In addition to the Lesula monkey, a new shrub species was also discovered (Sosef et al. 2019).

The climate in Lomami NP is sub-equatorial, warm, and humid, with an average of 1870 mm annual rainfall over the 2008–2016 period in the Obenge station located in the northern part of the park, and 1720 mm over the 2009–2021 period in Katopa in the southern part (Figure 1b). The short dry season, centered on June–July, lasts no more than 2 months. The average annual temperature is 26°C and varies little during the year.

The region is mainly covered by dense moist forests, but savanna patches are found in the southern part of the park, and large expanses of seasonally flooded forests locally called "Sende" are found along main rivers notably in the eastern part of the park. Flooding in the park is mainly due to rising water levels in the Lomami River during the rainy season in a region with relatively flat topography. Although the frequency of floods is highly predictable, flooding levels vary from year to year depending on rainfall.

2.2 | Forest Plots and Tree Measurements

A stratified sampling approach was developed for the plot network (Figure 1). We first selected 5 km × 5 km blocks in the four edaphic combinations (seasonally flooded clay soil; seasonally flooded sandy soil; *terra firme* clay soil; *terra firme* sandy soil), both in the northern and the southern part of the park. Selection of blocks was based on data from Lomami NP surveillance patrols who systematically georeferenced seasonally inundated zones as they were encountered, either by presence of standing water or by water-saturated substrate. Patrol data covered multiple years and was evaluated using satellite imagery in which seasonally flooded riverine forests can be distinguished from

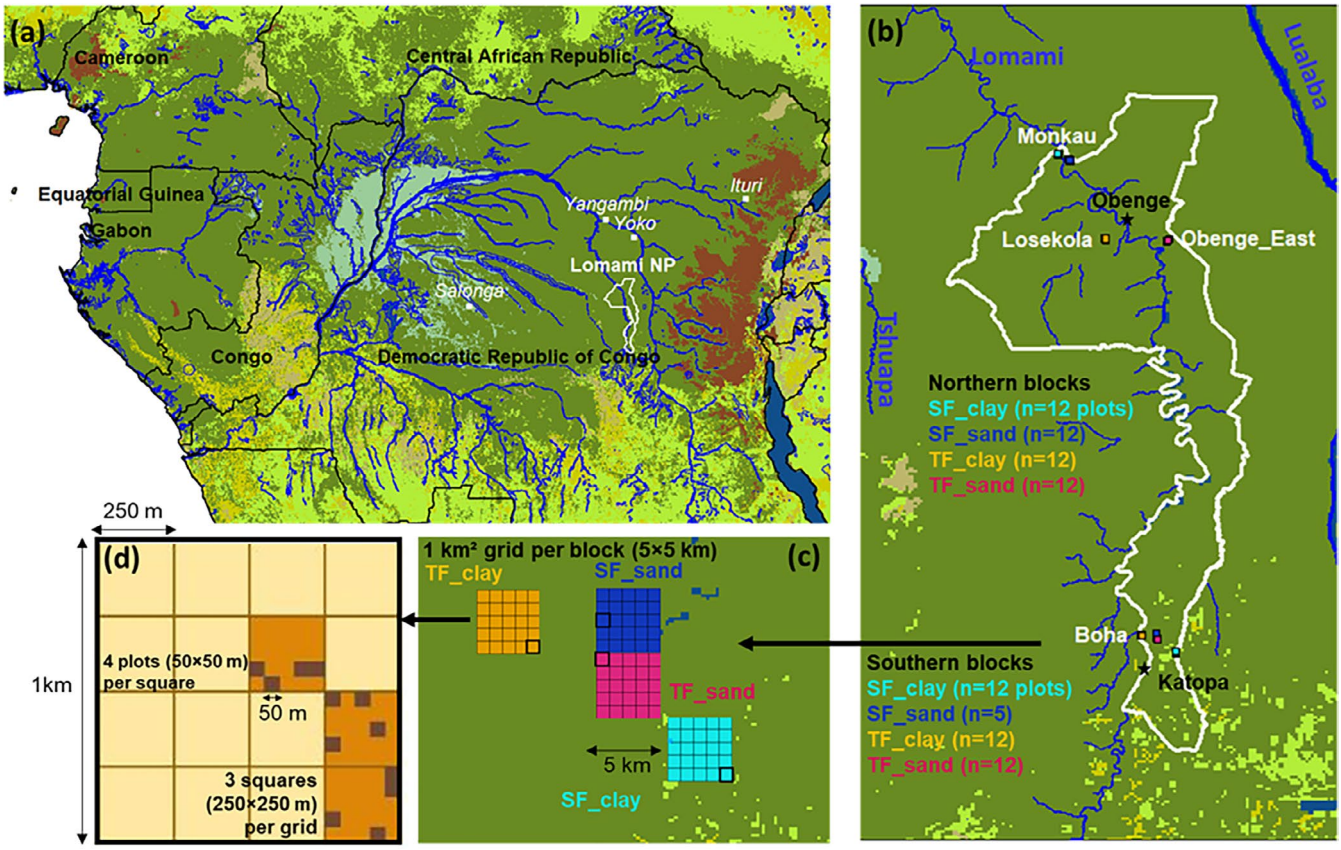


FIGURE 1 | Location of Lomami National Park (NP) and plot network within the park. (a) Location of the Lomami NP and four other sites (Yoko, Yangambi, Salonga and Ituri) in the DRC with a base map of vegetation types according to Global Landcover Map 2000 (Mayaux et al. 2003). The colours indicate closed canopy forest (dark green), open forest (light green), swamp forest (marine green), altitudinal vegetation (brown), shrub savanna (yellow), and grass savanna (khaki). Rivers and major water bodies (blue) are also indicated. (b) The plot network is distributed over four blocks in the north (two in the Monkau zone, one in Obenge_East, one in Losekola) and four blocks in the south (all in the Boha zone). Each block represents a combination of flooding regime and soil type, with SF_clay = seasonally flooded on clay soil, SF_sand = seasonally flooded on sandy soil, TF_clay = *terra firme* on clay soil, and TF_sand = *terra firme* on sandy soil. The two meteorological stations installed in the Obenge and Katopa villages are also indicated (black stars). (c) A block is 5 km × 5 km (*bright turquoise*, golden orange, bright pink, and *royal blue*) subdivided in 1 km × 1 km grid cells. (d) Each 1 km × 1 km grid cell is then subdivided in squares of 250 m × 250 m each (dark orange). Each square is then subdivided in 50 m × 50 m plots (brown). Within each block, we first selected one grid cell (c), then three squares per grid (d), then four plots per square (d) leading to 12 plots following this nested procedure (1 grid × 3 squares × 4 plots).

adjacent *terra firme* areas by visual differences in the imagery. Seasonally flooded and *terra firme* blocks were then selected in areas where patrol data and satellite imagery matched. In each block, soil texture was then visually characterised in the field, following a simplified protocol described by Coche and Laughlin (1985). Specifically, 20 cm deep profiles were dug after removing the litter and organic matter to collect only the mineral soil. The soil samples were then moistened and pressed by hand. If the soil formed a stable cylindrical column, it was classified as clayey. Conversely, if no solid ball formed, the soil texture was classified as sandy. After the exact location of plots was determined (see below for details), we repeated this protocol at the corners of each plot.

