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### ► To cite this version:

Juliette Picard, Maïalichah M Nungi-pambu Dembi, Nicolas Barbier, Guillaume Cornu, Pierre Couteron, et al.. Combining satellite and field data reveals Congo's forest types structure, functioning and composition. *Remote Sensing in Ecology and Conservation*, In press, 10.1002/rse2.419 . hal-04739747

HAL Id: hal-04739747

<https://hal.inrae.fr/hal-04739747v1>

Submitted on 16 Oct 2024

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## RESEARCH ARTICLE

# Combining satellite and field data reveals Congo's forest types structure, functioning and composition

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## Keywords

Deep learning, North Congo, satellite data, tropical forests, vegetation map, water drainage depth

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## Funding Information

This work was supported by the DESSFOR project funded by the French National Research Agency (ANR-20-CE32-0010).

Editor: Prof. Mat Disney  
Associate Editor: Dr. Rocio Hernandez-Clemente

Received: 2 February 2024; Revised: 22 June 2024; Accepted: 12 August 2024

doi: 10.1002/rse2.419

## Introduction

Behind the homogeneous green carpet often illustrated in maps or considered by global models, tropical forests are known to harbour a complex mixture of forest types organized at different spatial scales (Brando et al., 2019; Chazdon, 2003; Couvreur, 2015). Ecologists and foresters

## Abstract

Tropical moist forests are not the homogeneous green carpet often illustrated in maps or considered by global models. They harbour a complex mixture of forest types organized at different spatial scales that can now be more accurately mapped thanks to remote sensing products and artificial intelligence. In this study, we built a large-scale vegetation map of the North of Congo and assessed the environmental drivers of the main forest types, their forest structure, their floristic and functional compositions and their faunistic composition. To build the map, we used Sentinel-2 satellite images and recent deep learning architectures. We tested the effect of topographically determined water availability on vegetation type distribution by linking the map with a water drainage depth proxy (HAND, height above the nearest drainage index). We also described vegetation type structure and composition (floristic, functional and associated fauna) by linking the map with data from large inventories and derived from satellite images. We found that water drainage depth is a major driver of forest type distribution and that the different forest types are characterized by different structure, composition and functions, bringing new insights about their origins and successional dynamics. We discuss not only the crucial role of soil–water depth, but also the importance of consistently reproducing such maps through time to develop an accurate monitoring of tropical forest types and functions, and we provide insights on peculiar forest types (Marantaceae forests and monodominant *Gilbertiodendron* forests) on which future studies should focus more. Under the current context of global change, expected to trigger major forest structural and compositional changes in the tropics, an appropriate monitoring strategy of the spatio-temporal dynamics of forest types and their associated floristic and faunistic composition would considerably help anticipate detrimental shifts.

have long identified major differences between forest types, leading to different ecosystem services (e.g. carbon stocks, water regulation, food supplies, etc.; Watson et al., 2018) and different floristic and faunistic compositions influencing conservation priorities (Asner et al., 2017; Cannon et al., 2007; Fonteyn et al., 2023).

However, the large-scale distribution of forest types and their underlying floristic and faunistic compositions are poorly known in tropical forests (Fonteyn et al., 2023; Ordway et al., 2022). The main reasons for this knowledge gap are the inherent difficulties of satellite-based approaches to detect subtle changes in the structure and composition of tropical dense forests, and the low signal/noise ratio and artefacts due to imperfect pre-processing (Hoekman et al., 2020; Jha et al., 2021). It considerably limits our understanding of the drivers and of the dynamics of forest type distribution and thus our ability to design appropriate management and conservation strategies in one of the most biodiverse and carbon-rich biomes on Earth.

Tropical forest dynamics have historically been studied through ground-vegetation surveys, notably in permanent forest plots (Anderson-Teixeira et al., 2015; ForestPlots-net et al., 2021). Because these plots are extremely labour-intensive, they can only cover a limited area and do not necessarily represent all forest types well, often being over-represented in mature terra firme forests. Larger commercial inventories have also been used to map forest types and characteristics (Réjou-Méchain et al., 2021; Ter Steege et al., 2006). While these inventories provide unique large-scale information, they are not reproduced over time and thus have limited value for monitoring forest ecosystems. By contrast, the increasing availability of remote sensing products, which provide repeated measurements over time, offers invaluable potential for continuous spatio-temporal monitoring of tropical forests. Although most current remote sensing data rapidly saturate with forest structure (Jha et al., 2021), some studies have shown that the spectral and/or textural information contained in satellite data have some potential to discriminate between tropical forest types (Gond et al., 2013; Thenkabail et al., 2003, 2004; Viennois et al., 2022).

Recent synergistic advances in remote sensing products and artificial intelligence open new perspectives in distinguishing and mapping different forest types. The increasing availability of satellite data with high spectral, spatial and temporal resolutions, such as Sentinel 2 data, offer a great potential, provided that careful image processing is made to minimize known biases, such as variability in sun-sensor acquisition conditions (bidirectional reflectance distribution function [BRDF]) or atmospheric pollution (Phiri et al., 2020). Indeed, many vegetation types can be distinguished from their specific textural and spectral signals (Ordway et al., 2022; Viennois et al., 2022). In the recent years, deep learning approaches also have permitted significant progress in forest properties mapping from space-borne data with the development of performant convolutional networks (e.g. Kattenborn et al., 2021; Wagner et al., 2019) and, more recently, of

vision transformer models (e.g. Fayad et al., 2023). However, so far, studies leveraging deep learning mostly focused on predicting quantitative metrics of forest structure (Li et al., 2020) to estimate carbon stocks (Huy et al., 2022) and their changes over time (Waldeland et al., 2022). Despite the need for new methods to monitor forest composition, relatively few studies have used deep learning approaches to predict tropical forest types from remote sensing images (Kattenborn et al., 2021). Even fewer have paired their forest type predictions with extensive field data to understand how the floristic, functional and faunistic compositions vary among predicted types (Gond et al., 2013).

Different factors are expected to drive the structure and composition of tropical forests at different spatio-temporal scales. Among these factors, water availability appears as a major driver. At the continental to regional scale, or along marked elevational gradients, climate water deficit and temperature have been shown to be the main ecological drivers of the distribution of forest types (Réjou-Méchain et al., 2021; Ter Steege et al., 2006). At the regional-to-landscape scale, investigated in this study, geological substrates, soil characteristics and topography are known to impact both water and nutrient availability and thus to have a significant impact on forest composition and structure (Fayolle et al., 2012). The effect of topography is, however, known to be context-dependent (Muscarella et al., 2020; Sousa et al., 2022) with for example, lower canopies in valley bottoms than in hilltops in high-rainfall areas (e.g. Ferry et al., 2010) while the reverse is observed in drier contexts (e.g. Detto et al., 2013). A recent study consistently showed that the functional composition of trees varies along gradients of soil-water availability in a non-linear way, with conservative strategies associated with very shallow water table depth due to anoxic conditions, acquisitive strategies in intermediate water table depth values and, again, conservative strategies in deep water table depth areas due to a marked water deficit in the soil (Costa et al., 2023). Another potentially important driver of forest composition and structure is the positive and negative feedbacks between megafauna and forest structure and composition (Malhi et al., 2016; Terborgh et al., 2016). For example, elephants and gorillas are known to be major ecosystem engineers: They are both important seed dispersers and can significantly modify forest structure through disturbances (Campos-Arceiz & Blake, 2011; Haurez et al., 2015), with potentially important impacts on forest composition (Beaune et al., 2013; Terborgh et al., 2008) and functions (Berzaghi et al., 2019).

Central Africa is home to the second largest tropical forest block worldwide and hosts some of the world's most iconic megafauna. As with any other large tropical

forest block, several forest types, with specific structure and functional and faunistic compositions, occur or co-occur along environmental gradients, from for example, permanently flooded to terra firme forests, semi-deciduous to evergreen forests or open to dense canopy forests (Fayolle et al., 2014; Fonteyn et al., 2023; Réjou-Méchain et al., 2014; Réjou-Méchain et al., 2021). Besides, central Africa is home to peculiar but widespread forest types which origins still remain debated, such as the monodominant *Gilbertiodendron dewevrei* forests (Hart et al., 1989; Katembo et al., 2020) and the so-called Marantaceae forests, a forest type with an understory dominated by giant herbs and hypothesized to correspond to an arrested succession (Pouteau et al., 2024). Central African forests and their fauna are, however, heavily threatened by both increasing human pressure (Lhoest et al., 2020; Vancutsem et al., 2021) and climate change (Bush et al., 2020; Kasongo Yakusu et al., 2023; Wimberly et al., 2023), highlighting the urgent need for characterizing and understanding the distribution of forest composition and structure at scales compatible with ecosystem management strategies.

