

Article

Vertical Canopy Gap Profiles Reveal Structural Divergence Among Central African Old-Growth Forest Types

Timothée Besisa Nguba ^{1,2} , Arthur Vander Linden ² , Jan Bogaert ² , Thalès de Haulleville ³, Antoine Plumacker ² , Trésor Selemani Mbavumoya ² , Thibault Collet ², Zoé Rousseau ², Wannes Hubau ^{4,5} , Sassan Saatchi ⁶ and Jean-François Bastin ^{2,*} 

- ¹ Ecole Régionale Postuniversitaire d'Aménagement et de Gestion Intégrés des Forêts et Territoires Tropicaux (ERAIFT), Université de Kinshasa, Kinshasa P.O. Box 15.373, Democratic Republic of the Congo; t.besisa@eraift-rdc.org
 - ² Teaching and Research Center (TERRA), Gembloux Agro-Bio Tech, Université de Liège, Passage des Déportés, 2, 5030 Gembloux, Belgium; arthur.vanderlinden@uliege.be (A.V.L.); j.bogaert@uliege.be (J.B.); antoine.plumacker@uliege.be (A.P.); tmselemani@uliege.be (T.S.M.); thibault.collet@uliege.be (T.C.); zoe.rousseau@uliege.be (Z.R.)
 - ³ Faculty of Bioscience Engineering, Department of Environment, Ghent University, 9000 Ghent, Belgium; thales.dehaulleville@ugent.be
 - ⁴ Laboratory for Wood Technology, Faculty of Bioscience Engineering, Ghent University, 9000 Ghent, Belgium; wannes.hubau@ugent.be
 - ⁵ Royal Museum for Central Africa, Service of Wood Biology, 3080 Tervuren, Belgium
 - ⁶ Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109, USA; sasan.s.saatchi@jpl.nasa.gov
- * Correspondence: bastin.jf@gmail.com or jfbastin@uliege.be

Highlights

What are the main findings?

- Monodominant *Gilbertiodendron dewevrei* (De Wild) J. Léonard forests exhibit consistently lower canopy openness and smaller gaps throughout the entire vertical canopy profile, indicating more continuous and homogeneous canopies.
- LiDAR-derived structural ratios normalizing gap area by basal area and canopy height provide robust indicators of canopy structure across contrasting forest types.

What are the implications of the main findings?

- Gap structure varies with canopy height and site conditions, reflecting differences in stand development and disturbance regimes.
- Integrating canopy gap metrics improves the assessment of forest structural dynamics and supports large-scale monitoring using remote sensing.

Abstract

Forest canopy gaps are key indicators of forest dynamics, yet their vertical organization remains poorly quantified across forest types. While canopy gaps are commonly interpreted as signatures of disturbance regimes, their size distribution and vertical organization may also reflect intrinsic differences in stand structure, crown architecture, and density-dependent interactions. We hypothesize that the vertical distribution of canopy gap size differs among forest types, reflecting contrasting structural organization and developmental trajectories. Using airborne LiDAR, we quantified vertical gap size distributions in two Central African old-growth forest types: monodominant *Gilbertiodendron dewevrei* (GIL) and MIXED forests, across two sites in the Democratic Republic of the Congo (Lileko and Yangambi). We also derived structural ratios normalizing gap area by basal area and canopy height. Results show clear divergence in vertical gap profiles. GIL forests



Academic Editor: Matteo Mura

Received: 8 June 2026

Revised: 8 July 2026

Accepted: 11 July 2026

Published: 22 July 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

consistently exhibit lower canopy openness than MIXED forests. Between heights of 10 and 20 m, total gap area per hectare ranged from 39.11 (95% CI: 19.84–83.5) to 567.56 (95% CI: 229.44–707.48) m² ha^{−1} in GIL forests, compared with 69.10 (95% CI: 55.28–123.51) to 1244.97 (95% CI: 784.73–1360.45) m² ha^{−1} in MIXED forests across both sites. Structural ratios further confirm that GIL forests maintain smaller gap areas relative to basal area and canopy height. Overall, the results support the three study hypotheses, demonstrating that vertical gap size distributions and their normalization by stand structural attributes provide robust and transferable indicators for discriminating among Central African old-growth forest types and developmental stages, highlighting the importance of structural context for interpreting tropical forest dynamics.

