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# Contrasts in forest structure, floristic diversity and aboveground carbon stocks between peat swamp forest and terra firme forest in northern Congo

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## Abstract

The Congo Basin plays a central role in global climate regulation and biodiversity conservation, yet plot-based comparisons among contrasting forest types remain limited. This study compares forest structure, floristic diversity and aboveground carbon stocks between peat swamp forest and terra firme forest in Likouala, northern Republic of the Congo. The analysis is based on 23 one-hectare plots, comprising 12 plots in peat swamp forest and 11 plots in terra firme forest. Forest structure was assessed using stem density, mean diameter at breast height (DBH), basal area and diameter-class distributions. Floristic diversity was analysed using species richness, family richness, Shannon, Simpson and Pielou indices, and floristic turnover. Aboveground biomass was estimated from DBH and wood specific gravity using a regional allometric equation developed for Congo Basin forests, and converted to carbon using a carbon fraction of 0.47.

The results show that peat swamp forest has a more developed structure, with a mean DBH of 22.63 cm, a basal area of 29.34 $m^2$ $ha^{-1}$ and an aboveground carbon stock of 166.16 Mg C $ha^{-1}$. Terra firme forest in Likouala has a slightly higher stem density, a basal area of 24.47 $m^2$ $ha^{-1}$ and an aboveground carbon stock of 125.80 Mg C $ha^{-1}$, but it supports higher species richness, with 155 species compared with 129 in peat swamp forest. Floristic overlap between the two forest types is extremely low, with only two shared species and a Jaccard index of 0.007. Large trees play a disproportionate role in carbon storage: trees with DBH ≥ 50 cm contribute 48.2% of aboveground carbon in peat swamp forest and 68.7% in terra firme forest. These findings indicate that peat swamp forest and terra firme forest in Likouala are not interchangeable: the former represents a major aboveground carbon reservoir, whereas the latter makes a substantial contribution to regional floristic diversity.

**Keywords:** Congo Basin; Peat Swamp Forest; Terra Firme Forest; Aboveground Biomass; Forest Carbon; Floristic Diversity**.**

## 1. Introduction

Tropical forests simultaneously provide climate-regulation functions, biodiversity conservation and support for human livelihoods. However, these functions are not distributed uniformly across forest types and landscapes. In the Congo Basin, forest ecosystems contribute to global climate regulation, regional hydrological cycling, biodiversity conservation and ecosystem services on which millions of people depend [1]. Despite this importance, the Congo Basin remains less

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well documented than Amazonia or Southeast Asia, particularly with respect to relationships among forest structure, floristic diversity and carbon stocks.

The peatlands of the Cuvette Centrale have profoundly reshaped scientific understanding of the Congo Basin. They constitute the largest tropical peatland complex currently known, covering approximately 167,600 km$^2$ and storing nearly 29–30 Pg of organic carbon in soils [2,3,5]. Recent studies and syntheses further emphasise that, despite their global importance, African tropical peatlands remain insufficiently documented in terms of biodiversity, greenhouse-gas dynamics, vegetation structure and long-term ecological trajectories [4,6]. This knowledge gap is particularly important for the aboveground tree component, which is less frequently assessed than soil carbon in peatland studies.

Terra firme forests remain essential components of the Congolese forest landscape. They may exhibit high floristic diversity, complex species assemblages and substantial structural heterogeneity. Studies conducted in northern Congo have shown that terra firme forests, seasonally flooded forests and hydromorphic forests differ in structure, floristic composition and biomass [7]. Similarly, work along the Impfondo–Dongou axis indicates that Likouala includes several forest facies, including primary terra firme forests, hydromorphic forests dominated by Lophira alata Banks ex C.F.Gaertn. or Guibourtia demeusei (Harms) J.Leonard, and degraded forests dominated by pioneer species such as Musanga cecropioides R.Br. and Macaranga spp. [8].

A central scientific question is therefore whether neighbouring peat swamp and terra firme forests represent a simple carbon–biodiversity contrast or a more complex ecological complementarity. Pantropical analyses show that tree diversity and aboveground carbon stocks are not always spatially congruent at the 1-ha plot scale [9]. It is therefore important to assess carbon-storage and biodiversity-conservation functions separately, particularly in regions where field data remain scarce.

The overall objective of this study is to compare forest structure, floristic diversity and aboveground carbon stocks between peat swamp forest and terra firme forest in Likouala, northern Congo. The specific objectives are to: (i) compare forest structure using stem density, mean DBH, basal area and diameter-class distributions; (ii) analyse differences in floristic diversity and composition; and (iii) compare aboveground carbon stocks and the contribution of diameter classes to carbon storage.