The aim of this study was to build a large-scale vegetation map in the North of the Republic of Congo and to assess the environmental drivers of the main forest types, their forest structure, their floristic and functional compositions and their faunistic composition. We selected an area known to contain a mosaic of contrasted forest types as well as high abundance of megafauna. First, we used very high (0.5 m) and high (10 m) resolution satellite images and recent deep learning architectures to map six vegetation types over 18 500 km<sup>2</sup> (Fig. 1). Then, we linked this map to a water table depth proxy (HAND, height above the nearest drainage index) and tested whether soil–water availability drives forest types distribution. Then, we combined the vegetation map with a large tree inventory dataset (2524 plots) to investigate how forest structure, floristic and functional compositions vary between forest types. Finally, we combined the vegetation map with a large megafauna inventory dataset (2667 observations) to compare the faunistic composition of the various forest types.

## Materials and Methods

### Study area

The study area is located in the North of the Republic of Congo (Fig. 2). It covers an area of 18 500 km<sup>2</sup> (135 × 137 km) and sits astride the Odzala-Kokoua National Park and the IFO-Interholco forestry concession (UFA Ngombé). Annual rainfall is about 1500 mm (Congo National Civil Aviation Agency, 2005–2015), with

a 3-months dry season during December to February. The average temperature is 25°C. The Sangha department is mostly covered by forests belonging to the mixed evergreen and semi-deciduous forest types (Réjou-Méchain et al., 2021).

### Pre-processing of the Sentinel-2 satellite image

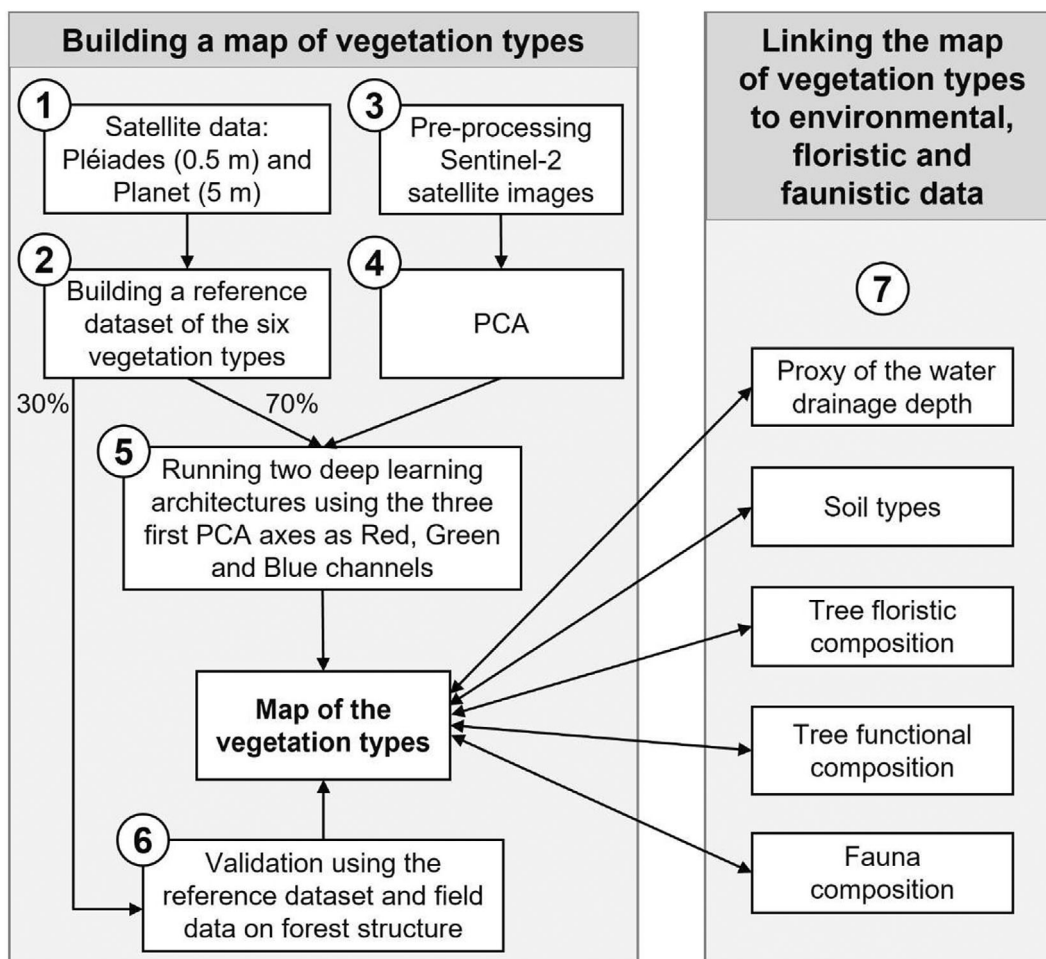
We used Sentinel 2 (S2) data from 11 January 2020 for wall-to-wall mapping of vegetation types over the study area. To improve the signal/noise ratio in the data, image processing consisted in applying three main corrections: (i) atmospheric effects enhanced correction and dehazing, (ii) bidirectional effects correction and (iii) instrumental artefacts correction. The full process is detailed in Appendix S.1.

### Reference dataset of vegetation types

Based on the review of regional literature and on our ability to visually discriminate forest types from very high-resolution images, we defined six main forest types of interest, and roads (Fig. 3). To build a reference dataset representing the six studied vegetation types plus the roads, we acquired 2320 km<sup>2</sup> of very high-resolution stereo Pleiades images (0.5 m resolution) between January and December 2022. Due to budget and cloud cover constraints, Pleiades images were not acquired for the entire study area (Figure S1). To improve the spatial representativeness of some forest types and study zones, we also used freely available Planet images (5 m resolution) as a secondary, lower priority option. Our final reference dataset consisted of 680 well-distributed 1-ha polygons (535 polygons based on Pleiades images and 145 on Planet images; Figure S1 and Table S1). Polygons labelling was made by a single expert (JP) based on image visual interpretation on QGIS version 3.22.9 (QGIS.org, 2022) using criteria such as canopy texture and 3D information from Pleiades-derived digital surface models obtained from stereo photogrammetry. All areas that burnt or experienced large-scale disturbance between 2020 and 2022 were excluded from this dataset. Moreover, a large area (12 000 ha), which burnt in the early 1970s (pers. comm.), was excluded from the reference dataset as its status was uncertain.

### Deep learning prediction and validation

We used two types of recent deep learning architectures to predict the different forest types: a convolutional neural network EfficientNet-B3 (Tan & Le, 2019), using pre-trained Noisy-Student weights (Xie et al., 2020), and



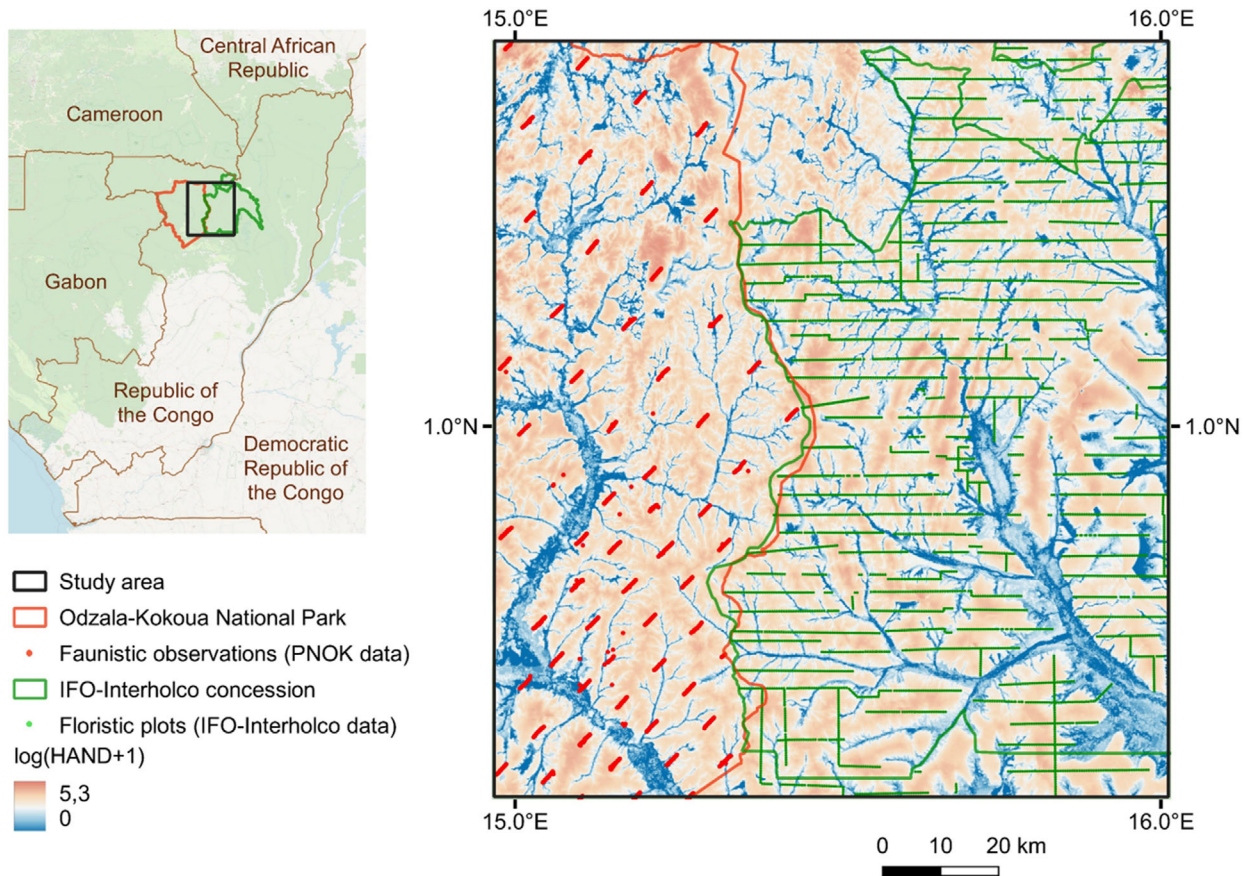
**Figure 1.** Methodological workflow.