In the southern region of the park, the four edaphic combinations were found within a single zone called Boha (Figure 1b). In the northern region, three different zones were selected on both sides of the Lomami River to cover the different combinations: Losekola (a 5 km × 5 km block corresponding to *terra firme* forest on clay soils), Obenge_East (two 5 km × 5 km blocks corresponding to *terra firme* and seasonally flooded forests, both on sandy soils), and Monkau (one 5 km × 5 km block representing seasonally flooded forests on clay soils). Each block was subdivided into 1 km × 1 km grid cells, which were subdivided into 250 × 250 m squares, which were finally subdivided into 50 m × 50 m plots, 0.25 ha each (Figure 1b–d). Within each block, we randomly selected 12 plots following a nested procedure. We first selected one grid cell, then three squares per grid, then four plots per square. We thus selected a total of 96 sample plots (8 blocks × 1 grid × 3 squares × 4 plots) covering 24 ha. Eighty-nine plots were inventoried between 2015 and 2022. The remaining seven plots of the sampling design (all in seasonally flooded forests on sandy soils in the south) could not be installed due to logistic and safety reasons and are thus missing.

In each 0.25 ha plot, all trees with a diameter at breast height (dbh) ≥ 10 cm were measured at 1.30 m from the ground, except in cases of trunk irregularities (such as buttresses, serrations, spines, or stilt roots), where the point of measurement (POM) was recorded. Trees were also labelled (using numbered aluminium tags and aluminium nails), mapped, and taxonomically identified. For multi-stemmed trees, the diameter was measured on the main stem below the point where the tree branches or for each stem separately, depending on where the branching occurs. For a leaning tree, the diameter was measured at 1.30 m along the stem. Botanical samples of each species in each plot were collected and dried. Herbarium samples ($n = 1118$) are stored at the University of Kisangani. The taxonomy was standardised according to the African Plant Database (www.ville-ge.ch/cjb/bd/africa/).

Height measurements were performed in all plots in 2022. A pre-selection of trees was made using the data of the 72 plots inventoried in the 2015–2018 field campaigns, to cover the diameter range in each plot and to adequately sample the largest trees. All trees with diameters ≥ 10 cm were divided into six diameter classes: 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, and ≥ 60 cm. Three trees were measured in each diameter class in each 0.25 ha plot. For the largest class, the height of all trees was measured, varying from zero to seven trees depending on the plots. For multi-stemmed trees with branching below 1.30 m, the height was measured on each stem. In case of a lack of trees for a certain diameter class in a certain plot, the number of trees for this diameter class was increased in the following plot. Pre-selected trees that were severely leaning or broken in the field were not considered for height measurements that were performed with the VERTEX IV (an ultrasonic instrument used to measure tree height, manufactured by Haglöf Sweden) at a distance equal to or greater than the total tree height. Several height measurements (three on average) from different locations were made for the same tree. In the end, total tree height was available for 1571 trees in 82 out of the 89 plots inventoried and covering the tree diameter range (10–140 cm).

2.3 | Forest Diversity Indices and Structural Attributes

To characterise tree species diversity at the 0.25 ha plot scale, we computed several diversity indices, including species richness (S_{obs}), Shannon (H) and Simpson (D) diversity indices, the number of singletons (#Sing), which is a good indicator of the sampling completeness, and the Fisher's alpha index (α). Diversity indices were computed with the vegan package (Simpson et al. 2022). To compare our species richness observed in 0.25 ha plots to that reported in one-ha plots for other sites in DRC (Makana et al. 2008, 2011; Kearsley et al. 2013; Doetterl et al. 2015) and across the tropics (Sullivan et al. 2017), we estimated the species richness per hectare (Sha) based on tree density per hectare (N) and Fisher's alpha (α) for each plot using the following equation (ter Steege et al. 2023): $\text{Sha} = \alpha \times \ln(1 + N/\alpha) \times 1$.

To characterise forest structure at the 0.25 ha-plot scale, we examined five structural attributes: tree density (N), basal area (G), basal-area weighted average wood density (gWD), Lorey's height (HL), and aboveground carbon (AGC). Tree density (≥ 10 cm) is simply counted as the number of trees per hectare (N). Basal area is the sum of the cross-sectional areas at breast height (G, in $m^2\ ha^{-1}$). Basal-area weighted average wood density (gWD, in $g\ cm^{-3}$) is calculated as the average wood density (WD) of each tree in the plot, weighted by its basal area. For each individual tree, wood density was extracted from the global wood density database (Chave et al. 2009). If available we used the species average, which has been demonstrated to be sufficient for accurate aboveground biomass estimation (Fayolle et al. 2013). Species average WD was assigned to most trees (80%). Alternatively, genus and family averages were used for partially identified trees or for missing taxa in the global database. Plot average WD was used for unidentified trees.

Lorey's height (HL, in m) is the average height of all trees in a plot, weighted by tree basal area. Height was only available for a subsample of trees (17.2%) and the prediction from a height-diameter allometric model was used for all trees. We fitted monotonic, second-degree polynomial, and asymptotic allometric models to the data following Fayolle et al. (2016). We used several criteria for model selection (Akaike and Bayesian Information Criteria, Residual Standard Error) and we examined the significance of

the model coefficients. We retained the log-linear polynomial model similarly to Ferry et al. (2010) in French Guiana but several model shapes showed good performance (Table S1). We tested the effect of the flooding regime (seasonally flooded vs. *terra firme*), soil texture (clay vs. sandy soils) and region (north vs. south) on the height-diameter allometry. Our final height-diameter model included the plot as a random effect and soil texture as a fixed effect since trees were found to be slightly but significantly smaller for the same diameter on sandy soils than on clay soils. We used the lm() and nls() functions for the model fitting in the basic open-source package of the R environment and the lme4 package for including fixed and random effects.

Total aboveground carbon (AGC, in Mg C ha^{-1}) in each plot was calculated as the sum of aboveground carbon of each tree. To estimate tree aboveground biomass (AGB, in kg), we used the most recent pantropical allometric equation (Chave et al. 2014) that was earlier validated for the Congo basin (Fayolle et al. 2018). This equation estimates tree AGB from three predictors: the tree diameter (D, in cm), the total height (H, in m), and the wood density (WD in g cm^{-3}). We assumed that AGC represents 45.6% of the tree AGB (Martin et al. 2018).