Keywords: remote sensing; unoccupied aerial vehicle; LiDAR; monodominant forests; dominant species; *Gilbertiodendron dewevrei*; Congo Basin

1. Introduction

Tropical forest canopy gap size and spatial distribution are key indicators of forest dynamics, reflecting the combined effects of tree growth, mortality, recruitment, succession, and anthropogenic disturbances such as shifting cultivation, selective logging, and clear-cutting [1–4]. Canopy gaps are generated by a range of endogenous processes, including individual tree mortality, windthrow, and branch fall [1,5,6]. By modifying light availability and local microclimatic conditions, canopy gaps regulate regeneration and successional trajectories, thereby influencing species composition and the development of forest structural complexity [7]. Within old-growth systems, the ecological outcome of gap formation depends not only on the surface area of the opening but also on the canopy height stratum at which it occurs. The size and frequency of canopy openings vary systematically across height levels, mediating regeneration trajectories and sustaining vertical biodiversity gradients [8,9]. Characterizing how gap size distributions vary across canopy height strata is therefore essential for accurately capturing disturbance regimes, structural heterogeneity, and long-term ecosystem functioning [10,11]. These structural differences across forest types are expected to generate contrasting canopy gap regimes, yet their vertical expression across old-growth forest types remains largely uncharacterized in Central Africa, which contains the second-largest area of tropical forest cover.

Despite this ecological role, remote sensing research on canopy gap dynamics in Central Africa has focused more on the impacts of selective logging [12], leaving several structural and functional dimensions underexplored. In particular, the potential of airborne Light Detection and Ranging (LiDAR) derived metrics to capture differences in vertical organization of gap size distributions across contrasting old-growth forest types remains poorly quantified in this region, a knowledge gap with direct consequences for biodiversity conservation, silvicultural management, and carbon accounting. Depending on their successional stage, ecological niche, and spatial distribution, forests can vary considerably in both composition and structure, even at the continental scale [13,14]. In tropical biomes, certain stages of forest succession can exhibit a disproportionate contribution to forest stem density and basal area by a single dominant species, forming what are commonly known as monodominant forests [15].

Different types of monodominant forests occur across tropical biomes. In Afrotropical and Neotropical regions, they are typically dominated by species from the *Fabaceae* (formerly *Caesalpiniaceae*) family, whereas in Asia, dominance is most associated with *Dipterocarpaceae* and *Lauraceae* [16–18]. In Central Africa, early successional forests are

frequently dominated by fast-growing pioneer species such as *Musanga cecropioides* and *Aucoumea klaineana* [19] and, in some cases of savannah colonization, by *Uapaca guineensis* [20], while late-successional forests are often characterized by the dominance of shade-tolerant species, notably *Gilbertiodendron dewevrei*, *Brachystegia laurentii*, *Cynometra alexandri*, and *Julbernardia seretii* [15,18,21].

Gilbertiodendron dewevrei (De Wild) J.Léonard (*G. dewevrei*) is among the most ecologically and biogeochemically significant tree species in Central Africa [22]. It has a long average lifespan and low adult mortality rate, creating endogenous conditions of low disturbance that sustain classical monodominant stands [18]. Monodominant *G. dewevrei* forests account for 29% of the 7858 Km² of the Sangha Trinational area [23], and *G. dewevrei* represents the dominant species in terms of biomass across several landscapes [24], with carbon stocks ranging from 160 Mg ha⁻¹ to 300 Mg ha⁻¹ [25] and a positive annual carbon sequestration rate of 1.1 Mg ha⁻¹, particularly due to diameter growth [26]. In most study sites in Central Africa, *G. dewevrei* trees represent more than 50% of forest basal area and biomass [26–28]. Yet structural differences between monodominant *G. dewevrei* forests (GIL) and adjacent mixed forests (MIXED) are not systematic across the region [25]. For example, significant differences in basal area are documented in the Dja Biosphere Reserve [27] but not in the Yangambi Biosphere Reserve [28,29], and stem density patterns vary across sites [25–27,30,31]. These inconsistencies across regions highlight the need for additional structural indicators beyond conventional plot-level metrics based on field data. In particular, the dominance of large-diameter trees and their effect on canopy gap structure across vertical strata have not been fully investigated to differentiate GIL from MIXED forests or to identify developmental stages within GIL forests, a knowledge gap that airborne LiDAR is particularly well-suited to address. Yet, despite its ecological and biogeochemical importance, the structural signature of GIL forests, particularly the vertical organization of their canopy gap size distributions, has never been explicitly quantified using innovative remote sensing tools, such as airborne LiDAR.