a Vision transformer (Dosovitskiy et al., 2021; Khan et al., 2022), pre-trained on ImageNet (Russakovsky et al., 2015). To benefit from the pre-trained weights of both networks, which were based on Red-Green-Blue (RGB) images, we reduced the dimensionality of the 13 bands of Sentinel data using a principal component analysis (PCA) and used the first three PCA axes to generate false-RGB images (code available at <https://github.com/MaximeRM/ScriptDeepLearningCongo>).

We used an ensemble-average approach to ensure the robustness and the accuracy of the predictions. Each architecture was trained separately three times each using our reference polygon dataset split into a calibration (70%) and validation (30%) datasets that preserved the proportion of the different forest types of the dataset. We then used these six models to predict forest types over the whole study area at 100-m resolution ( $10 \times 10$  pixels). Post-training, the probabilities from the six models were averaged, resulting in the probability for

each  $10 \times 10$  pixels corresponding to the seven different classes (Fig. 3). The assigned class was determined by the highest averaged probability.

The validation of the map was done using the six original maps and their corresponding validation datasets to build a global confusion matrix and calculate the global accuracy (ratio of well-classified elements to the total number of elements). We additionally validated our final map using independent field- and satellite-based metrics of forest structure. Field-based metrics were drawn from Ploton et al. (2020) and included the mean above ground biomass per ha (in  $\text{Mg ha}^{-1}$ ), the number of trees per ha with diameter at breast height (DBH)  $\geq 20$  cm and the mean quadratic diameter of trees with DBH  $\geq 20$  cm (in cm). Satellite-based metrics were obtained from products derived from the LiDAR GEDI mission (Dubayah et al., 2020). We used estimates of the mean canopy height (rh100 in m, L3 version 2) and of the above ground biomass per ha (in  $\text{Mg ha}^{-1}$ , L4B version 2), both



**Figure 2.** Study area, floristic and faunistic data location and HAND index variations in the North of the Republic of Congo (map background was taken from OpenStreetMap).

downloaded from <https://webmap.ornl.gov/ogc/> on the 7/11/2023 (Duncanson et al., 2022).

## Crossing the map of vegetation types with environmental, floristic and faunistic data

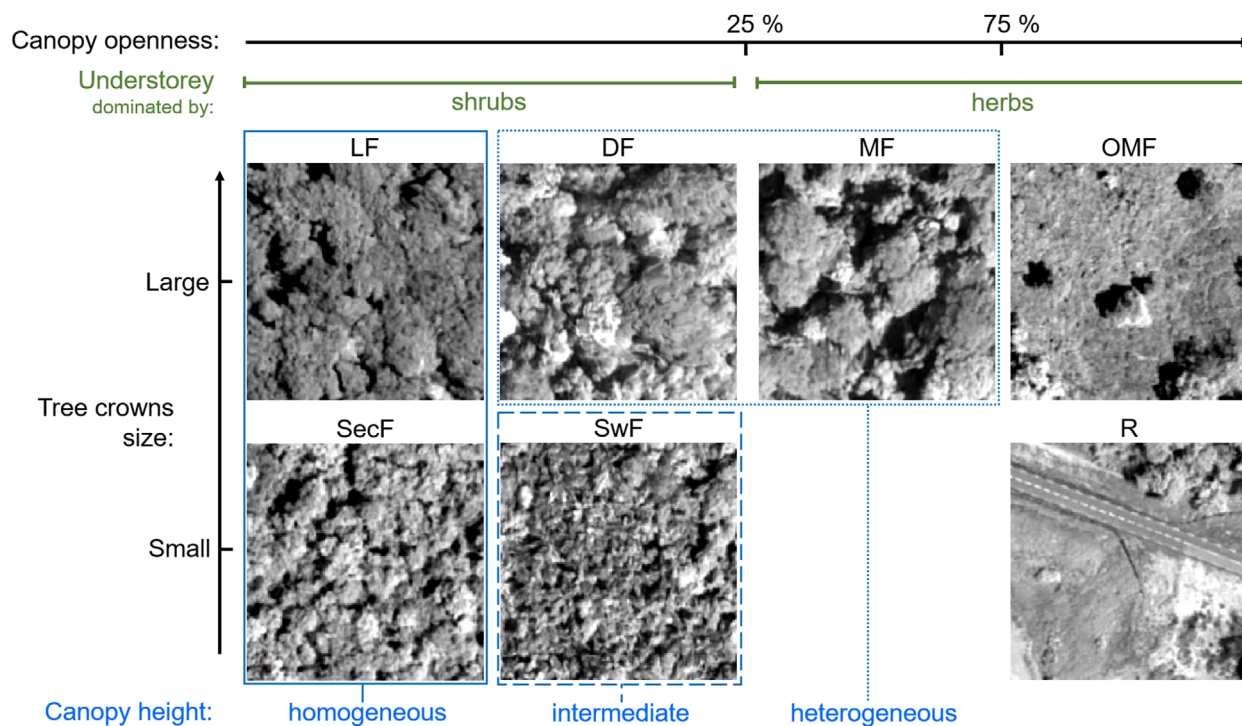
### Topographical variable: A proxy for water drainage depth

The altitude of our study area varied between 330 and 680 m, mainly according to the hydrological network (Fig. 2). We thus used an index that captured most of the topographical variation over our study area: the height above the nearest drainage (HAND; Nobre et al., 2011). This index was built using the method developed by Rennó et al. (2008) based on data from the shuttle radar topography mission (SRTM; 30-m resolution). By normalizing topography according to the local relative heights found along the drainage network, this index captures the local draining potentials and thus the local soil–water conditions (water drainage depth), known to

influence forest composition (Guitet et al., 2015). The lower the HAND index value, the shallower the drainage level. Because the distribution of the HAND index values was right-skewed, we log-transformed ( $\ln + 1$ ) its values in subsequent analyses.

### Soil types

Information on soil type composition and structure is scarce in central Africa and global soil maps often result from interpolation approaches partly based on remote sensing products, partly leading to circularity issues in vegetation studies. We thus used a 1:2 000 000 scale map of soil types (de Boissezon et al., 1969), which is still likely the most accurate one for this region (Figure S2). The map encompassed six soil types from ferrallitic desaturated modal soils to hydromorphic soils. Hydromorphic soils are mainly mineral in our study area, and are subject to hydromorphy that is either total, but not permanent, or partial. We merged them with organic hydromorphic



**Figure 3.** The six studied forest types illustrated with  $100 \times 100$  m patch examples taken from Pleiades images acquired in 2022 in the study area. The main criteria that distinguish them (i.e. canopy openness, tree crown size and understory composition) are displayed in the figure. LF, monodominant *Gilbertiodendron* forests; DF, dense forests; MF, Marantaceae forests; OMF, open Marantaceae forests; SecF, secondary forests; SwF, swamp forests; R, roads.

soils, which occupy a very small part of the study area, and are waterlogged part of the year and flooded the rest of the time. On the contrary, ferrallitic desaturated modal soils are well-drained soils, even if they can also experience waterlogging periods depending on their topographical location (plateau, slope or valley bottom).

### Floristic data

We used a floristic dataset of 2524 plots obtained from forest management inventories conducted in the IFO-Interholco concession in 2001–2004. Most of the plots were 0.5 ha in size ( $200 \times 25$  m<sup>2</sup>; 91%), the remaining being 1 ha ( $400 \times 25$  m<sup>2</sup>; 8%). All trees with a DBH  $\geq 20$  cm were identified using vernacular or commercial names and then converted to scientific names whenever possible (see the general methodology in Réjou-Méchain et al. (2011)). We conducted a selection of seemingly well-identified taxa based on expert knowledge and using distributional ranges reported in the RAINBIO dataset (Dauby et al., 2016). We ended up with 159 taxa and removed an additional 16 species that were represented by  $<100$  individuals in the dataset. The studied 143 taxa were identified at the species ( $n = 61$ ) or genus

( $n = 82$ ) levels and represented 83% of the originally inventoried individuals.