## 2. Materials and methods

### 2.1. Study design and sampling units

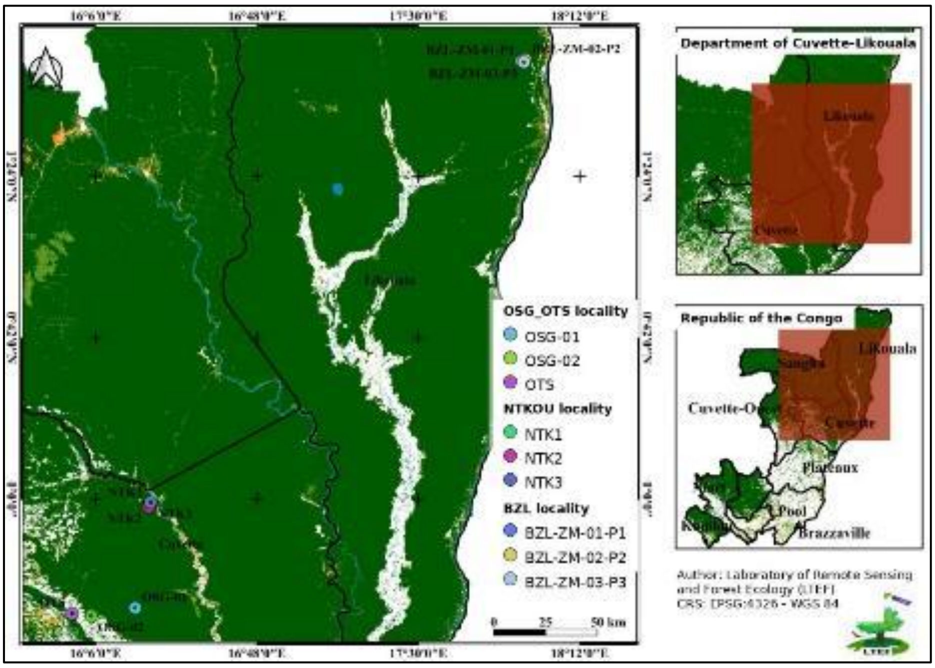


**Figure 1** Study area

The study compares two contrasting forest types in northern Congo: peat swamp forest and terra firme forest in Likouala. The analysis is based on 23 one-hectare plots, including 12 plots in peat swamp forest and 11 plots in terra firme forest. Each plot was treated as a comparable 1-ha sampling unit. This design allows direct comparison of structural, floristic and carbon attributes between the two forest types.

### 2.2. Forest-structure analysis

Stem density was calculated as the ratio between the total number of recorded stems and the inventoried area: $D = N / A$, where D is density expressed as stems $ha^{-1}$, N is the number of stems and A is area in hectares. The basal area of each stem was calculated as $BA = \pi \times (DBH/200)^2$, where DBH is expressed in centimetres and BA in $m^2$. Diameter-class distributions were established to assess stand structure, regeneration and the relative presence of large trees.

### 2.3. Floristic diversity and similarity

Floristic diversity was assessed using species richness, family richness, the Shannon index, the Simpson index and Pielou evenness. The Shannon index was calculated as $H' = -\Sigma(p_i \ln p_i)$, the Simpson index as $1 - \Sigma(p_i^2)$, and Pielou evenness as $J = H' / \ln(S)$, where pi is the relative abundance of species i and S is total species richness. Floristic similarity between the two forest types was estimated using the Jaccard index: $J = a / (a + b + c)$, where a is the number of shared species, b the number of species restricted to the first site and c the number of species restricted to the second site.

### 2.4. Aboveground biomass and carbon stock

Tree aboveground biomass was estimated from diameter measured at 1.30 m (DBH, in cm) and wood specific gravity (WSG, in g $cm^{-3}$), using regional model 12 proposed by Fayolle et al. [10], developed for Congo Basin forests:

$$AGB = \exp[0.046 + 1.156 \log(WSG) + 1.123 \log(D) + 0.436(\log(D))^2 - 0.045(\log(D))^3]$$

where AGB is aboveground biomass in kg per tree, WSG is wood specific gravity and D is DBH in cm. Wood specific gravity values were obtained from the Global Wood Density Database where available [11]. For species lacking a species-level value, the tropical African mean wood density of 0.65 g $cm^{-3}$ was used. Aboveground biomass was then converted to aboveground carbon stock by applying a carbon fraction of 0.47. Carbon stocks were aggregated at plot level and expressed as Mg C $ha^{-1}$.