2.4 | Data Analysis

Accumulation curves showing the accumulation of the number of species observed with the number of plots sampled were drawn separately for flooding regime (seasonally flooded vs. *terra firme*), soil texture (clay vs. sand), and region (north vs. south). The rarefy() function of the vegan package was used for this analysis. To account for potential effects of interactions between factors, multiple linear models including the three factors and their interactions (flooding regime × soil texture, soil texture × region) were fitted using the lm() function. In addition, a spatial autoregressive error model (*Spatial Error Model*) was fitted using the errorsarlm() function from the spdep package (Bivand et al. 2005) to test for the existence of potential spatial autocorrelation. As this model did not significantly improve performance (non-significant λ, similar AIC), the multiple linear models were retained for interpreting environmental effects on diversity indices and structural attributes.

A non-symmetric correspondence analysis (NSCA) was used to detect the gradients in species composition. NSCA is known to emphasise frequent/abundant species whereas the more classical Correspondence Analysis (CA) is highly sensitive to particular correspondences between species-poor plots and rare species (Couteron et al. 2003). We used the dudi.nsc() function of the ade4 package for this analysis (Jombart et al. 2022). The NSCA was applied to the abundance (tree number) matrix of 416 species in the 89 plots. Morphospecies ($n = 30$) were not considered here. The first three NSCA axes representing 48% of total inertia were retained. To test the influence of the flooding regime, soil texture, and region on species composition, we applied a set of analyses of similarity (ANOSIM) tests on the dissimilarity matrix (Bray Curtis index) using the anosim() function of the vegan package. The NSCA was complemented by analyses of the indicator species for the flooding regime, soil type, and region, separately. The indicator values, which represent the association between species and specific environmental conditions, were computed with the IndVal() function of the indicspecies package (Jansen and Dell 2022). Relative species abundance in the plots, expressed as the ratio of the number of trees of the same species to the total number of trees in the plot, was also computed to illustrate the dominance (top five species).

Finally, to test the strength of the relationships between structural attributes, diversity indices, and species composition gradients revealed by the first three NSCA axes, a Principal Component Analysis (PCA) and pairwise Pearson correlation tests were used.

3 | Results

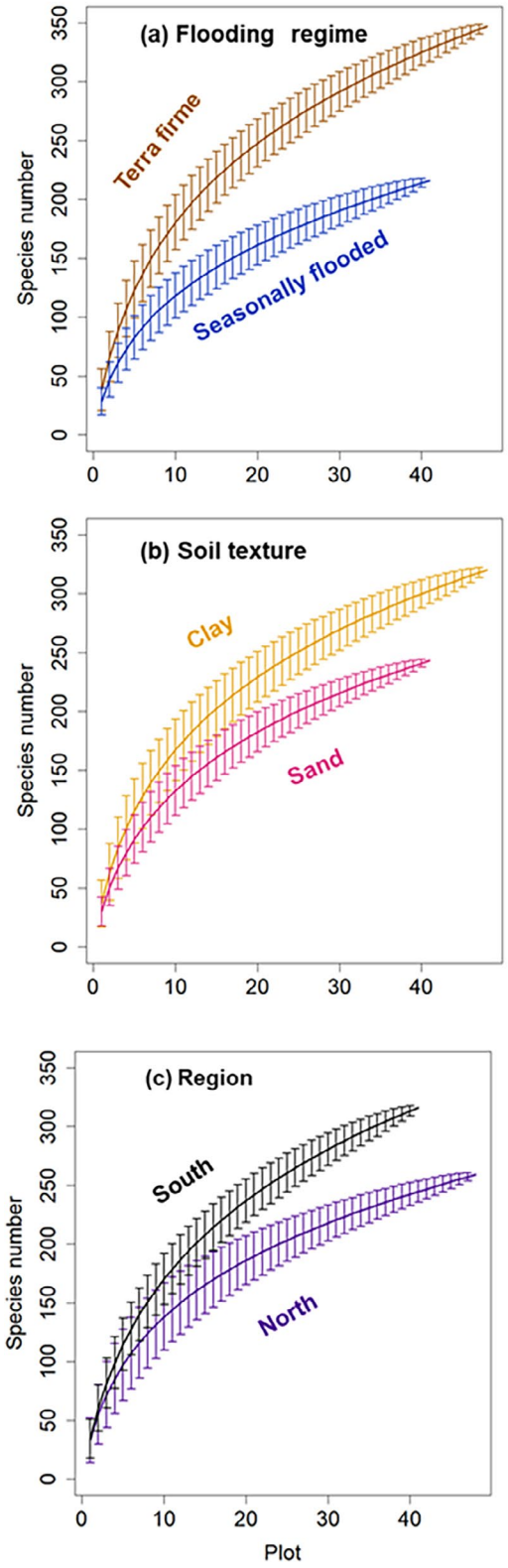
3.1 | Tree Species Diversity and Dominance

A total of 9156 trees ≥ 10 cm dbh belonging to 47 families, 193 genera, and 416 tree species (and 30 morphospecies) were recorded in the 89 plots. The species accumulation curves did not flatten for any of the forest types (Figure 2a–c), and the number of singletons was high (Table 1), which suggested that many more species could have been added with additional survey efforts. Fabaceae was the most speciose family (93 species), followed by Sapotaceae (30 species), and Annonaceae (25 species). *Gilbertiodendron dewevrei* (Fabaceae) was the most abundant species (666 trees, 7.4%), followed by *Baikiaea insignis* (Fabaceae; 537 trees, 6%), *Cleistanthus caudatus* (Euphorbiaceae; 397 trees, 4.4%), Greenwayodendron *suaveolens* (Annonaceae; 319 trees, 3.5%), and *Guibourtia demeusei* (Fabaceae; 264 trees, 2.9%) (Figure 2d–f). These five most abundant species accounted for 24.2% of all trees. Seasonally flooded forests showed the highest level of dominance, with the five most abundant species accounting for 38.5% of all trees, whereas in *terra firme* forests, the five most abundant species accounted for only 20%.

Average plot richness was 34 ± 9.1 species, with a Shannon index of 3.0 ± 0.4, a Simpson index of 0.92 ± 0.04, a Fisher's alpha of 19.7 ± 9.82, and 17.6 ± 6.59 singletons. Flooding regime and region significantly affected all diversity indices (Table 1) with tree diversity consistently higher in *terra firme* forests than in seasonally flooded forests. Although no significant effect of soil texture was detected, significant interactions were found between soil texture and both flooding regime and region, for all indices. Species accumulation curves support these findings, showing that *terra firme* forests were richer in species than seasonally flooded forests (Figure 2d), whereas region exhibited a weak effect on tree species diversity (Figure 2c).