### Functional traits

The functional trait dataset was compiled from various sources. We selected two quantitative traits (wood density and maximum diameter) and three qualitative traits (deciduousness, seed dispersal mode and shade tolerance) known to vary between forest types and successional status (Réjou-Méchain et al., 2014). See details on the traits database construction in Appendix S.2.

### Faunistic data

The faunistic dataset was composed of 2667 direct and indirect observation points of forest elephants (*Loxodonta cyclotis*) and western lowland gorillas (*Gorilla gorilla gorilla*) recorded by field teams of the Odzala-Kokoua National Park in August 2016–January 2017 (1113 observations), February–March 2020 (2585 observations) and November 2022 (1539 observations; Fig. 2). These data were collected as part of 3-yearly line-transect distance sampling surveys to assess wildlife population trends

(Buckland et al., 2001; Odzala-Kokoua-Lossi Foundation, 2023). The 2.5-km transects were randomly positioned along a systematic grid using Distance 7.3 (Release 2; Thomas et al., 2010) and the 'systematic segmented trackline' option. Elephant dung piles and gorilla nests were recorded and the perpendicular distance was measured from the centreline. Nearly 98% of the perpendicular observations were made at a distance <10 m. Direct observations were also taken when travelling between transects. Note that dung and nest decay rates vary according to many factors (Morgan et al., 2016) and may thus generate density-biased estimates between forest types.

## Data analyses

To determine whether the different forest types were associated with different topography, soil, floristic and faunistic characteristics, we used non-parametric torus translation tests to account for spatial autocorrelation (Harms et al., 2001). These robust tests perform random two-dimensional translations in the four cardinal directions to partially rearrange the forest type map preserving coarse spatial structures in both the response and explanatory variable. We generated 999 simulated maps of vegetation types and compared the value of the observed association statistic,  $Stat_{obs}$  (specific to each variable, see Appendices S.3–S.5), with the distribution of the simulated statistic,  $Stat_{sim}$ , and computed the  $P$ -value as  $P = (N(Stat_{sim} \geq Stat_{obs}) + 1) / (N_{sim} + 1)$ , where  $N$  gives the number of achievements and  $N_{sim}$  the number of simulations. To ensure accurate matches between forest types and environmental or compositional variables, we excluded all pixels having an average probability of classification <70% (39% of pixels).

For the floristic analysis, we performed a correspondence analysis (CA) to detect the main floristic gradients in our dataset and used a canonical correspondence analysis (CCA) to assess whether and how the different forest types differed in taxa composition. Functional composition was assessed through the mean value (quantitative traits) and the frequency (one modality for each qualitative trait), weighted by abundance, of the five functional traits at the community level for each plot. For both floristic and functional analyses, all plots located in areas that burned between 2002 and the acquisition of satellite images in 2020 were excluded from the dataset. To ensure reliable floristic and functional estimates while minimizing sampling errors, we also discarded plots with fewer than 20 trees (1.3% of plots). Note that this arbitrary threshold is likely conservative, as a lower threshold of 10 trees per plot led to similar results (not shown). Thus, analyses were run on 2524 plots.

## Results

### Mapping forest types

The vegetation map achieved an overall accuracy of 83%. Most classification errors were due to confusion involving pairs of forest types linked by progressive forest structure transitions. For instance, dense versus Marantaceae forests and Marantaceae versus open Marantaceae forests represented 61% of the errors (Table 1 and Fig. 4). The map is openly available in DataSuds-geo repository (IRD, France) at <https://doi.org/10.23708/59ed1234-bb7f-4914-be50-aadeadf67aa0>.

The dominant forest type in the area was Marantaceae forests (48% of the total predicted area), followed by open Marantaceae forests (21%), swamp forests (22%), dense forests (4%), secondary forests (2%) and monodominant *Gilbertiodendron* forests (2%). Vegetation types presented a structured mosaic with notable big patches of open Marantaceae forests (up to 10 000 ha) and with monodominant *Gilbertiodendron* forests mostly distributed along the rivers in the eastern part of the study area, in the close vicinity of swamp forests. Dense forests were mainly located in the north, but with smaller patches scattered across the rest of the study area. Interestingly, our model classified the large forest patch that burnt in 1970 as secondary forest, while all reference areas for secondary forests were on areas that burnt after 2002 and mainly in 2016.

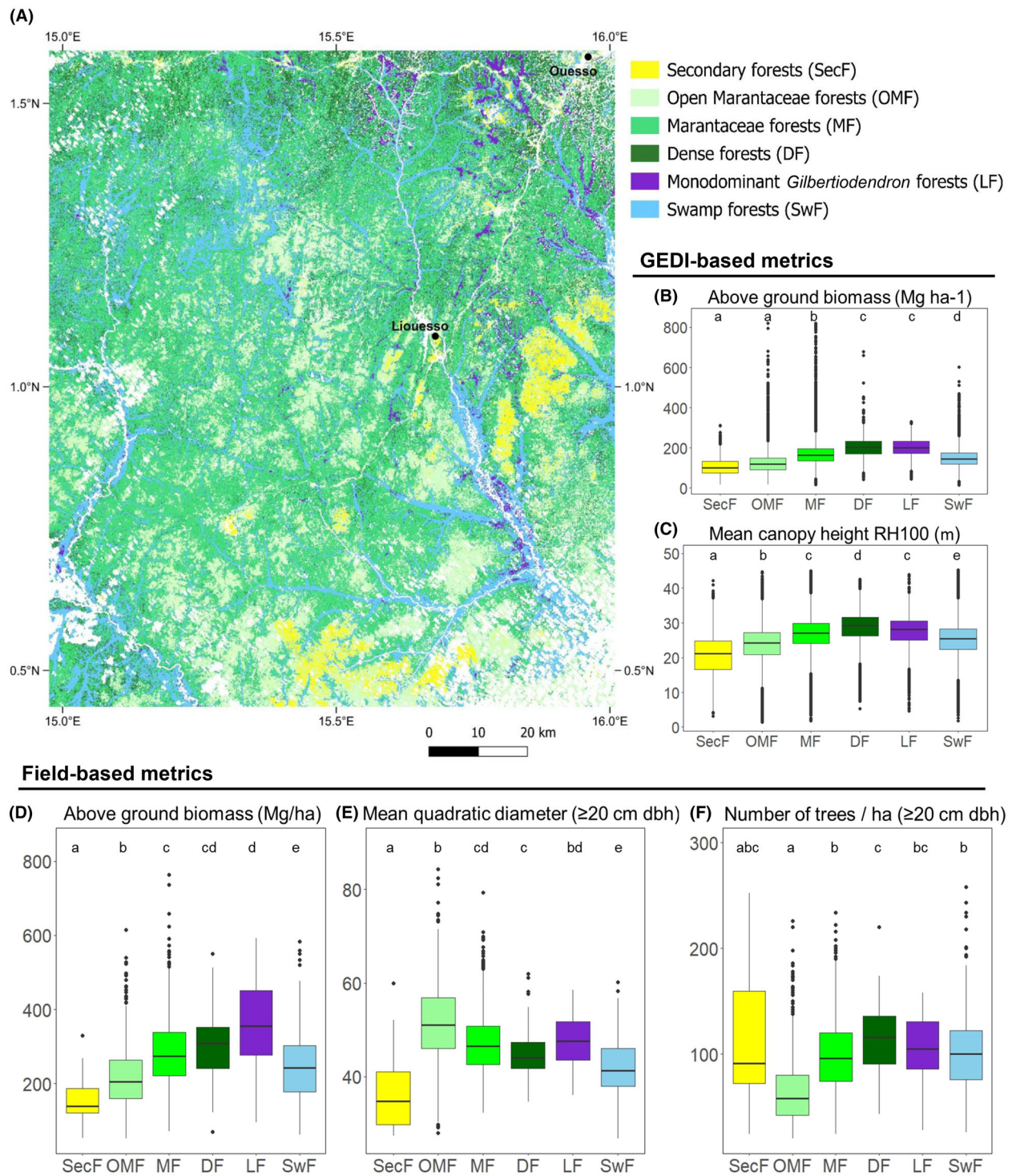
Combining this map with forest inventory data and GEDI products consistently revealed significant structural

**Table 1.** Confusion matrix summarizing the validation of the six predictive models.

Prediction	Reference							Total confusion error (%)
	DF	LF	MF	OMF	R	SecF	SwF	
DF	56	2	10	0	1	0	2	21
LF	0	77	0	0	0	0	3	4
MF	41	5	181	29	7	2	10	34
OMF	0	0	38	223	11	17	0	23
R	0	0	2	0	105	0	0	2
SecF	0	0	0	2	3	57	0	8
SwF	4	1	4	0	0	0	216	4
Total	45	9	23	12	17	25	6	
confusion error (%)								

A total of 204 validation polygons spread over the seven vegetation types were repeatedly used to validate the six models (DF, dense forests; LF, monodominant *Gilbertiodendron* forests; MF, Marantaceae forests; OMF, open Marantaceae forests; R, roads; SecF, secondary forests; SwF, swamp forests). Green: correct classification.