### 2.5. Contribution of diameter classes to carbon stock

The contribution of each diameter class to carbon stock was calculated by summing the carbon of all stems within that class and dividing this value by the total carbon stock of the forest type considered. The contribution of large trees was assessed using thresholds of DBH ≥ 30 cm, DBH ≥ 50 cm, DBH ≥ 70 cm and DBH ≥ 100 cm. This approach distinguishes the numerical contribution of stems from their functional contribution to carbon storage.

### 2.6. Statistical analyses

Descriptive statistics were calculated at plot and forest-type levels. When comparisons between forest types were required, plot-level values were used as independent statistical units. Non-parametric tests, particularly the Mann-Whitney test, were favoured when assumptions of normality and homoscedasticity were not met. Statistical results are interpreted cautiously because of the limited number of plots and the internal ecological variability of tropical forests.

## 3. Results

### 3.1. General contrast in structure, diversity and carbon

Peat swamp forest and terra firme forest in Likouala differ markedly in structure, floristic richness and carbon stocks. Peat swamp forest includes 6,085 stems across 12 ha, with a density of 507.08 stems $ha^{-1}$, a mean DBH of 22.63 cm and a basal area of 29.34 $m^2$ $ha^{-1}$. Terra firme forest in Likouala includes 5,692 stems across 11 ha, with a density of 517.45 stems $ha^{-1}$, a mean DBH of 17.65 cm and a basal area of 24.47 $m^2$ $ha^{-1}$. Thus, peat swamp forest shows a more developed structure in terms of diameter and basal area, whereas terra firme forest has a slightly higher stem density.

**Table 1** Summary of the main structural, floristic and carbon attributes of the two forest types.

| Variable | Peat swamp forest | Likouala terra firme forest |
|---|---|---|
| Number of plots | 12 | 11 |
| Inventoried area (ha) | 12 | 11 |
| Number of stems | 6,085 | 5,692 |
| Density (stems $ha^{-1}$) | 507.08 | 517.45 |
| Mean DBH (cm) | 22.63 | 17.65 |
| Basal area ($m^2$ $ha^{-1}$) | 29.34 | 24.47 |
| Species richness | 129 | 155 |
| Family richness | 52 | 44 |
| Shannon index | 3.70 | 3.83 |
| Simpson index (1-D) | 0.960 | 0.953 |
| Aboveground carbon stock (Mg C $ha^{-1}$) | 166.16 | 125.80 |