3.2 | Tree Species Composition

An NSCA was applied to the abundance matrix of the 416 species in the 89 plots to assess the variability in tree species composition across Lomami NP (Figure 3). The first NSCA axis explained 22.6% of the total variance and showed that differences in species composition were primarily driven by flooding regime, contrasting seasonally flooded and *terra firme* forests. The ANOSIM test confirmed the strong and significant dissimilarity between seasonally flooded and *terra firme* forests ($p < 0.001$ and R^2 close



Dominant species		Indicator species	
(d) Seasonally flooded vs terra firme			
Gilbertiodendron dewevrei (12.5)	*Greenwayodendron suaveolens* (5.6)	*Guibourtia demeusei* (0.9***)	*Greenwayodendron suaveolens* (0.8***)
Baikiaea insignis (10.4)	*Cleistanthus caudatus* (4)	*Gilbertiodendron dewevrei* (0.8***)	*Anonidium mannii* (0.8***)
Guibourtia demeusei (6.2)	*Leonardoxa bequaertii* (4)	*Diospyros iturensis* (0.8***)	*Diospyros canaliculata* (0.7***)
Cleistanthus caudatus (4.9)	*Diospyros canaliculata* (3.4)	*Baikiaea insignis* (0.8***)	*Diospyros zenkeri* (0.7***)
Dialium corbisieri (4.5)	*Scorodophloeus zenkeri* (3)	*Napoleonaea vogelii* (0.7***)	*Strombosia pustulata* (0.7**)
(e) Clay vs sand			
Gilbertiodendron dewevrei (8.6)	*Cleistanthus caudatus* (6.9)	*Diospyros melocarpa* (0.7***)	*Leonardoxa bequaertii* (0.8***)
Baikiaea insignis (5.6)	*Baikiaea insignis* (6.5)	*Diospyros iturensis* (0.7***)	*Cynometra pedicellata* (0.7***)
Guibourtia demeusei (3.6)	*Leonardoxa bequaertii* (6.4)	*Dacryodes klaineana* (0.7**)	*Baphia longepedicellata vel.sp.aff* (0.7***)
Greenwayodendron suaveolen (3.6)	*Gilbertiodendron dewevrei* (5.9)	*Diospyros cinnabarina* (0.7***)	*Xylopia phloiodora* (0.7***)
Dichostemma glaucescens (3.4)	*Scorodophloeus zenkeri* (3.5)	*Diospyros canaliculata* (0.7***)	*Barteria nigritana* (0.6**)
(f) North vs south			
Gilbertiodendron dewevrei (9.3)	*Baikiaea insignis* (8)	*Lebrunioden-dron leptan thum* (0.9***)	*Dichostemma glaucescens* (0.7***)
Cleistanthus caudatus (7.4)	*Gilbertiodendron dewevrei* (5.4)	*Cleistanthus caudatus* (0.9***)	*Barteria nigritana* (0.7***)
Leonardoxa bequaertii (5.1)	*Greenwayodendron suaveolens* (5.4)	*Diospyros melocarpa* (0.7***)	*Anthonotha macrophylla* (0.7***)
Dialium corbisieri (4.4)	*Dichostemma glaucescens* (4.5)	*Dacryodes klaineana* (0.7***)	*Xylopia phloiodora* (0.6***)
Baikiaea insignis (4)	*Diospyros iturensis* (3.7)	*Normandiodendron romii* (0.7***)	*Synsepalum longecuneatum* (0.6**)

FIGURE 2 | Species accumulation curves of inventoried plots for (a) flooding regime, (b) soil texture, and (c) region. The five most abundant species and the five species with the highest indicator values are presented for flooding regime (d), soil texture (e) and region (f), using the same colour code. The relative abundance (% stem) and the indicator value (between 0 and 1) are given in brackets for dominant and indicator species, respectively. The significance level is also indicated for the indicator value (*** for $p < 0.001$; ** for $p < 0.01$; and * for $p < 0.05$).

TABLE 1 | Results of multiple linear models testing the effects of flooding regime (seasonally flooded vs. *terra firme*), soil texture (clay vs. sand), region (north vs. south), and their interactions on (a) diversity indices and (b) structural attributes. Diversity indices: Number of species observed (Sobs), Shannon (H), Simpson (D) diversity index, number of singletons (#Sing), and Fisher's α. Structural attributes: Tree density (N), basal area (G), Lorey's height (HL), wood density weighted by basal area (gWD), and aboveground carbon (AGC). Significant differences are highlighted by the significance level (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$).

(a) Tree species diversity	**Sobs**			**H**			**D**			**#Sing**			**Fisher's**		
Predictors	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***
Intercept	30.88	28.02 to 33.73	0.001***	2.86	2.74 to 2.99	0.001***	0.90	0.89 to 0.92	0.001***	16.02	13.67 to 18.37	0.001***	17.24	14.32 to 20.16	0.001***
Texture soil [Sand]	−3.18	−7.30 to 0.94	0.129	−0.09	−0.27 to 0.09	0.313	−0.01	−0.03 to 0.01	0.483	−3.07	−6.46 to 0.32	0.075	−3.87	−8.09 to 0.34	0.071
Flooding regime [*Terra firme*]	16.25	12.96 to 19.54	0.001***	0.71	0.57–0.86	0.001***	0.06	0.04 to 0.07	0.001***	9.96	7.25 to 12.67	0.001***	17.94	14.57 to 21.31	0.001***
Region [South]	−3.83	−7.13 to −0.54	0.023*	−0.27	−0.41 to −0.12	0.001***	−0.02	−0.04 to −0.01	0.005**	−2.12	−4.83 to 0.58	0.123	−7.17	−10.54 to −3.80	0.001***
Texture soil [Sand] × Flooding regime [*Terra firme*]	−14.56	−19.51 to −9.60	0.001***	−0.55	−0.77 to −0.33	< 0.001***	−0.03	−0.06 to −0.01	0.010*	−9.36	−13.43 to 5.29	0.001***	−16.01	−21.07 to −10.94	0.001***
Texture soil [Sand] × Region [South]	8.47	3.52 to 13.42	0.001**	0.41	0.19 to 0.63	0.001***	0.03	0.01 to 0.06	0.012*	5.69	1.62 to 9.77	0.007**	11.21	6.15 to 16.27	0.001***
Observations		89			89			89			89			89	
R^2/R^2 adjusted		0.625/0.602			0.604/0.581			0.452/0.419			0.516/0.487			0.663/0.643	

(b) Structural attributes	**N (ha^{-1})**			**G ($m^2\ ha^{-1}$)**			**HL (m)**			**gWD ($g cm^{-3}$)**			**AGC (Mg C ha^{-1})**		
Predictors	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***
Intercept	398.75	374.89 to 422.61	0.001***	28.96	26.67 to 31.24	0.001***	30.28	29.34 to 31.21	0.001***	0.74	0.72 to 0.76	0.001***	195.95	178.24 to 213.65	0.001***
Texture soil [Sand]	−7.65	−42.11 to 26.81	0.660	−4.52	−7.82 to −1.22	0.008**	−2.33	−3.68 to −0.97	0.001**	−0.01	−0.04 to 0.02	0.363	−47.28	−72.85 to −21.71	0.001***

(Continues)

TABLE 1 | (Continued)