**Figure 4.** Predicted vegetation map over the study area (A); GEDI-derived characterization of forest types (B, C) and ground-based derived characterization of forest types (D–F). The statistical differences between the distribution of forest structure values are illustrated with letters in panels B to F (different letters indicate statistical differences with a 5% risk for the torus test on Wilcoxon effect size).

differences between the six forest types with a similar ranking of forest types. However, GEDI's above ground biomass (AGB) estimates were 41% lower than the field estimates on average ( $153$  vs  $260$   $\text{Mg ha}^{-1}$ ; Fig. 4). Open Marantaceae forests were characterized by a significantly lower number of trees per hectare (but of larger trunk diameter on average) and a lower mean canopy height than almost all other forest types, resulting in small AGB values (mean of  $219 \pm 6.2$   $\text{Mg ha}^{-1}$  using field estimates vs  $124 \pm 0.2$   $\text{Mg ha}^{-1}$  using GEDI estimates), similar to the swamp forests (mean of  $247 \pm 11$  vs  $149 \pm 0.2$   $\text{Mg ha}^{-1}$ ) but higher than the secondary forests (mean of  $153 \pm 22.4$  vs  $106 \pm 0.6$   $\text{Mg ha}^{-1}$ ). By contrast, the highest AGB values were observed for the monodominant *Gilbertiodendron* (mean of  $356 \pm 27.3$  vs  $202 \pm 0.7$   $\text{Mg ha}^{-1}$ ) and dense forests (mean of  $306 \pm 16.7$  vs  $201 \pm 0.5$   $\text{Mg ha}^{-1}$ ) while Marantaceae forests exhibited intermediate values (mean of  $286 \pm 4.9$  vs  $167 \pm 0.2$   $\text{Mg ha}^{-1}$ ). The mean quadratic diameter and number of trees per hectare of secondary forests displayed a large variance, probably reflecting the different age of the forests.

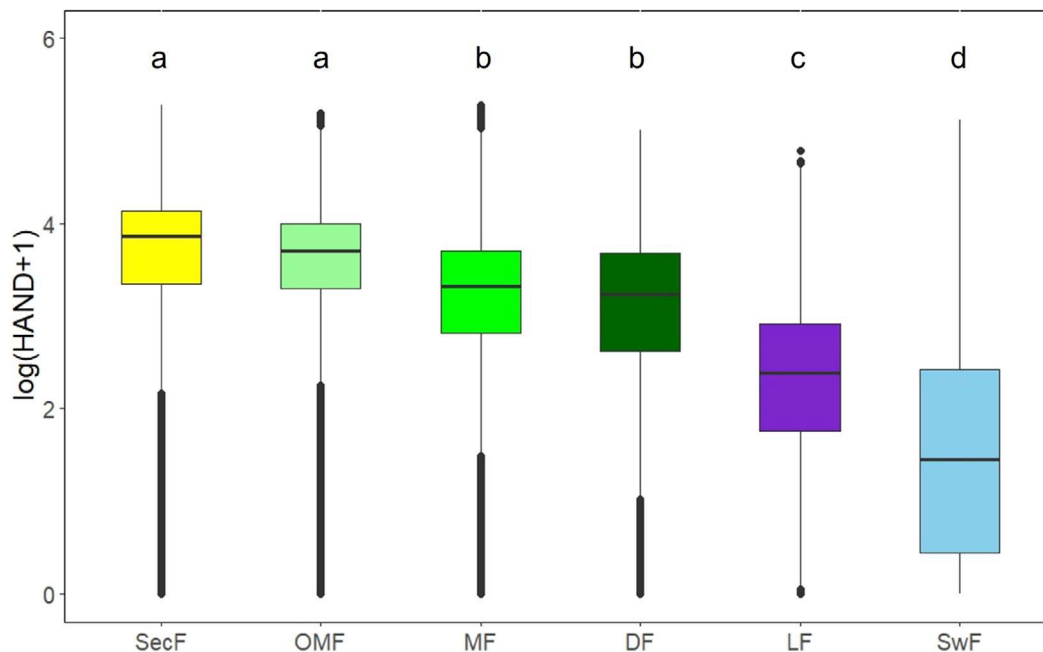
### Linking forest types to topography

Vegetation types were significantly associated with topographical gradient (HAND index), with significant

differences in HAND values between all forest types except between open Marantaceae forests and secondary forests, and between Marantaceae forests and dense forests (Fig. 5). Secondary and open Marantaceae exhibited the highest HAND index values indicating the highest elevation above nearest drainage, *Gilbertiodendron* and swamp forests had the lowest values, and Marantaceae forests and dense forests showed intermediate values.

### Testing the role of soil types on forest types distribution

We found an overall significant association between vegetation types and soil types ( $\chi^2 = 99\,507$ ; torus test  $P = 0.003$ ). However, our post hoc test based on pairwise associations revealed that only a few associations between vegetation and soil types were significant (Table 2). As expected, swamp forests were significantly associated with hydromorphic soils but significantly scarce on ferrallitic soils on sandstone and quartzite. Dense forests were significantly associated with ferrallitic soils on sandstone and quartzite. Monodominant *Gilbertiodendron* forests were also significantly, albeit weakly, associated with ferrallitic soils on sandstone and quartzite. Open Marantaceae forests were scarcer on hydromorphic soils and were significantly associated with ferrallitic soils on material from the clayey-sandy series, along with secondary forests, which



**Figure 5.** HAND index distribution for the different vegetation types (SecF, secondary forests; OMF, open Marantaceae forests; MF, Marantaceae forests; DF, dense forests; LF, monodominant *Gilbertiodendron* forests; SwF, swamp forests). Different letters indicate significant differences (torus test on Wilcoxon effect size,  $P = 0.001$ ).

**Table 2.** Observed and null distributions of the frequency of vegetation types in the different soil types (DF: dense forests, LF: monodominant *Gilbertiodendron* forests, MF: Marantaceae forests, OMF: open Marantaceae forests, SecF: secondary forests, SwF: swamp forests).

	Ferralitic, highly desaturated, impoverished, modal soils, on material from the clayey–sandy series	Ferralitic, highly desaturated, modified, modal, undifferentiated soils	Ferralitic, highly desaturated, modified, modal soils, on sandstone and quartzite	Ferrallitic, highly desaturated, modified, modal soils, on shale	Hydromorphic mineral and organic soils	Juxtaposition: highly desaturated, impoverished, yellow ferralitic soils + undifferentiated hydromorphic soils on alluvial deposits
DF	19.9 [14.9–53.5]	15.0 [9.5–46.4]	<b>33.2 [7.6–27.1]</b>	14.7 [1–15.9]	9.1 [7–21]	3.3 [1.2–17]
LF	23.2 [11.7–49.6]	13.7 [5.3–59.6]	<b>38.1 [2.7–37.4]</b>	6.0 [0.8–14.7]	15.6 [3.8–29.4]	3.8 [0.6–19.8]
MF	29.1 [23.6–36.3]	32.6 [20.7–36]	18.1 [12.4–21.7]	5.6 [3–7.5]	11.3 [11.3–17.2]	<b>2.3 [3.2–8.5]</b>
OMF	<b>47.4 [19–44.1]</b>	22.0 [15–42.4]	12.6 [8.5–25.5]	1.0 [0.8–10.1]	<b>6.4 [8.3–20.8]</b>	9.0 [1.6–10.2]
SecF	<b>72.2 [5.8–70.3]</b>	<b>2.6 [5.1–54.1]</b>	8.7 [0.5–47.1]	0.9 [0.1–23.6]	<b>6.3 [2–32.7]</b>	9.5 [0.2–19.3]
SwF	28.2 [24.9–36.3]	28.4 [22.7–33]	<b>10.3 [11.4–21.1]</b>	5.6 [3.3–7.6]	<b>21.7 [10.7–18.5]</b>	4.8 [4–8.1]

Observed values are first reported and then compared to the 0.025 and 0.975 quantiles of the null distribution (obtained from the toroidal translations) reported in square brackets. Values in dark grey indicate that the vegetation type is more frequent, and in pale grey less frequent, on the soil type than by chance at a 5% risk.

avoid ferralitic undifferentiated soils. Finally, Marantaceae forests avoided the juxtaposition of ferralitic and hydromorphic soils.