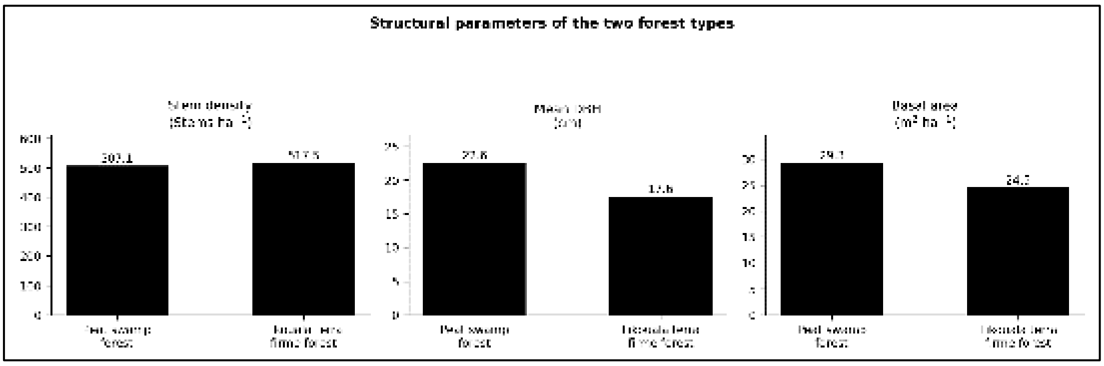


**Figure 2** Comparison of the main structural parameters between peat swamp forest and terra firme forest in Likouala.

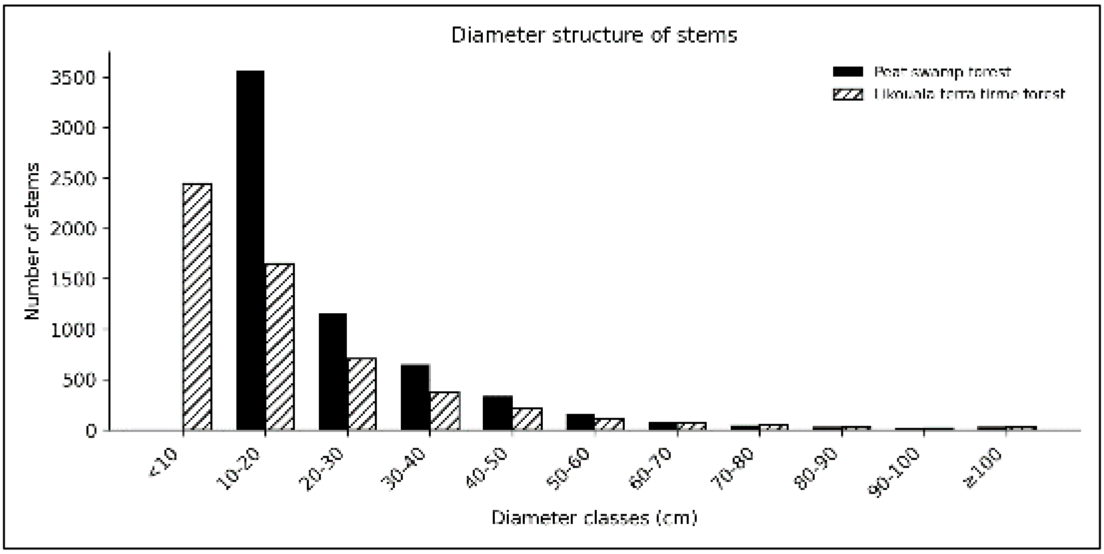


**Figure 3** Stem distribution by diameter classes in peat swamp forest and terra firme forest in Likouala.

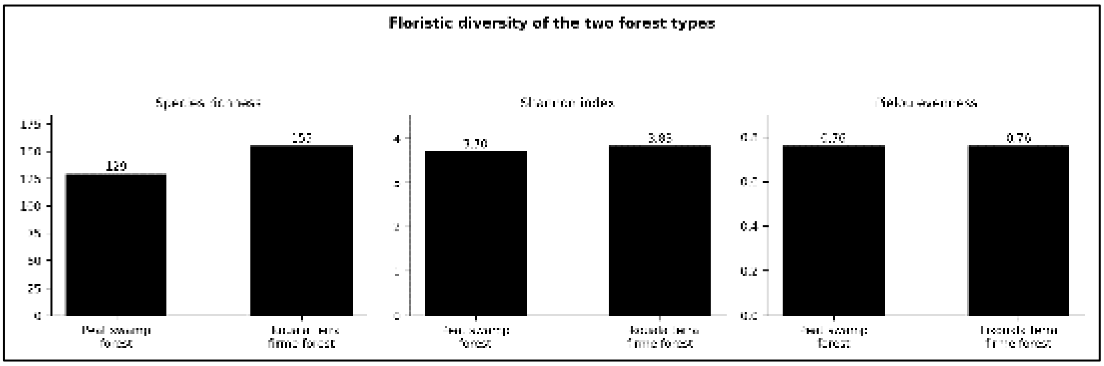


**Figure 4** Comparison of the main floristic diversity indicators between the two forest types.

### 3.2. Floristic differentiation

Floristic overlap between the two forest types is extremely low. Only two species are shared by peat swamp forest and terra firme forest in Likouala, corresponding to a Jaccard index of 0.007. Terra firme forest supports higher species richness, with 155 species compared with 129 species in peat swamp forest. This low similarity indicates that the two forests host distinct floristic assemblages and contribute complementarily to regional biodiversity.