Airborne LiDAR is an active remote sensing technology that emits laser pulses and records the time of return from vegetation surfaces to reconstruct three-dimensional canopy structure at high spatial resolution [32]. By generating dense point clouds from which canopy height models (CHMs) are derived, LiDAR enables the delineation of canopy gaps through successive height thresholds applied to the CHM, allowing calculation of gap number, gap area, and gap fraction across multiple canopy strata [2,32,33]. At the global scale, the NASA Global Ecosystem Dynamics Investigation (GEDI) spaceborne full-waveform LiDAR mission, operational since 2019, has demonstrated the value of LiDAR-derived vertical canopy profiles for characterizing forest structure, aboveground biomass, and canopy height on a near-global extent [34,35]. Fusion of GEDI waveform data with Sentinel-2 imagery has further enabled global canopy height mapping at 10 m resolution [36,37], confirming that highly complex and tall canopies are concentrated in the tropics. In Amazonia, vertical LiDAR canopy profiles are notably used to assess gap-related metrics essential for capturing functional and structural differences among forest types [10,11,38]. However, the application of airborne LiDAR to quantify vertical canopy gap structure specifically across contrasting old-growth forest types in Central Africa remains virtually absent from the literature. Existing airborne LiDAR surveys in the region have focused primarily on biomass and canopy height estimation at landscape and regional scales [37,39], without addressing the vertical distribution of gap size across forest types. This represents a major research gap in our understanding of these ecologically unique and carbon-dense forest systems.

To our knowledge, no study has yet quantified the vertical distribution of canopy gap size across contrasting old-growth forest types in Central Africa using airborne LiDAR. This

study addresses this gap by combining high-resolution LiDAR data with field-based forest inventories across two sites in the Democratic Republic of the Congo (DRC) (Lileko and Yangambi) to test whether vertical gap profiles can discriminate between monodominant *G. dewevrei* (GIL) and mixed (MIXED) old-growth forests. Beyond gap detection, we introduce two integrative structural indicators, the gap area-to-basal area ratio (GAP/BA) and its fully remote-sensing-based equivalent, the gap area-to-canopy height ratio (GAP/TCH), which normalize canopy openness by stand development level, providing transferable metrics for large-scale structural monitoring across Central African forest landscapes. Specifically, we tested three hypotheses: (1) The vertical size-frequency distribution of canopy gaps differs significantly between forest types, with MIXED forests dominated by larger gaps and GIL forests by smaller ones, reflecting contrasting stand architecture and disturbance regimes. (2) Structural differences between forest types are maintained across the entire vertical canopy profile, with canopy openness consistently lower in GIL forests than in MIXED forests at multiple canopy strata, demonstrating the added value of LiDAR-derived metrics that capture vertical structure. (3) For a given basal area and canopy height, canopy gaps are smaller in GIL forests than in mixed forests, reflecting denser canopy packing and distinct structural organization. If consistent across sites, such structure-normalized gap metrics may provide transferable indicators for large-scale mapping of monodominant forest structure and developmental trajectories in Central Africa.

2. Materials and Methods

2.1. Study Area

This study is based on existing forest inventory and airborne LiDAR data from the Yangambi study site, supplemented by new data collected at the Lileko study site. Figure 1 shows the location of the two study sites within the Yangambi biosphere reserve (YBR) landscape, DRC. The Lileko site is located approximately 35 km (as the crow flies) northwest of the YBR administrative boundary within the same continuous forest block, whereas the Yangambi site lies within the YBR core zone. Panel (A) in Figure 1 presents the Lileko study site, where an airborne LiDAR survey conducted in 2023 covered approximately 240 ha and where a total of 242 1-ha grid cells were photo-interpreted as GIL or MIXED old-growth forest. Panel (B) in Figure 1 presents the Yangambi study site, where an airborne LiDAR transect acquired in 2014 covered approximately 2000 ha and where a total of 422 1-ha grid cells were photo-interpreted for the vertical canopy gap profile analysis. At the Lileko site, all eight field inventory plots are located within the photo-interpreted grid. At the Yangambi site, two field inventory plots are located within the photo-interpreted grid, while three additional plots located outside the grid were used for floristic characterization and calibration of the relationship between LiDAR-derived top-of-canopy height (TCH) metrics and field-based basal area data (Figure 1).