## Floristic composition

The first two axes of the correspondence analysis (CA) explained 11.0% of the total variance in floristic composition (Fig. 6). The axes of the CA were very structured (cf. bar plot of eigenvalues, Fig. 6) and therefore displayed marked floristic gradients. *Gilbertiodendron dewevrei* was the most represented taxa on the first axis, leading to negative site scores for the monodominant *Gilbertiodendron* forest plots. Note that some areas classified as swamp forests by our model also showed negative scores along this axis, probably illustrating the local coexistence of both forest types within the 1-ha predicted pixels. The second axis mostly opposed pioneer taxa, such as *Maesopsis eminii* and *Macaranga* spp. to taxa known to characterize mature forests in this area, such as *Manilkara* spp. and *Scotellia* spp. This axis consistently opposed secondary forests, and to a lesser extent, open Marantaceae forests, to swamp, dense and Marantaceae forests. Thus, as expected, the predicted forest types from our vegetation map exhibit marked differences in their tree composition.

The canonical correspondence analysis (CCA) constrained by the vegetation types explained a total of 7.6% of the variance (the first two axes expressed 70.8% of the explained variance) (Fig. 7). The torus test indicated that this part of explained variance was significantly explained by the vegetation types ( $P = 0.001$ ), confirming that forest types exhibited contrasted tree compositions. The first axis mostly opposed monodominant *Gilbertiodendron* forests to the other forest types, and the second axis, again

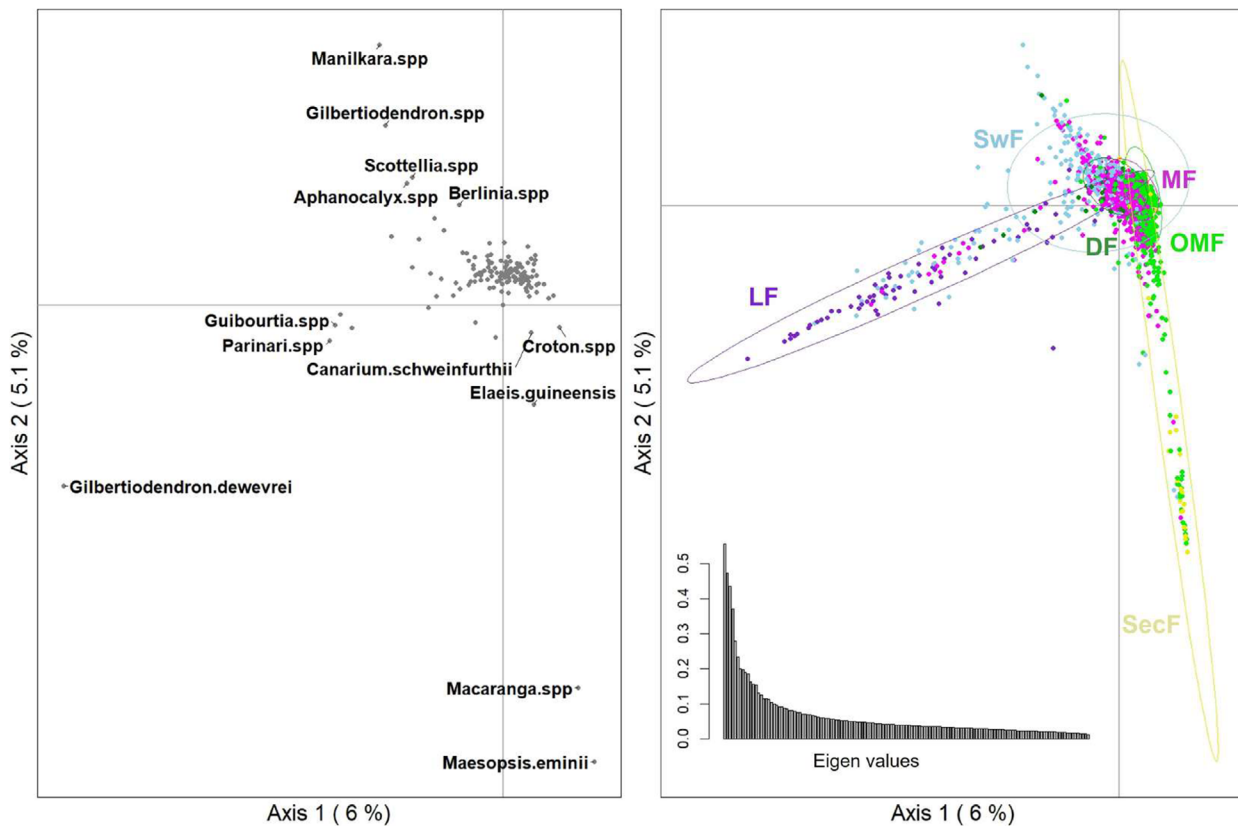
contrasting taxa with different successional affinities, mainly opposed secondary and open Marantaceae forests to Marantaceae and dense forests.

## Functional composition

The forest types expressed significant differences in functional composition (Fig. 8). All the studied traits followed a gradient from secondary forest, open Marantaceae and Marantaceae forests, to dense and monodominant *Gilbertiodendron* forests (except for the deciduous proportion in secondary forests). Secondary forests displayed a large variance in wood density and pioneer proportion. They also had among the lowest mean wood density, maximum diameter and proportion of deciduous trees, and the highest pioneer and anemochorous tree species proportions. Note that *Macaranga* spp., which is highly abundant in this forest type (65% of the tree individuals) is mostly responsible for some of these patterns. Open Marantaceae and, to a lesser extent, Marantaceae forests were characterized by low maximum diameter and wood density, and a high proportion of deciduous, pioneer and anemochorous trees, compared to the other forest types. By contrast, monodominant *Gilbertiodendron* forests had the highest wood density and maximum diameter, and the lowest proportion of deciduous, pioneer and anemochorous trees, but, here again, *Gilbertiodendron dewevrei* drove these patterns with 46% of individuals in this forest type.

## Megafauna composition

Across the 2667 observation points, 2149 were attributed by local spotters to elephants and 518 to gorillas. Our



**Figure 6.** Distribution of the tree taxa (left) and the plots (right) on the first two axes of a correspondence analysis (SecF, secondary forests in yellow; OMF, open Marantaceae forests in green; MF, Marantaceae forests in magenta; DF, dense forests in dark green; LF, monodominant *Gilbertiodendron* forests in purple; SwF, swamp forests in pale blue).

torus tests revealed that elephant occurrences were over-represented in Marantaceae forests (66.4% of occurrences in Marantaceae forests against the 5% confidence interval of 6.6–33.8%). Moreover, gorillas were over-represented in open Marantaceae forests (40.3% of occurrences against the 5% confidence interval of 0–22.7%) and in Marantaceae forests (45.8% of occurrences against 3.3–42%). No other significant difference between forest types was detected for these two species.

## Discussion

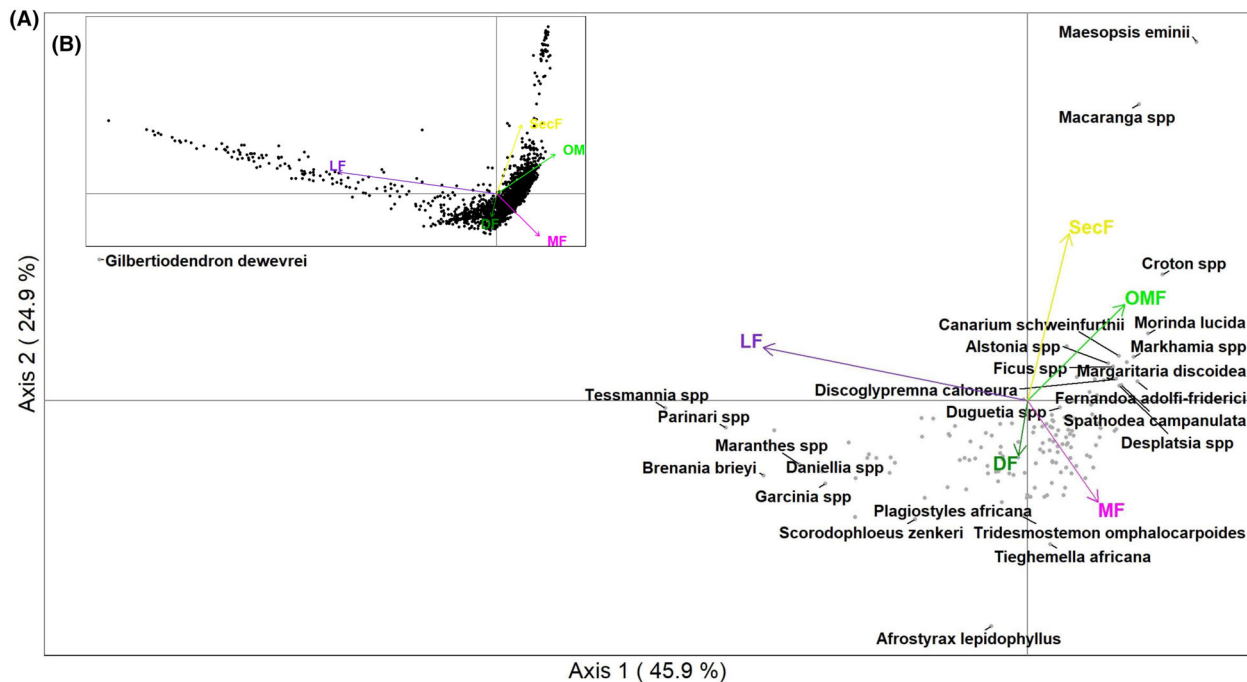
In this paper, we combined up-to-date remote sensing approaches and extensive field- and satellite-based forest metrics to map the large-scale distribution of forest types and characterize their structure, composition, function and environmental drivers in a poorly studied area in central Africa. Our work demonstrates that such a combination of data has the potential to generate knowledge on forest ecology and to support forest management and conservation strategies at the regional scale. We specifically found that water drainage depth is a major driver of

forest type distribution and described the different structure, composition and functions of the different forest types, bringing new insights into the potential mechanisms responsible for their establishment and maintenance.