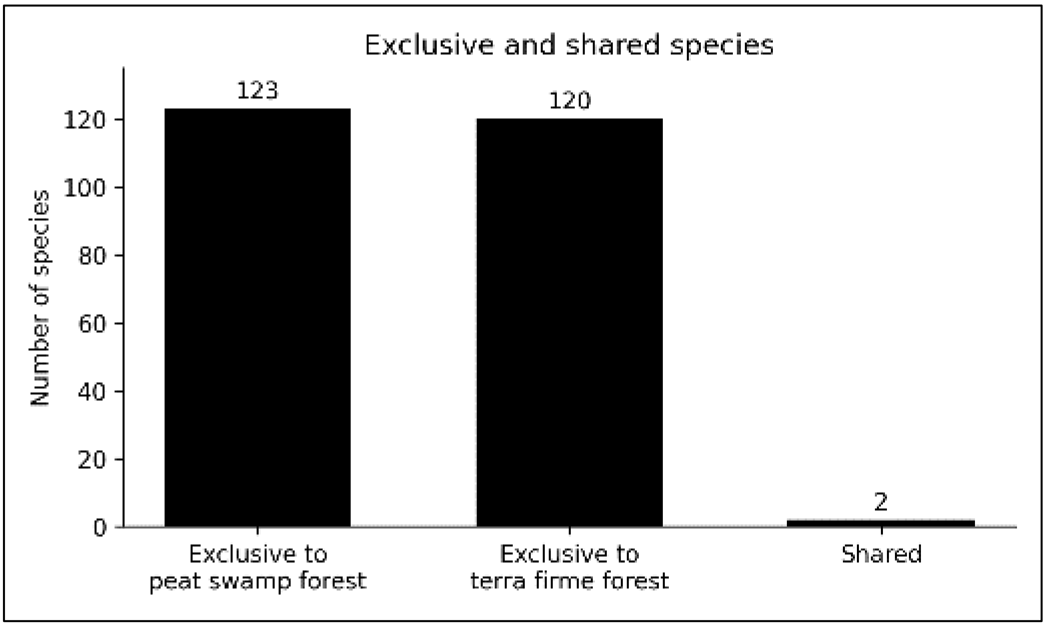


**Figure 5** Exclusive and shared species between peat swamp forest and terra firme forest in Likouala.

### 3.3. Aboveground carbon stock and contribution of diameter classes

Aboveground carbon stock is higher in peat swamp forest than in terra firme forest. Peat swamp forest stores 166.16 Mg C ha$^{-1}$, compared with 125.80 Mg C ha$^{-1}$ in terra firme forest in Likouala. Analysis by diameter classes shows that large trees contribute disproportionately to carbon storage in both forest types. Trees with DBH ≥ 50 cm contribute 48.2% of aboveground carbon in peat swamp forest and 68.7% in terra firme forest. These results confirm that carbon storage depends more on tree size and basal area than on total stem density.