(b) Structural attributes	N (ha^{-1})			G ($m^2\ ha^{-1}$)			HL (m)			gWD (gcm^{-3})			AGC (Mg C ha^{-1})		
Predictors	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***	**Estimates**	**Confidence interval**	***p***
Flooding regime [*Terra firme*]	−6.83	−34.38 to 20.72	0.623	0.12	−2.52 to 2.75	0.930	0.34	−0.74 to 1.42	0.536	−0.07	−0.09 to −0.05	0.001***	−20.11	−40.55 to 0.33	0.054
Region [South]	54.83	27.28 to 82.38	0.001***	−0.46	−3.10 to 2.17	0.728	−1.77	−2.86 to −0.69	0.002**	−0.02	−0.05 to −0.00	0.044*	−21.15	−41.59 to −0.71	0.043*
Texture soil [Sand] × Flooding regime [*Terra firme*]	−21.36	−62.77 to 20.04	0.308	2.61	−1.35 to 6.58	0.193	1.64	0.01 to 3.27	0.048*	0.06	0.02 to 0.09	0.002**	42.94	12.21 to 73.66	0.007**
Texture soil [Sand] × Region [South]	−30.97	−72.38 to 10.44	0.141	−2.49	−6.45 to 1.47	0.215	−0.06	−1.69 to 1.57	0.940	−0.00	−0.04 to 0.03	0.851	−12.06	−42.78 to 18.67	0.437
Observations		89			89			89			89			89	
R^2 / R^2 adjusted		0.295/0.252			0.215/0.168			0.304/0.262			0.382/0.345			0.273/0.229	

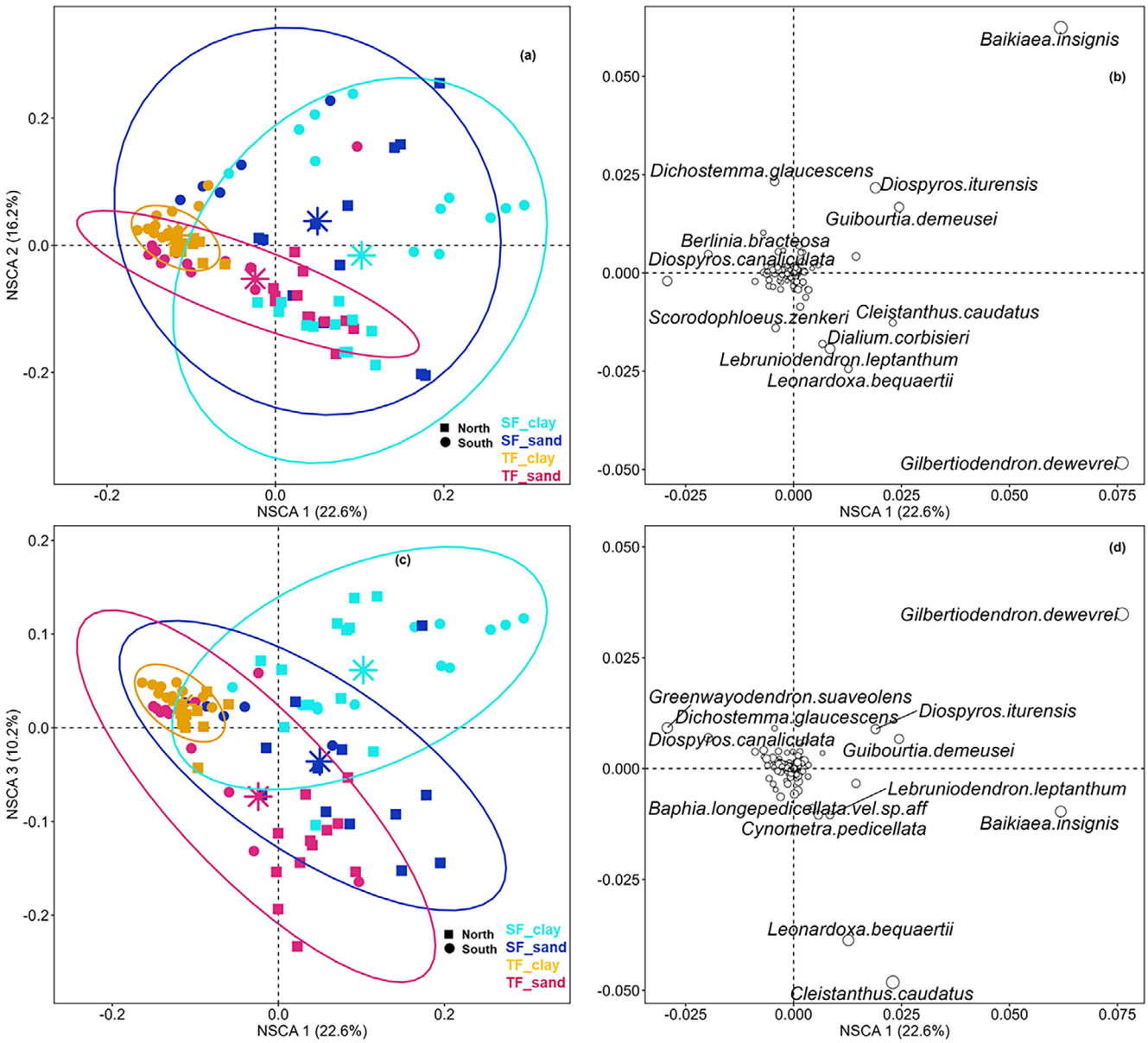


FIGURE 3 | Variation in trees species composition as revealed by a non-symmetric correspondence analysis (NSCA). (a) and (c) show the projection of the 89 0.25-ha plots onto the first three NSCA axes, with stars indicating the centroid of each group. (b) and (d) display the projection of the 15 most discriminatory species, based on their contributions to the first three NSCA axes. The size of symbols is proportional to the species abundance and the type and colour of symbols used for plots dependency on flooding regime (in blue, SF = seasonally flooded vs. TF = *terra firme* forests), soil texture (in light colour, clay vs. sand) and region (square = north vs. circle = south).

to 1). The second NSCA axis explained 16.2% of the variance and showed differences among seasonally flooded forests, with plots in the north (positive scores, squares) characterised by a greater abundance of *G. dewevrei* and plots in the south (negative scores, circles) characterised by a higher abundance of *Baikiaea insignis* and *Guibourtia demeusei* (Figure 3a,b). All three species belong to the Fabaceae family. The third NSCA axis explained 10.2% of the variance and showed a slight effect of soil texture discriminating *terra firme* forests on sandy soils (golden orange) from seasonally flooded forests on clay soils (*bright turquoise*) in the northern part of the park (squares, Figure 3c,d).

Analyses of dominant and indicator species confirmed the species distribution patterns identified by NSCA (Figure 2d–f). The three species associated with the second axis were among the most significant indicator species of seasonally flooded forests, together with *Diospyros iturensis* and *Napoleonaea vogelii*. *Greenwayodendron suaveolens*, the dominant species in terra firme, also emerged as a major indicator species (Figure 2d). Four of the five indicator species on clay soils belonged to the genus *Diospyros* (Figure 2e).