## Towards an accurate monitoring of tropical forest types and functions

So far, tropical forests have often been remotely sensed as a uniform forest type, and most current research efforts have concentrated on improving the monitoring of deforestation, and to a lesser extent forest degradation (Dupuis et al., 2020). However, further efforts are also needed to characterize the diversity and composition of tropical forests at larger scales to better anticipate and monitor their response to upcoming pressures, such as functional shifts or possible critical transitions, and to significantly improve management and conservation strategies.

Recent progress has been made to distinguish and characterize forest types using airborne LiDAR data (Scheeres et al., 2023). However, airborne LiDAR data are often



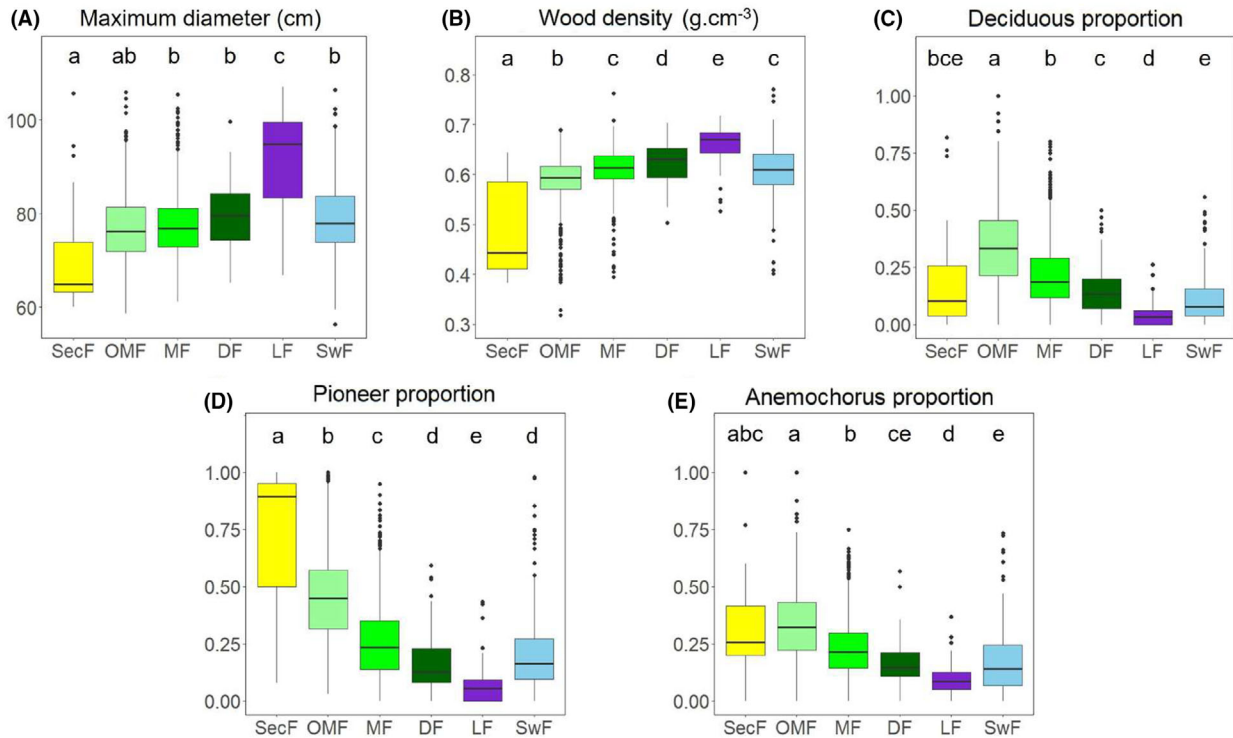
**Figure 7.** Result of the canonical correspondence analysis (CCA) constraining ordination by vegetation types. Distribution of: (A) tree species and (B) plots, on the first two axes of the CCA according to vegetation types (SecF, secondary forests in yellow; OMF, open Marantaceae forests in green; MF, Marantaceae forests in magenta; DF, dense forests in dark green; LF, monodominant *Gilbertiodendron* forests in purple).

restricted to relatively small-scale areas (Mascaro et al., 2014). Large-scale LiDAR data, readily available from the GEDI mission, now plays a crucial role in characterizing forest structure in the absence of extensive field measurements. Our study demonstrates that GEDI estimates consistently rank forest types based on structural metrics, providing valuable insights into relative differences in forest structure. However, we found that GEDI products significantly underestimate above ground biomass (AGB) by 41% compared to field-derived estimates in our study area, consistent with findings from another study in central Africa (Hunka et al., 2023). Therefore, while these products offer substantial assistance in characterizing differences between forest types, caution is warranted when interpreting their absolute values.

We demonstrated that combining state-of-the-art deep learning approaches with well-processed Sentinel 2 data has the potential to generate accurate forest type maps. Given that Sentinel-2 satellites provide weekly data globally, under cloud-free conditions, our framework has the potential to accurately monitor the spatio-temporal dynamics of forests at both fine spatial and temporal scales, moving beyond the classical forest and non-forest dichotomy often used in forest change detection algorithms (Decuyper et al., 2022). It opens several new perspectives, such as the improvement of (i) forest carbon

maps, where inversion models would account for allometries specific to forest types (Djomo et al., 2016); (ii) global vegetation models, where forest types would be modelled according to their own composition, function and dynamics (Scheiter et al., 2013); (iii) ecosystem service assessments, where the spatio-temporal dynamics of services would be better anticipated (Alamgir et al., 2016; Lhoest et al., 2019); (iv) wildlife management, where the quality, fragmentation and connectivity of habitats would be better assessed (Foerster et al., 2016); and (v) management and conservation strategies, where decisions would be guided by a deeper understanding of forest composition and functions and of the complementarity of forest types (Gavin, 2009).

Thus, further efforts are needed to expand our study scheme to other tropical regions. Large-scale field datasets or independent satellite products, such as GEDI or the upcoming BIOMASS mission (Le Toan et al., 2011), can be leveraged in combination with these forest type maps to provide a better understanding of the structure of forest types. However, mapping tropical vegetation types should ideally also provide insights into their functionality. Recent research suggests that satellite data have the potential to predict functional traits derived from field-based or airborne measurements, such as leaf mass per area and canopy phosphorus (Aguirre-Gutiérrez



**Figure 8.** Distribution of the community mean values of five traits among the vegetation types. SecF, secondary forests; OMF, open Marantaceae forests; MF, Marantaceae forests; DF, dense forests; LF, monodominant *Gilbertiodendron* forests; SwF, swamp forests. Different letters indicate significant differences (torus test on Wilcoxon effect size,  $P < 0.05$ ).

et al., 2021; Durán et al., 2019; Ordway et al., 2022). Furthermore, recent advancements in hyperspectral sensors, such as EnMAP, offer new perspectives in this area (Guanter et al., 2015). Given that the response of tropical forests to environmental change will likely depend on their functional characteristics, and considering the significant lack of field-based trait measurements in central Africa (Kattge et al., 2020), the use of satellite data to characterize the functional composition of tropical forests holds great potential for forecasting their future.