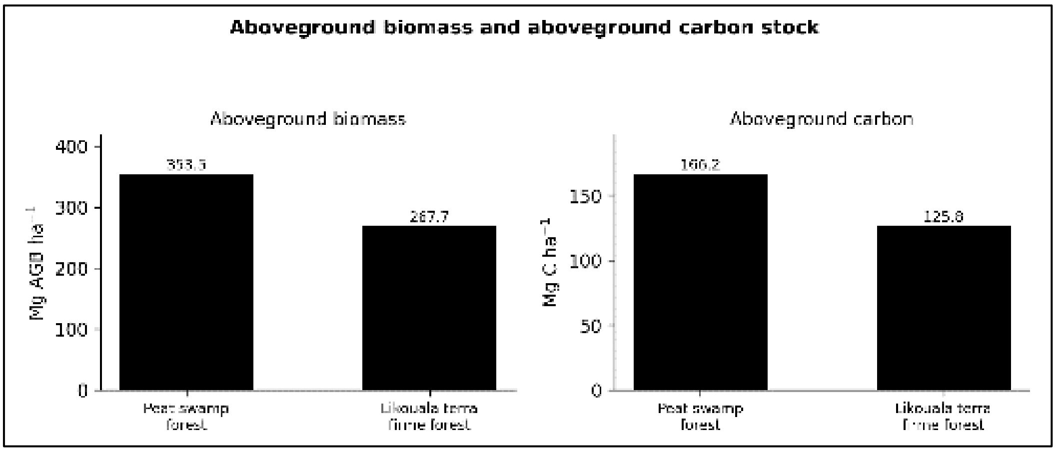


**Figure 6** Aboveground biomass and aboveground carbon stock in peat swamp forest and terra firme forest in Likouala.

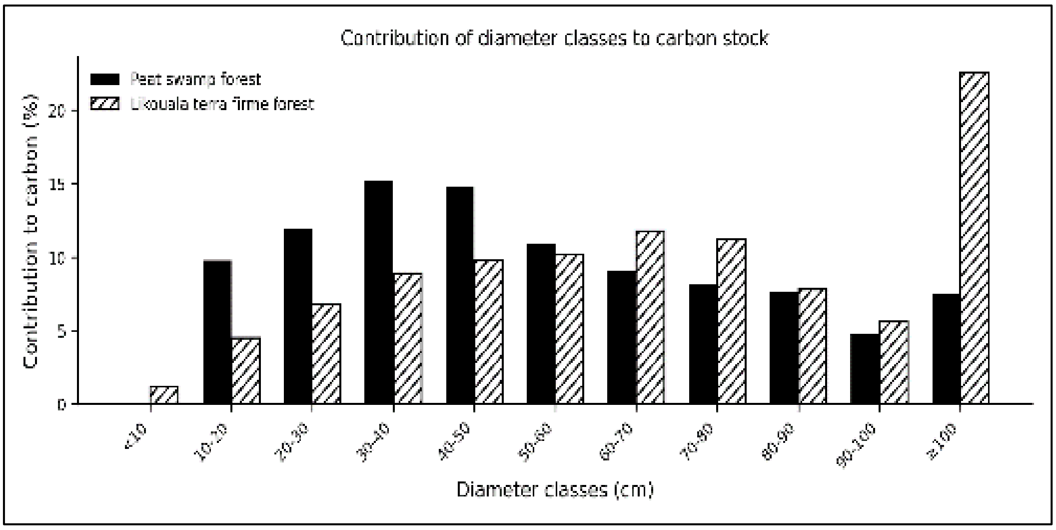


**Figure 7** Contribution of diameter classes to aboveground carbon stock.

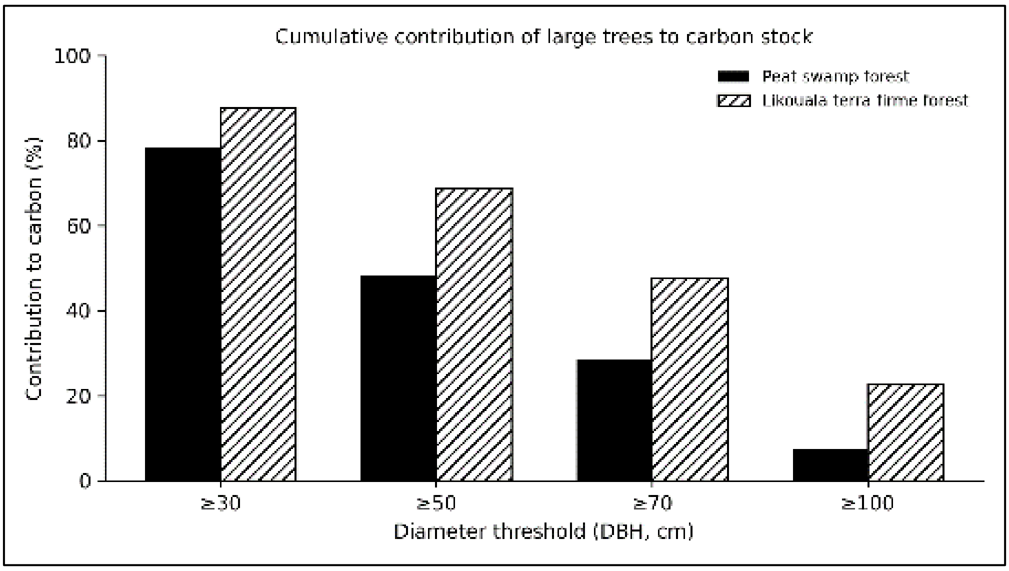


**Figure 8** Cumulative contribution of large trees to aboveground carbon stock under different DBH thresholds.

## 4. Discussion

### 4.1. An ecological contrast rather than a simple site effect

The structural and floristic differentiation observed between peat swamp forest and terra firme forest in Likouala is consistent with previous work along the Impfondo–Dongou axis in northern Congo. Koubouana et al. [8] identified several distinct forest facies in this landscape, including primary terra firme forest, hydromorphic forests dominated by Lophira alata Banks ex C.F.Gaertn. or Guibourtia demeusei (Harms) J.Leonard, and degraded forests dominated by pioneer taxa such as Musanga cecropioides and Macaranga spp. Their results show that forest structure and floristic composition vary according to substrate conditions, flooding regime and disturbance history. This supports the interpretation that peat swamp forest and terra firme forest in Likouala should not be considered simple variants of the same forest type, but rather distinct ecological systems shaped by hydrology, edaphic conditions and stand history.

This point helps avoid an overly descriptive interpretation of the observed differences. The two forest types represent different ecological filters. Peat swamp forest is associated with hydromorphic and peaty conditions, where waterlogging, low soil oxygenation and the organic properties of the substrate may select for particular species and functional strategies. Terra firme forest, being better drained, may offer a greater diversity of microhabitats and edaphic conditions, which is consistent with the higher species richness observed in this study.

### 4.2. Ecological significance of the reverse-J diameter structure

The reverse-J diameter distribution observed in both forest types corresponds to a typical uneven-aged tropical forest structure, characterised by high abundance of small stems and a progressive decline in the number of individuals towards larger diameter classes. Ecologically, this structure suggests continuous regeneration, associated with progressive mortality and increasing competition as individuals move into larger diameter classes. In northern Congo, Koubouana et al. [8] show that diameter distributions may reflect the shade-tolerant or light-demanding temperament of species, soil properties, hydrological conditions and the sylvigenetic stage of stands.