3.3 | Forest Structural Attributes

Across all plots, mean tree density was 405 ± 55.5 trees ha^{-1}, basal area was $27 \pm 5\,m^2\,ha^{-1}$, Lorey's height was $29 \pm 2.2\,m$, and wood density weighted by basal area was $0.70 \pm 0.05\,g\,cm^{-3}$. Forest structural attributes varied markedly across the analysed factors (Table 1). Region had the broadest influence, significantly

affecting tree density ($p < 0.001$), Lorey's height ($p = 0.002$), wood density weighted by basal area ($p = 0.044$), and aboveground carbon stocks ($p = 0.043$). Tree density was higher in the south than in the north (427 vs. 387 trees ha^{-1}), whereas Lorey's height (29.7 m vs. 28.2 m), wood density (0.72 vs. 0.69 g cm^{-3}), and aboveground carbon stocks (173 vs. 151 Mg C ha^{-1}) were higher in the north. Soil texture significantly affected basal area ($p = 0.008$), Lorey's height ($p < 0.001$), and aboveground carbon stocks ($p < 0.001$), with clay soils showing higher values than sandy soils. Height–diameter allometry did not differ significantly between *terra firme* and seasonally flooded forests, but for a similar diameter, trees were shorter on sandy than on clay soils (Figure S1). Flooding regime only influenced wood density weighted by basal area, which was significantly higher in seasonally flooded forests than in *terra firme* forests ($p < 0.001$). Significant interactions were found between soil texture and flooding regime for Lorey's height ($p = 0.048$), wood density weighted by basal area ($p = 0.002$) and aboveground carbon stocks ($p = 0.007$).

3.4 | Relationship Between Forest Structure, Diversity, and Composition

The first PCA axis explains 41.3% of the total variance and reveals a strong correlation among all diversity indices, which are associated with a specific species composition (NSCA1) and higher wood density weighed by basal area (Figure 4b). The second PCA axis explains 23.4% of the variance and shows that structural attributes are highly positively correlated, except tree density (N) which is negatively correlated with the other structural attributes. This illustrates a difference between plots with large trees (high basal area, Lorey's height and carbon stock) vs. plots with many small trees (Figure 4a). This structural variation is not necessarily driven by the edaphic conditions (a combination of flooding regime and soil texture) but is associated with a particular species composition (NSCA2), and the location in the park; that is, southern plots tend to have more small trees, a lower canopy, and less basal area and carbon (Figure 4b). Our results show that structural attributes (PCA axis 2) are completely orthogonal to diversity indices (PCA axis 1), though there is a weak but significant relationship between structural attributes such as tree density, basal area, height, and diversity indices (Figure S2).

The plot network at Lomami NP covers the variations in carbon stocks (80–300 Mg C ha^{-1}) and tree species richness (20–100 tree species ha^{-1}) both per hectare, observed across DRC (Figure 5a) and tropical Africa (Figure 5b). Tree species richness per hectare is however more restricted for tropical forests in the inner Congo basin, across Lomami NP or elsewhere in DRC, than that of the other tropical regions, where tree species richness can reach up to 300 tree species per hectare. Finally, across Lomami NP, carbon stocks and species richness are uncorrelated, and this pattern holds when Lomami data are integrated with 1-ha forest plots from the DRC and across the tropics (Figure 5a,b).

4 | Discussion

Species diversity across Lomami NP was significantly higher in *terra firme* than in seasonally flooded forests, and higher in northern than in southern forests. While soil texture alone did not significantly affect tree diversity, it showed significant interactions with both flooding regime and region. Species composition was primarily driven by flooding regime, with little overlap in dominant species between species-rich *terra firme* and species-poor seasonally flooded forests. We also found high structural variability between forests on clay soils and those on

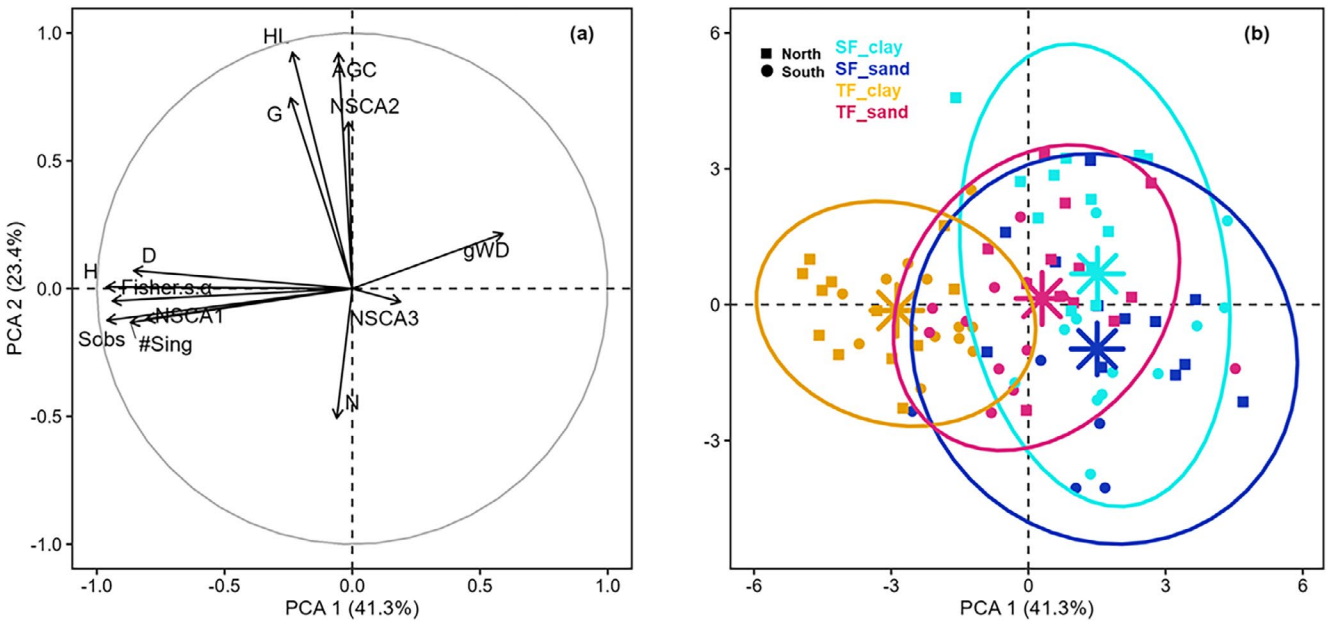


FIGURE 4 | Principal Component Analysis (PCA) testing relationships between forest structural attributes including tree density (N), basal area (G), Lorey's height (HL), and aboveground carbon (AGC), wood density weighted by basal area (gWD), diversity indices including species richness (S_{obs}), Simpson (D) and Shannon (H), the number of singletons (#Sing), Fisher's alpha (α), and species composition gradients (NSCA axes 1–3, Figure 3). (a) Correlation circle of the PCA. (b) Projection of the plot scores on the first two ordination axes of the PCA, with stars representing the centroid of each group.