The YBR, which is part of UNESCO's Man and the Biosphere (MAB) program, is 100 km west of Kisangani town, in the Tshopo province, Democratic Republic of the Congo (DRC) (Figure 1). The region's climate is warm and humid, with an average annual precipitation of about 1800 mm and a mean annual temperature of 25.1 °C [40,41]. The vegetation of the Yangambi landscape is mainly composed of two types of old-growth forests: (i) moist semi-deciduous rainforest with high variability in floristic composition, in which *Scorodophloeus zenkeri* Harms is widely distributed across the landscape and often shows strong local dominance; (ii) evergreen monodominant rainforest dominated either by *Gilbertiodendron dewevrei* (De Wild) J. Léonard or by *Brachystegia laurentii* (De Wild) Louis ex Hoyle [42].

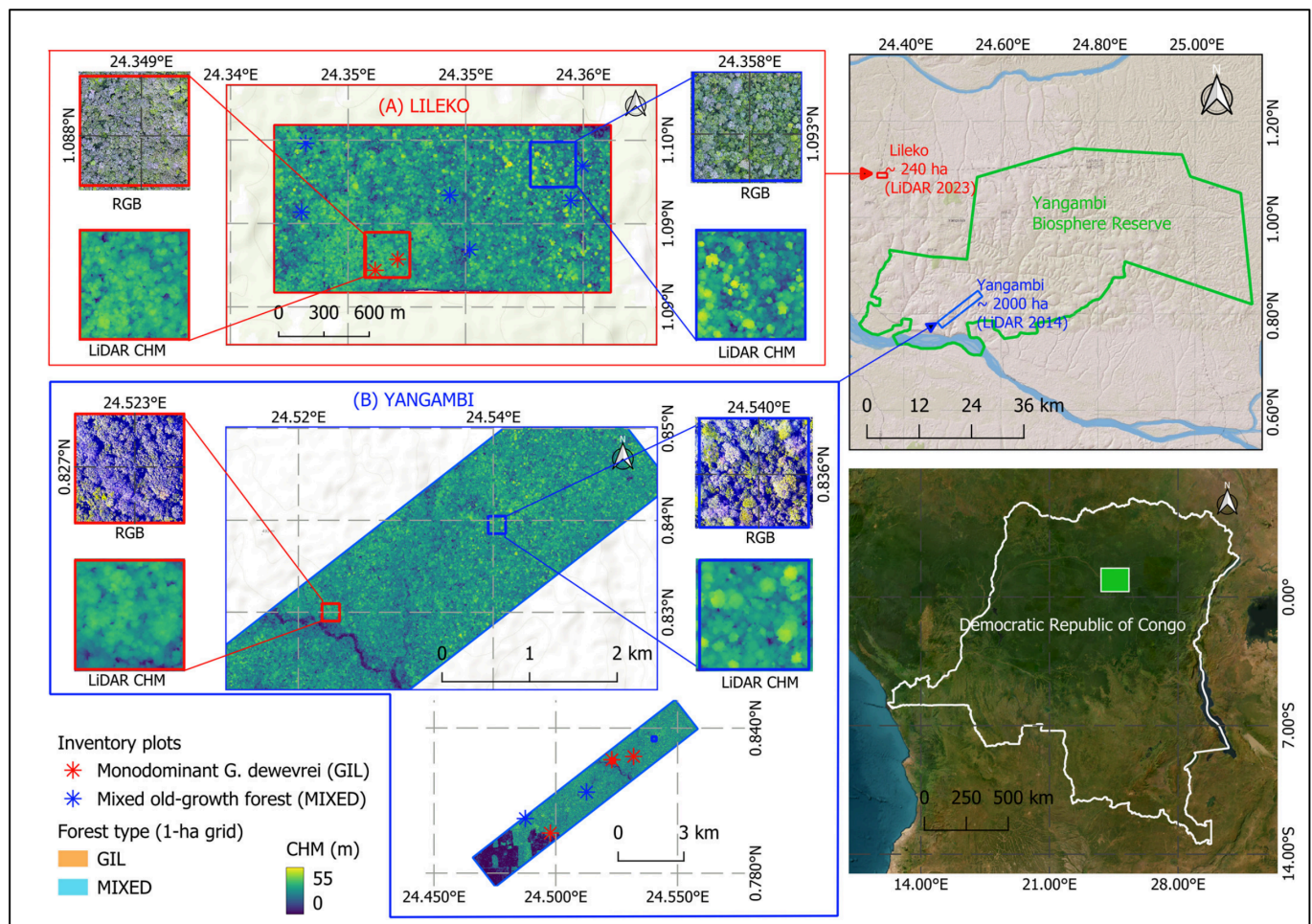


Figure 1. Study sites within the Yangambi forest landscape, Democratic Republic of the Congo. The central map (Top, right) shows the spatial context of both study sites within and adjacent to the Yangambi Biosphere Reserve (green boundary). The Lileko site (red rectangle) is located approximately 35 km (as the crow flies) northwest of the YBR administrative boundary within the same continuous forest block, while the Yangambi site (blue rectangle) lies within the YBR core zone. The inset shows the location of the study area within the Democratic Republic of the Congo. Panel (A) shows the Lileko study site, where an airborne LiDAR survey was conducted in 2023 covering approximately 240 ha. Panel (B) shows the Yangambi study site, where an airborne LiDAR transect was acquired in 2014 covering approximately 2000 ha. The five GIL and eight MIXED field inventory plots are indicated by asterisks. RGB and LiDAR-derived canopy height model (CHM) insets illustrate the contrasting canopy structure between GIL and MIXED forest types at the two sites.

2.2. Forest Inventories

We established 8 1-ha (100 m × 100 m) forest inventory plots at the Lileko study site in 2023 for the present study: 2 plots in the GIL forests and 6 in the MIXED forests (Table 1, Figure 1). To ensure geolocation accuracy and reduce bias when associating ground and remote sensing data [43], we collected GPS coordinates every 25 m using a Garmin GPSMAP 65s and