The meaning of this reverse-J structure is not identical in the two forests. In peat swamp forest, recruitment and survival of young stems are probably filtered by the hydrological and edaphic constraints of water-saturated organic soils. These conditions may limit the establishment of certain species while favouring taxa adapted to waterlogging. In terra firme forest, better-drained soils may allow recruitment from a more diverse floristic pool, which is consistent with the higher species richness observed. Ifo et al. [7] noted that, in seasonally flooded and terra firme forests of northern Congo, flood depth and duration can influence small-stem density, species richness and stand structure.

This diameter structure is also central to interpreting carbon. Small stems dominate numerically, but their contribution to aboveground biomass and carbon remains limited because biomass increases non-linearly with tree diameter. Conversely, medium- and large-diameter trees are far less numerous but contribute strongly to basal area, biomass and carbon stock. This result agrees with Ifo et al. [7], who showed that mean DBH, basal area and large-tree density are better indicators of biomass than total stem density. It is also consistent with the synthesis of Sullivan et al. [9], which shows that diversity and carbon are not always spatially congruent at the 1-ha plot scale.

### 4.3. Forest structure explains the carbon contrast better than stem density

The higher aboveground carbon stock of peat swamp forest is primarily explained by its structural development rather than by its stem density. Peat swamp forest has a slightly lower density than terra firme forest, but a higher mean DBH and basal area. This combination shows that the total number of stems is insufficient to explain carbon stocks. Tree diameter, basal area and the presence of large-diameter trees are the main determinants of stored biomass.

The basal-area values observed in this study fall within the range reported for structurally developed forests of northern Congo. Work along the Impfondo–Dongou axis reported mean values of approximately 28.44 $m^2\ ha^{-1}$ in primary forests and 19.21 $m^2\ ha^{-1}$ in degraded forests [8]. In the present study, peat swamp forest reaches 29.34 $m^2\ ha^{-1}$, while terra firme forest in Likouala reaches 24.47 $m^2\ ha^{-1}$. This suggests that peat swamp forest has a structural development comparable to that of primary stands, whereas terra firme forest also remains well structured, although its basal area is lower than that of peat swamp forest.

### 4.4. Peat swamp forest as an aboveground carbon-rich forest, beyond the soil-carbon threshold

Peatlands are usually discussed first as soil-carbon reservoirs. This perspective is justified by the very large quantities of organic carbon accumulated under hydromorphic and oxygen-poor conditions. The central peatland complex of the

Congo Basin is described as the largest tropical peatland complex currently known, with nearly 29–30 Pg of carbon stored in soils [2,3,5]. However, the persistence of these carbon stocks depends strongly on hydrological stability. Palaeoenvironmental evidence indicates that past hydroclimatic drying altered peat accumulation in the central Congo Basin, while process-based modelling suggests that changes in water-table dynamics can shift tropical peatlands from long-term carbon accumulation towards carbon loss [12,13].

However, our results show that the aboveground component of peat swamp forest should not be neglected. Peat swamp forest stores 166.16 Mg C $ha^{-1}$ in living aboveground biomass, a value higher than that estimated for Likouala terra firme forest. This result does not imply that all Congo Basin peat swamp forests necessarily have higher aboveground stocks than all terra firme forests, but it shows that, in this landscape, peat swamp forest combines high belowground carbon potential with a substantial aboveground stock.

The need to interpret aboveground carbon together with belowground processes is reinforced by recent field estimates of fine-root production in the central Congo Basin. Repeat minirhizotron observations in palm-dominated peat swamp forest, hardwood-dominated peat swamp forest and terra firme forest showed fine-root production of 2.6 ± 0.3, 1.9 ± 0.5 and 1.7 ± 0.1 Mg C $ha^{-1}$ $yr^{-1}$, respectively [14]. These results suggest that carbon cycling in Congo Basin forests involves both standing aboveground biomass and active belowground production, making integrated forest and peat monitoring essential.

### 4.5. Large trees as disproportionate components of carbon storage

A central finding of this study is the disproportionate contribution of large trees to aboveground carbon stock. In both forest types, trees with DBH ≥ 50 cm represent a small proportion of stems but contain a large share of the carbon. In peat swamp forest, they contribute 48.2% of aboveground carbon; in terra firme forest in Likouala, they contribute 68.7%. This observation confirms that large trees are major functional components of carbon storage in tropical forests and that stand structure should be interpreted alongside species richness when assessing forest climate functions.