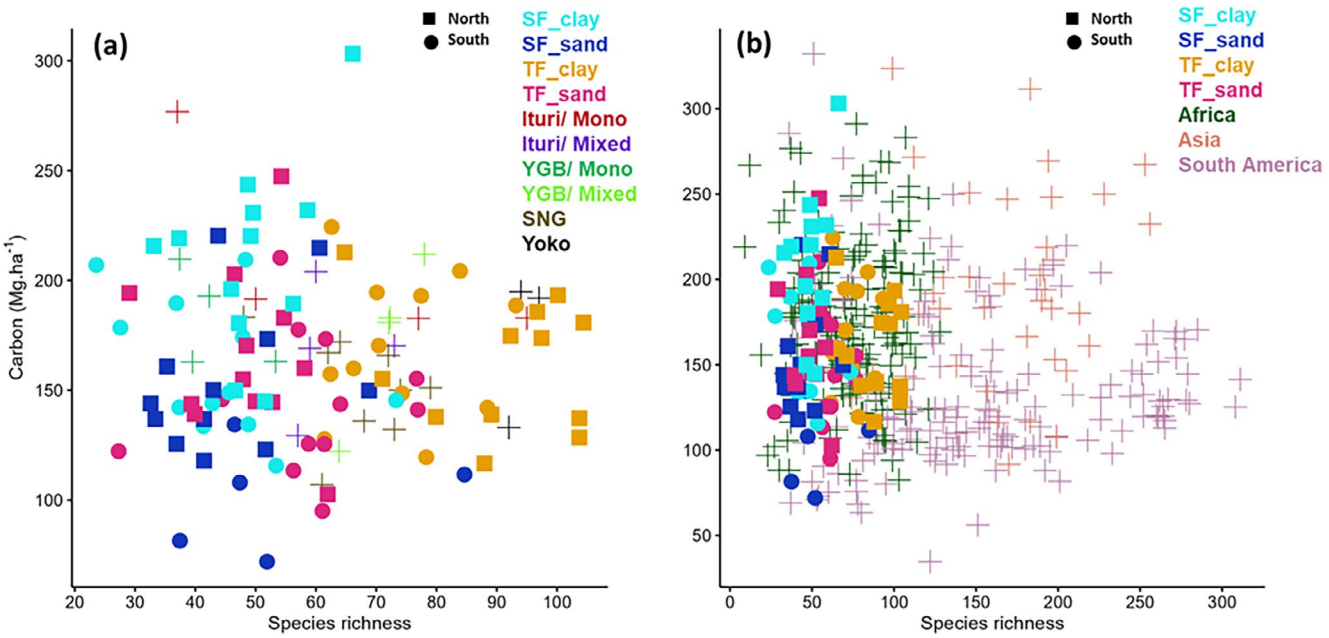


FIGURE 5 | Carbon stocks and species richness per hectare. The estimates for the Lomami NP (this study, squares and circles) for seasonally flooded (SF) and *terra firme* (TF) forests on clay and sandy soils are confronted with available data for other sites (a) in the DRC (crosses) including Yoko from Doetterl et al. (2015), Salonga (SNG) from Makana et al. (2008), Ituri from Makana et al. (2011), Yangambi (YGB) from Kearsley et al. (2013), separately for mixed forest (Mixed) and monodominant *Gilbertiodendron dewevrei* forests (Mono), and (b) across the tropics (crosses) from Sullivan et al. (2017).

sandy soils, with the former having significantly higher basal area, tree height, and carbon stocks. No significant main effect of flooding regime on structural attributes was detected, except for wood density weighted by basal area. Finally, carbon stocks and species richness were independent in mature forests, confirming earlier findings across the tropics.

4.1 | Tree Species Diversity and Dominance

Overall tree species richness (416 species) for Lomami NP is greater than that recorded in Ituri forests, where 278 tree species were found in four plots totaling 40 ha (Makana et al. 2004). This result shows the greater floristic diversity of Lomami NP in comparison to other forests in DRC. The importance of this region for biodiversity conservation is further confirmed by the discovery of new species in recent times (Hart et al. 2012; Sosef et al. 2019). The Fabaceae, which is an important and diverse family in tropical Africa and in South America (Silva de Miranda et al. 2022), appeared extremely diverse in Lomami NP, with 93 species, and 42 genera inventoried. However, the plot richness and diversity remain low compared to many moist forests in Asia or in the Neotropics (Sullivan et al. 2017).

At the local scale, alpha diversity was lower in seasonally flooded forests than in *terra firme* forests, and on sandy soils when compared to clay soils. The same trend has been reported in the Amazon (Hawes et al. 2012; Roa-Fuentes et al. 2022). Low diversity in seasonally flooded forests is likely due to strong constraints imposed by periodic waterlogging, which only a few species tolerate, leading to low species richness and strong dominance by a few species. High dominance by a single tree species is also associated with low species richness in the monodominant *Gilbertiodendron dewevrei* forest in the Ituri region (Hart et al. 1989), but *Gilbertiodendron*-dominated forests are not always associated with seasonal flooding. In addition, the greater diversity found on clay soils is likely due to better nutrient and water retention, leading to higher fertility (Gautam et al. 2016; Nadeau and Sullivan 2015).

When extrapolating species richness to the scale of 1 ha-plots using Fisher's alpha and tree density, the *terra firme* forest of Lomami NP shows a higher species richness than other forests of the DRC, such as Salonga, Ituri, and Yangambi. This observation could be attributed to the specific location of Lomami NP, within the Congolese sub-center of endemism (White 1986).

Some of the patterns we observe could be driven by species characteristics rather than edaphic conditions. Particularly the presence of *Gilbertiodendron dewevrei* can strongly impact community composition (Glick et al. 2021; Hall et al. 2020). This species often occurs in monodominant stands, probably driven by efficient acquisition of nutrients from soil organic matter, limiting nutrient availability for co-occurring species. *G. dewevrei* is the only species with the highest score on both the first and second ordination axes in Figure 3. However, several other observations contradict competition by *G. dewevrei* as the main driver of the patterns we observed. First, *G. dewevrei* obtains a maximum of 12.5% of the total stem density, particularly in seasonally flooded forests. The species can therefore not be classified as monodominant in the Lomami NP, as monodominance is set to at least 50% of total stem abundance (Connell and Lowman 1989). Secondly, seasonally

flooded forests in Lomami have higher stem density and lower basal area than *terra firme* forests (Table 1), while competition by *G. dewevrei* generally leads to significantly lower stem density and higher basal area than surrounding mixed forests (Hart et al. 1989; Makana et al. 2004, 2011; Glick et al. 2021). Third, we found no significant correlation between the abundance of *G. dewevrei* (% stem density) and total plot-level stem density ($r^2 = 0.008$). Finally, we reproduced our calculations by extracting plots where *G. dewevrei* exceeded 5% of the stem density and where it was below 5% and found similar results (Table S2).

4.2 | Tree Species Composition

Our results show a variation in species composition due to the flooding regime and spatial configuration (region), and to a lesser extent, soil texture, within the forests of Lomami NP. Tree species on sandy soils in the north and south are very dissimilar from each other on the NSCA axis, showing a strong floristic heterogeneity as shown by Potts et al. (2002) in Asia. The same kind of floristic differentiation was also observed in the Amazon between flooded and *terra firme* forests (Tuomisto et al. 2003), between clay and sandy soils in the Central African Republic (Gourlet-Fleury et al. 2011) and in the DRC (Vleminckx et al. 2015).