aggregated the 25 geolocations per plot by computing their centroid to reconstruct the spatial geometry of each sampling unit. In each plot, all living tree stems with a diameter at breast height (DBH at 1.30 m height) superior or equal to 10 cm were inventoried. For each tree, we recorded its taxonomic identification with the assistance of botanists from the Institut National d'Etude et Recherche Agronomiques of Yangambi (INERA Yangambi) and measured the diameter at breast height (DBH). Tree heights were

estimated using DBH measurements and a three-parameter exponential height-diameter allometric model calibrated specifically for the central Congo Basin by Kearsley et al. [25]:

$$H = (a - b) \times e^{-cD} \quad (1)$$

where H is tree height (m), D is DBH (cm), a is the maximum asymptotic height, b is the difference between minimum and maximum height, and c is the shape parameter. Forest type-specific parameters were applied: for monodominant *G. dewevrei* forests, $a = 35.04$, $b = 30.43$, $c = 0.0246$ (RSE = 4.05, $n = 452$); for mixed forests, $a = 36.36$, $b = 31.66$, $c = 0.0221$ (RSE = 4.22, $n = 487$). Only living trees were included in basal area calculations; standing dead trees were not recorded during field inventories and were therefore excluded from all structural metrics.

Table 1. Main data and structural characteristics of the 1-ha field plots (TCH: top-of-canopy height, P95: percentile 95, X_coord and Y_coord: X and Y geographic coordinates in decimal degrees (WGS84; EPSG:4326) of 1-ha rectangle plot centroid).

Forest Type	Site	Number of Stems	Basal Area (m ² /ha)	TCH_mean (m)	TCH_P95 (m)	X_coord (Esthern)	Y_coord (North)
GIL	Lileko	342	39.48	34.15	40.32	24.349	1.088
GIL	Lileko	279	34.06	37.34	43.95	24.348	1.087
GIL	Yangambi	342	31.8	32.83	39.03	24.523	0.827
GIL	Yangambi	435	32.14	29.02	34.87	24.532	0.828
GIL	Yangambi	376	30.58	32.00	38.53	24.498	0.797
MIXED	Lileko	433	28.37	28.11	42.40	24.343	1.091
MIXED	Lileko	431	34.37	27.49	39.85	24.353	1.088
MIXED	Lileko	400	37.42	30.98	40.83	24.343	1.095
MIXED	Lileko	437	34.62	28.72	37.69	24.352	1.092
MIXED	Lileko	518	39.87	30.55	44.59	24.360	1.093
MIXED	Lileko	412	38.75	31.38	42.04	24.359	1.091
MIXED	Yangambi	559	34.78	29.15	38.03	24.513	0.814
MIXED	Yangambi	331	26.95	29.47	39.64	24.488	0.803