### The importance of soil–water depth

We found that water drainage depth is an important driver of forest type distribution at landscape scale. Swamp forests and monodominant *Gilbertiodendron* forests were, as expected, found in areas where the water drainage depth is shallow; dense and Marantaceae forests were associated with intermediate water drainage depths; and both open Marantaceae and secondary forests were associated with the highest water drainage depth values. This result confirms that soil–water content significantly affects forest structure, composition and functioning, as found in other continents (Jucker et al., 2018; Muscarella

et al., 2020; Sousa et al., 2022). We consistently found that swamp forests were significantly associated with hydromorphic soils and avoided ferralitic soils on sandstone while dense forests tended to be slightly over-represented on the latter. By contrast, open Marantaceae forests were under-represented on hydromorphic soils and were, along with secondary forests, significantly associated with ferralitic soils on material from the clayey–sandy series, where the strongest drainage capacity occurred in the study area. The soil–vegetation analysis thus confirms that soil–water availability has a major impact on the distribution of vegetation types in our study area, even though the contrasted effect of the juxtaposition of ferralitic and hydromorphic soils on Marantaceae forests remains unclear. More generally, the lack of information on soil composition and structure in central Africa constitutes a major limitation for understanding the role of soil nutrient and water content in the distribution of forest types. Several global soil datasets were developed during the last decade, some of which focused on soil hydraulic characteristics (Dai et al., 2019). However, most of these products rely on passive remote sensing data that heavily follow vegetation characteristics, raising important circularity issues when causal links

between soil and vegetation characteristics are investigated. Therefore, future efforts to develop soil products independently of vegetation are necessary, even if they require extensive ground sampling and the development of new extrapolation or modelling approaches.

If some forest types exhibited significant differences between their water drainage depth values, an overlap in HAND values existed between some forest types, for example, between SecF, OMF, MF and DF. This suggests either that other environmental or historical factors are in play or that a form of multistability occurs, such as recently found for forests and savannas where hydrology acts as an important mechanism driving their local coexistence (Mattos et al., 2023). This result is of importance given that the climate of central African forests is forecasted to be hotter and drier (Fotso-Nguemo et al., 2017), suggesting that water availability may be lower in the future. This could trigger important transitions between forest types and thus shifts in functions and animal composition. It is already known that droughts affect forests globally (Tao et al., 2022), and the forest responses to drought can differ, notably according to topography (Schwartz et al., 2019). Extreme drought events also worsen fire risk, for example, fires that occurred in 2016 mostly in areas with the highest water drainage depths in our study area (Verhegghen et al., 2016).

### Ecological insights on poorly understood, yet widespread forest types

By producing information on the spatial distribution of forest types and on their structure and composition, our work contributed to a better knowledge of the ecology of central African forests. In particular, both Marantaceae and monodominant *Gilbertiodendron* forests constitute widespread but poorly understood forest ecosystems.

Monodominant *Gilbertiodendron* forests are dominated by *Gilbertiodendron dewevrei* (De Wild.) J. Leonard, a tall evergreen and shade-tolerant species belonging to the Detarioideae Burmeist. subfamily and quasi absent from any other forest type (Hart et al., 1989). Monodominant *Gilbertiodendron* forests have a peculiar structure and composition with a high AGB (Heimpel, 2023; Umunay et al., 2017); the highest of all forest types in our study area. The processes and factors explaining the establishment and maintenance of this forest type has been debated for a long time (Hall et al., 2020; Peh et al., 2011; Torti et al., 2001). The validation of our model suggests a very accurate identification of monodominant *Gilbertiodendron* forest patches, confirming a highly specific spectral and/or textural signature of this forest type (Barbier et al., 2016; Viennois et al., 2013).

This opens new perspectives to better understand its spatial distribution and thus, potentially, of its environmental drivers, if any. So far, monodominant *Gilbertiodendron* forests were hypothesized to be mostly distributed along the rivers, notably due to their seed dispersal (Kearsley et al., 2017), but monodominant *Gilbertiodendron* forests can also be found on plateaus (Katembo et al., 2020; Lokonda et al., 2018). Closer investigations could also be carried out on their stability over time, as they appear to have resisted dry climatic episodes and maintained over 2000 years at least (Tovar et al., 2019).

Marantaceae forests are characterized by a dense continuous understorey of giant perennial herbs from the *Zingiberales* order (Pouteau et al., 2024). Such understorey prevents tree regeneration, leading to a lack of intermediate sized trees and a quite open to very open canopy (Hecketsweiler et al., 1991; White & Abernathy, 1996). In this study, Marantaceae and open Marantaceae forests were predicted to cover 69% of the study area, illustrating that they constitute major forest types in central Africa. While these forest types exhibit a much lower carbon potential than other mature forest types, as revealed here, their importance for megafauna has long been recognized (Blake, 2002; Doran et al., 2002; White et al., 1995). Our results consistently showed a higher abundance of gorillas in Marantaceae and open Marantaceae forests, and of elephants in Marantaceae forests, suggesting potential positive feedbacks between megafauna and giant herbs. Indeed, being attracted to Marantaceae forests, notably due to the availability of food sources and nesting areas, megafauna may also contribute to their maintenance. For example, while elephants are known to physically damage small trees and tree seedlings, giant herbs appear to be little affected by elephants as they can re-sprout easily thanks to their hardy rhizomes (Brncic, 2003; Scalbert et al., 2023). However, the role of megafauna in the maintenance and spread of Marantaceae forests is still debated (Pouteau et al., 2024).

More broadly, the origin of Marantaceae forests is still highly uncertain (Pouteau et al., 2024). While some authors have argued that this system corresponds to a successional transition stage between savannas and dense forests (White, 2001), others state that Marantaceae forests would colonize a forested area after a large-scale disturbance. For instance, it has been shown that fire could be a factor in the establishment and maintenance, over >1000 years, of Marantaceae forests (Brncic, 2003; Tovar et al., 2014). In our study area, most secondary forests were former Marantaceae forest patches that burnt in the past (e.g. 83.1% of the burnt areas during the El Niño event in 2016 were open Marantaceae forests; Verhegghen et al., 2016). Moreover, a careful inspection of aerial

photographs taken in 1959 over our study area confirmed that the large patch that burnt in the late 1960s was an open Marantaceae forest before the fire (results not shown). Fifty years after the fire event, this forest patch remains spectrally more similar to a young secondary forest than to any other type of forest according to our model, suggesting in agreement with the field data that its canopy is still dominated by the species that recruited after the fire. Whether these secondary forests will follow a usual successional pathway towards a mature dense forest composition or will come back again to a Marantaceae forest state after the pioneer cohort disappears is uncertain. Fire could thus have two effects: reinitiate the vegetation succession by triggering a bifurcation in forest trajectory, or contribute to maintaining Marantaceae forests in the long term due to well-known positive feedbacks of fires on the herbaceous compartment (De Faria et al., 2021; Flores et al., 2016). Temporal surveys are needed to understand which hypothesis is the most likely. Using a time series approach with 12 years of data, a recent study in the Brazilian rainforest showed that recurrent fires can lead forests into an arrested succession with striking differences in community structure and functional composition compared to old-growth forests (Mata et al., 2022). However, in the case of the Marantaceae forests, multi-decadal data (e.g. Cuni-Sanchez et al., 2016), or even historical ecology approaches (e.g. Tovar et al., 2014), would be necessary to reach robust conclusions due to the expected low temporal dynamics of these systems.

## Conclusion

By combining satellite information and recent deep-learning architectures with field and satellite data, we were able to accurately map forest types in the north of Congo and reveal their contrasting floristic, functional and megafauna compositions. Our work confirms that the commonly pictured 'green carpet' of tropical forests in the Congo Basin is a mosaic of forest types with different functions, among which understudied forest types such as monodominant *Gilbertiodendron* forests and Marantaceae forests exist. Our approach paves the way for a better understanding of the spatio-temporal dynamics of tropical forests. It may also constitute an important tool for designing better management and conservation strategies to tackle carbon and biodiversity challenges, for instance, within the framework of the global 30 × 30 initiative launched during the 15th UN Biodiversity Conference (COP-15). We specifically hope that the development of such approaches will help to anticipate ecosystem transitions in the current context of global change.

## Acknowledgements

We thank the Odzala-Kokoua National Park and the forest company IFO-Interholco for sharing field data and Hervé Goeau for his useful advices on deep-learning analyses. This work was supported by the DESSFOR project funded by the French National Research Agency (ANR-20-CE32-0010). We also thank the One Forest Vision initiative (CEA, CIRAD, CNRS, IRD, INRAE, and MNHN), under the supervision of the Ministère de l'enseignement supérieur et de la recherche et du Ministère de l'Europe et des affaires Etrangères.

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## Supporting Information

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

**Appendix S1.** Corrections on satellite images.

**Appendix S2.** Functional traits data.

**Appendix S3.** Topography.

**Appendix S4.** Soil types.

**Appendix S5.** Floristic, functional and faunistic compositions.

**Table S1.** Distribution of the polygons and validation polygons in the vegetation types.

**Figure S1.** Localisation of the 680 calibration and validation polygons used to create the vegetation map in the

study area (red points) using Pleiades images (from January to December 2022, 0.5-m resolution, panchromatic) and Planet images (February 2020, 5-m resolution, NIR band).

**Figure S2.** Map of soil types in our study area, digitised from a part of the map by de Boissezon et al. (1969).