When considering all forest types together, only 39% of the dominant species across Lomami NP (7 out of 18) are also listed as abundance hyperdominant species in a previously published pan-African dataset showing that 77 species comprise 50% of trees throughout central Africa (Cooper et al. 2024). Furthermore, only 22% of the dominant species across Lomami NP (2 out of 9) are also listed as biomass hyperdominant species in a previously published dataset showing that 18 species comprise 50% of biomass throughout central Africa (Bastin et al. 2015). This relatively small overlap between the dominant species in Lomami NP and the hyperdominant species across central Africa suggests that tree species composition is quite different in Lomami NP. Therefore, inventory data from the Lomami NP should be considered for future large-scale analysis of tropical tree biodiversity and (hyper)dominance since earlier studies did not include any data from the south-eastern part of the inner Congo basin (see plot distribution maps in Bastin et al. 2015; Cooper et al. 2024).

4.3 | Forest Structural Attributes

Our results show that forest structural attributes in Lomami NP (Table 1) are highly variable and more strongly affected by the region (north vs. south) and soil texture (clay vs. sand) than by the flooding regime. Our results also show that carbon stocks are higher in forests on clay soils than in those on sandy soils. This is consistent with findings from other wet tropical regions, such as in Amazonia (Paoli et al. 2008; Laurance et al. 1999; de Castilho et al. 2006). In contrast, our results differ from findings in the Amazon regarding the influence of the flooding regime on structural attributes, where *terra firme* forests have significantly higher carbon stocks compared to seasonally flooded forests (Hawes et al. 2012). The contradiction is probably due to differences in basic structural parameters between the two continents. Amazonian forests are typically characterised by smaller trees and higher tree density (Lewis et al. 2013; Feldpausch et al. 2011, 2012) leading to lower carbon stocks (Slik et al. 2013). In addition to the similarity in stand structure between *terra firme* and seasonally flooded forests in Lomami NP, we also found that height-diameter allometry was not significantly affected by the flooding regime, unlike in the Amazon (Asner et al. 2013) and in French Guiana (Ferry et al. 2010), where tree height is significantly lower for the same diameter in seasonally flooded forest than in *terra firme* forest.

Our results are the first to shed light on forest structural attributes in the southeastern part of the understudied inner Congo basin (Hubau et al. 2020; Kearsley et al. 2013; Lewis et al. 2013). In Lomami NP, average tree density (405 trees ha^{-1}) and basal area (25–29 $m^2 ha^{-1}$) fall within the lower range of values reported for other well-studied mixed forest sites in DRC, such as Salonga, Ituri, Yangambi, and Yoko (Makana et al. 2004, 2008, 2011; Kearsley et al. 2013; Doetterl et al. 2015). The lower values in Lomami and Salonga may reflect their remoteness and limited disturbance, where self-thinning could reduce stem density over time (Lewis et al. 2013). Carbon stocks in Lomami NP (148–198 Mg C ha^{-1}) are also comparable to those reported for mixed forests in DRC (Makana et al. 2008, 2011; Kearsley et al. 2013; Doetterl et al. 2015).

When examining structural variations across central Africa (Lewis et al. 2013), Lomami NP exhibits a lower carbon stocks (148 to 173 Mg C ha^{-1}) compared to the average carbon stocks (204 Mg C ha^{-1}) in Gabon but higher than the lowest carbon stocks (147 Mg C ha^{-1}) observed in the Central African Republic according to Lewis et al. (2013). However, many uncertainties are associated with AGC estimates and maps (Mitchard et al. 2011), and within-site variation can be important as demonstrated here. This is even more true when plot size is small, and the size of one-quarter of a hectare is recognised as the minimum plot size (Chave et al. 2014).

Our results are important for the carbon prioritisation and conservation approach promoted under REDD+ by providing knowledge of the spatial variation of carbon stocks, tree species diversity, and composition and a vast forest area that has never been inventoried before. We emphasise that forests in the Lomami NP are important because they are characterised by a high degree of structural variability, high tree species richness and carbon stocks. Forests need to be further studied in this region, with specific attention to seasonally flooded forests that are less diverse than *terra firme* forests but harbour a unique tree species composition and important carbon stocks. Our findings also raise important questions about the ecological niche of *Gilbertiodendron dewevrei*, which emerged as one of the most abundant species in seasonally flooded forests. Although monodominant stands dominated by *G. dewevrei* are typically found on well-drained soils in central and western Africa (Connell and Lowman 1989; Hart 1990), this species has also been regularly reported in sparse occurrences along rivers (Kearsley et al. 2017; Barbier et al. 2017; Glick et al. 2021). The trait-based assessment of *G.*

dewevrei by Kearsley et al. (2017) suggests that certain traits related to water use and transport could favour its presence near forest rivers. These observations underscore the need for more targeted ecological studies to refine our understanding of this species' niche, which may be broader than currently recognised.

Author Contributions

Modestine Kompanyi: conceptualization, methodology, funding acquisition for the inventory campaign, data collection, analysis, writing the original manuscript, review, and editing. **Wannes Hubau:** conceptualization, methodology, validation, writing the original manuscript, review, and editing. **Jean-Remy Makana:** conceptualization, methodology, supervision of data collection, writing the original manuscript, review, and editing. **Terese Hart and John Hart:** conceptualization, methodology, and funding acquisition for the inventory campaign and review. **Adeline Fayolle:** conceptualization, methodology, validation, writing the original manuscript, review, and editing.

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Disclosure

Permission to reproduce material from other sources: Estimates of carbon stocks and tree species richness for plots spread over DR Congo (Makana et al. 2008, 2011; Kearsley et al. 2013; Doetterl et al. 2015) and across the tropics (Sullivan et al. 2017) were extracted from published studies, either in the main text or in Supporting Information.

Ethics Statement

The authors have nothing to report.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Plot-level data underlying analysis in this paper can be found on Dryad: https://doi.org/10.5061/dryad.rv15dv4hw. Full tree-by-tree data can be obtained from the authors on demand.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70118-sup-0001-AppendixS1.zip.

Biographies

Modestine Kompanyi is a Ph.D. candidate in Gembloux Agro-Bio Tech, University of Liège. Her research focuses on the variations in forest structure and diversity (including composition) across the Lomami National Park.

Wannes Hubau is a research scientist whose primary research interests include carbon stocks and dynamics in tropical forests in the Congo basin.

Jean-Remy Makana is a senior researcher at the University of Kisangani, and **John Hart** and **Teresa Hart** are senior researchers at Lukuru Wildlife Research Foundation. Their research interests focus on the ecology and conservation of tropical forests in the Democratic Republic of Congo.

Adeline Fayolle is a research scientist whose research interests include tree allometry and carbon stocks, tree biodiversity and biogeography in Africa.