The inventory data were supplemented by existing data from 5 1-ha (100 m × 100 m) forest inventory plots in Yangambi (3 in the GIL forest and 2 in the MIX forest) that are part of the Congo Basin Integrated Monitoring for Forest carbon mitigation and biodiversity (COBIMFO) project [44]. The locations of these plots fall within the footprint of an airborne LiDAR transect performed in 2014 (Figure 1B) over the Yangambi biosphere reserve [39]. Potential errors in entering scientific names were corrected by the TNRS package version 0.3.6 of the R software [45].

2.3. Remote Sensing Data Acquisition and Processing

LiDAR Data Acquisition and Processing

We acquired new LiDAR data over the Lileko study site in 2023 using a DJI Matrice 300 RTK UAV equipped with a Zenmuse L1 sensor. The flights used a terrain-follow mode with a lateral overlap exceeding 50% and triple-echo recording, resulting in an average point density of approximately 500 pts/m². Raw point clouds were extracted via DJI Terra using GNSS data from a DJI D-RTK2 mobile station. The base station position was corrected using the Precise Point Positioning (PPP) method to ensure a positioning error below 1 cm horizontally and 10 cm vertically. This step was essential to guarantee spatial consistency between the different flights performed over the study area. At the Yangambi site, airborne LiDAR data were acquired in 2014 over 2000 ha using an Optech ALTM 3100 sensor with an average density of 5 pts/m². Similar to the Lileko campaign, the reference

station position was corrected via PPP, and full acquisition details can be found in [39]. The two study sites differ in the timing of both their LiDAR acquisitions (2023 at Lileko and 2014 at Yangambi) and their field inventories (2023 at Lileko and 2012 at Yangambi). At Yangambi, the two-year interval between field inventories (2012) and LiDAR acquisition (2014) is considered acceptable given the slow structural dynamics of undisturbed old-growth tropical forests, where stand-level attributes such as basal area and stem density change at decadal rather than annual timescales [46,47]. The nine-year difference between the LiDAR acquisitions is due to the absence of a more recent airborne dataset providing complete coverage of the Yangambi GIL–MIXED forest mosaic, including the small and spatially fragmented *G. dewevrei* stands required for robust landscape-scale comparisons.

To evaluate the comparability of the two LiDAR datasets, canopy height metrics were compared within their spatial overlap in the Yangambi landscape (353 one-hectare grid cells after excluding edge cells). The 2023 UAV–LiDAR survey, previously used by Wan et al. [37] to validate satellite-derived canopy height estimates across African tropical forests, showed good agreement with the 2014 airborne LiDAR acquisition (TCH p95: $R^2 = 0.644$). The mean difference was -1.0 m (2023–2014), corresponding to approximately 3% of the mean canopy height (~ 30 m), with 95% limits of agreement of -5.16 to $+3.16$ m (Appendix A Figure A1A,B). Although these limits correspond to approximately $\pm 17\%$ of mean canopy height, they are consistent with the combined effects of measurement uncertainty and genuine structural change accumulated over the nine-year interval and remain within the range expected for undisturbed old-growth tropical forests [46,47].

Because subsequent analyses rely on relative structural differences between GIL and MIXED forests rather than on absolute canopy-height agreement, we further assessed whether temporal discrepancies differed between forest types. A stratified Bland–Altman analysis showed comparable mean differences for GIL ($n = 30$; -0.8 m) and MIXED forests ($n = 323$; -1.0 m), with no significant difference between forest types (two-sample t -test: $t = 0.358$, $df = 21$, $p = 0.724$; Appendix A Figure A1C). This indicates that temporal uncertainty affects both forest types similarly and is therefore unlikely to introduce systematic bias into GIL–MIXED structural comparisons. If anything, such non-differential variability would tend to reduce, rather than exaggerate, the observed contrasts. Overall, these analyses support the use of the two LiDAR datasets for inter-site comparisons. The main acquisition characteristics are summarized in Table 2.

Table 2. Main characteristics of LiDAR data acquisitions at the Lileko and Yangambi study sites.