The two forests differ, however, in how carbon is distributed among diameter classes. In peat swamp forest, the 30–40 cm class makes the largest contribution to carbon, suggesting a relatively broad contribution from medium to large trees. In terra firme forest in Likouala, the ≥100 cm class makes the largest contribution, indicating that carbon stock is more strongly concentrated in a small number of very large trees. This difference reinforces the idea that the two forest types do not have the same structural strategy of carbon storage.

### 4.6. Floristic richness of Likouala terra firme forest and the biodiversity function

Terra firme forest in Likouala has higher species richness than peat swamp forest, with 155 species compared with 129. This difference is consistent with the idea that better-drained soils may provide more varied ecological conditions and favour the coexistence of a larger number of species. Work by Ekoungoulou et al. [15] on lowland evergreen forests in Likouala also shows that stands in this region can exhibit high diversity and substantial variation in structure and floristic composition among sites.

The higher richness of terra firme forest does not mean that peat swamp forest has low conservation value. Floristic similarity between the two forests is extremely low, with only two shared species. This indicates that the two forests support very different assemblages. Conservation of one forest type therefore cannot compensate for the loss of the other. Peat swamp forest contributes primarily to the carbon function and to the specificity of hydromorphic habitats, whereas terra firme forest contributes strongly to regional floristic richness.

The contrast observed in this study fits within a broader debate on relationships between carbon and biodiversity in tropical forests. Sullivan et al. [9], using a pantropical dataset of 360 plots, showed that the relationship between tree diversity and aboveground carbon at the 1-ha scale is weak or absent depending on region. This means that the areas richest in carbon are not necessarily the richest in species, and vice versa.

Our study illustrates this decoupling at the scale of a northern Congo landscape. Peat swamp forest stores more aboveground carbon, whereas terra firme forest has higher species richness. This is not a universal trade-off, but rather a local complementarity between two ecological functions. A conservation strategy focused only on carbon could underestimate the value of Likouala terra firme forest, whereas a strategy focused only on species richness could underestimate the carbon value of peat swamp forest.

The regional importance of aboveground carbon is also highlighted by forest carbon mapping studies. Xu et al. [16] showed, using LiDAR data, field plots and satellite modelling, that forest carbon stocks vary strongly across the landscape and that field observations remain necessary for calibrating maps and reducing uncertainty. Our results therefore provide complementary information that is useful for forest carbon monitoring, reporting and verification systems.

### 4.7. From the plot to the ecological function of the Congo Basin

The relevance of this study extends beyond comparison of two local datasets. Bauters et al. [1] emphasise that Congo Basin ecosystems contribute simultaneously to carbon storage, hydrological regulation, biodiversity and human livelihoods. Our results provide a plot-scale illustration of this multifunctionality: two neighbouring forest types can contribute differently to carbon and biodiversity functions.

These results also have implications for REDD+ and MRV systems. Forest classes that are too broad may mask important ecological differences. A generic carbon value for all forests could underestimate peat swamp forests rich in aboveground carbon or neglect the floristic value of terra firme forests. Monitoring programmes should therefore integrate carbon stocks, floristic composition, diameter structure and local ecological conditions simultaneously.

## 5. Conclusion

This study shows that peat swamp forest and terra firme forest in Likouala differ strongly in structure, floristic diversity and aboveground carbon stock. Peat swamp forest has a higher mean DBH, basal area and carbon stock, indicating stronger structural development and an important carbon function. Terra firme forest in Likouala has higher species richness and a highly distinct floristic composition, underscoring its value for biodiversity conservation.

The analysis of diameter classes confirms the disproportionate role of large trees in carbon storage. Small stems dominate numerically, but large-diameter trees control a large share of aboveground carbon. These results show that stem density, species richness and aboveground carbon should be interpreted together rather than separately.

Overall, the two forest types are complementary. Peat swamp forest contributes strongly to carbon storage, whereas terra firme forest contributes strongly to floristic diversity. Conservation, carbon-monitoring and sustainable-management strategies in northern Congo should therefore integrate both forest types simultaneously in order to preserve the climate and biodiversity functions of the Congo Basin.

## Compliance with ethical standards

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*Disclosure of conflict of interest*

The authors declare that they have no financial or non-financial conflicts of interest.

*Statement of ethical approval*

This study was based on forest inventory data and did not involve human participants, animal experimentation or protected personal information. No specific ethical approval was required.

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