Parameter	Lileko	Yangambi
Acquisition year	2023	2014
Platform	DJI Matrice 300 RTK	Fixed-wing aircraft
Sensor	Zenmuse L1	Optech ALTM 3100
Average point density (pts m ²)	500	5
Echo recording	Triple return	Triple return
Horizontal positioning error	<1 cm (PPP)	PP-corrected
Vertical positioning error	<10 cm (PPP)	PP-corrected
Area covered (ha)	240 ha	2000
CHM resolution	1	1
Reference	This study	[39]

Raw point clouds from both sites followed a common processing workflow implemented in the R environment using the lidR package [32]. Ground points were classified using the Cloth Simulation Filter algorithm (resolution 1 m, rigidness 2, threshold 1.2 m) with slope smoothing enabled. Following classification, point heights were normalized using a Triangulated Irregular Network (TIN) interpolation of ground points, with nearest-

neighbor inverse distance weighting applied for edge extrapolation. Finally, a Canopy Height Model (CHM) was generated at a 1-m resolution using the pit-free algorithm to eliminate data pits while preserving natural canopy gaps. This method employed triangulation across a series of height thresholds (0 to 60 m) to ensure a robust representation of the upper canopy surface.

2.4. Forest Type Spatial Delineation

A 1-ha (100×100 m) grid was overlaid on each study site to match the sampling unit of the field inventories and provide sufficient spatial support for canopy gap analyses. Each grid cell was manually assigned to a forest type based on visual interpretation of the high-resolution RGB imagery acquired simultaneously with the LiDAR survey. A cell was classified as GIL when the characteristic dark-green, dense canopy of *G. dewevrei*, with relatively indistinct individual crowns (Figures 1 and 2), covered more than 50% of the cell area; cells with more than 50% mixed-species canopy were classified as MIXED. Cells dominated by palm trees, affected by edge effects or incomplete data, or lacking a clear majority (>50%) of either forest type were excluded from the analysis, thereby minimizing misclassification at forest-type boundaries.



Figure 2. Aerial overview of canopy structure in Central African old-growth forests, illustrating differences in canopy organization and image spectral patterns between monodominant *G. dewevrei* (GIL) and mixed (MIXED) forest types.

Manual photointerpretation was preferred over automated classification for two reasons. First, the spectral separability of GIL and MIXED forests in optical imagery is inherently limited, as recently demonstrated for Sentinel-2 classifications in the Congo Basin [23,48], and the available field dataset (13 inventory plots: 5 GIL and 8 MIXED) was insufficient to develop and independently validate a robust supervised classification model. The interpretation criteria were therefore based on canopy color, texture, and spatial pattern, informed by repeated field surveys at both sites during which the canopy architecture of monodominant *G. dewevrei* stands was directly observed and systematically compared with the corresponding RGB imagery. As a complementary consistency check, the resulting classification was compared with the known forest type of the 10 inventory plots located within the photo-interpreted area. All 10 plots were correctly assigned (100% agreement; exact Clopper–Pearson 95% CI: 69.2–100%), although this result is reported as descriptive support rather than as a formal accuracy assessment because of the limited sample size. At Lileko, 187 of the 242 grid cells were classified as MIXED forest and 46 as GIL forest, while 9 cells were excluded. At Yangambi, 392 of the 422 grid cells were classified as MIXED forest and 30 as GIL forest.

2.5. Gap Detection, Extraction and Definition

To capture the vertical structure of the forest, we calculated gap size at 12 canopy height levels: at 5 m and every meter from 10 to 20 m. This vertically explicit approach follows evidence that canopy gap size distributions vary systematically with height [10]. Gap measurements above 20 m height were excluded from the analysis because this threshold corresponds to the mean canopy height of dominant trees in both GIL and MIXED forests as estimated from the locally calibrated height-diameter allometric model of Kearsley et al. [25], above which gap formation events become structurally less frequent and ecologically less relevant for regeneration dynamics [10].

Canopy gaps were defined as contiguous areas where CHM values fell below the height threshold, with a minimum gap area of 20 m². This threshold does not correspond to a specific tree diameter class or crown area of the fallen tree, because treefall gaps typically exceed the projected crown area of the fallen tree owing to collateral damage, crown breakage, and, occasionally, multiple tree falls [49]. The 20 m² threshold used in this study is therefore best understood as a conservative detection floor rather than a precise ecological size class tied to a specific DBH value.

This threshold was set primarily by analogy with established operational precedents in the treefall gap detection literature. Brokaw's original transect-based method for treefall gap turnover at Barro Colorado Island (BCI) proposed a minimum detectable gap size of 20–40 m², based on the criterion that a gap must be readily distinguishable from surrounding canopy complexity [50]. Independently, field-based inventories at the same site demonstrated that the dominant treefall gap size class in undisturbed old-growth forest ranges between 25 and 75 m² [51], converging on a comparable lower bound for ecologically meaningful gap detection. This value is also consistent with minimum gap area thresholds applied in LiDAR-based gap studies in other tropical forests, where thresholds of 10–20 m² have been used based on analogous considerations [52–54]. The selected threshold is also broadly consistent, as a complementary cross-check, with the projected crown area of a small canopy tree (DBH $\approx$ 10 cm, corresponding to the minimum stem diameter recorded in the field inventories) according to the Central African crown area–diameter allometry of Blanchard et al. [55]. To evaluate the sensitivity of the analyses to the minimum gap area threshold, gap size distributions and GIL–MIXED contrasts were assessed using four threshold values (10, 20, 25, and 50 m²) at three canopy height levels (10, 12, and 20 m). Statistical significance was evaluated using the Benjamini–Hochberg false discovery rate (FDR) correction described in Section 2.9. The results of this sensitivity analysis are presented in Appendix A, Figure A2.

To identify forest gaps, we used a three-step detection workflow implemented in R version 4.5+ software and applied to the CHM, following the workflow described in the ForestGapR R package [33]. First, a height threshold was applied to the CHM to classify pixels below the threshold as potential gap areas, a step repeated 12 times for the 12 height levels considered. Second, contiguous gap pixels were aggregated into distinct patches using 8-neighbor connectivity via the *patches()* function from the terra R package [56], assigning a unique identifier to each spatially connected gap cluster. Gap clusters were then vectorized into polygons using the *as.polygons()* function from the terra R package [56] with *dissolve = TRUE*, and the total area of each gap polygon was recalculated from the reconstructed geometry using the *st_area()* function from the sf R package [57]. Finally, the area-based filter was applied to retain only gap patches above the 20 m² minimum area threshold, excluding isolated artifacts.

Gap area metrics were computed after correcting for border effects arising from the intersection of gap polygons with the 1-ha grid. Specifically, gap polygons were first reconstructed to their original spatial extent by dissolving intersection fragments

sharing the same identifier using *st_union()* from the *sf* R package [57], and their total area was recalculated from the reconstructed geometry. The minimum gap area threshold (20 m^2) was applied to the total gap area, while the gap area attributed to each grid cell corresponded to the actual intersected area within that cell, which was calculated using the *st_intersection()* function from the *sf* R package [57]. This correction ensures that gaps straddling cell boundaries are neither erroneously excluded due to fragmentation below the threshold nor double-counted in the aggregation. Because cumulative gap area increases with canopy height threshold by construction of the multi-level CHM detection approach, we also summarized the percentage of 1-ha grid cells containing at least one canopy gap at each height threshold (Appendix A Table A1).

2.6. Characterization of Monodominance in the Vertical Profile

We characterized monodominance across canopy height strata using field inventory data by comparing stem density and basal area (BA) of *G. dewevrei* and other species per plot across DBH classes and forest types. For each DBH class group, i.e., 10–30, 30–50, 50–80, and beyond 80, the proportions of stems and BA contributed by the dominant species were also calculated. DBH classes were identified to provide a better understanding of the contribution of *G. dewevrei* to the different layers of the forest. Statistical comparisons between forest types within each DBH class were performed as described in Section 2.9.

To confirm the dominance of *G. dewevrei* in the upper canopy layer, a supplementary analysis using a species accumulation model was applied to individual-based samples [58], ordered by decreasing tree height. Tree diversity in the upper canopy layer was subsequently compared between forest types by examining differences in their rarefaction curves.

2.7. Analysis of the Vertical Profile Distribution of Gap Areas

To characterize how canopy openness varies across forest types and canopy height strata, we compared gap area (equivalent to gap fraction expressed in $\text{m}^2 \text{ ha}^{-1}$) distributions across the 12 height levels and both forest types (Figure 3) at each study site. For each height level, total gap area per 1-ha grid cell was computed as described in Section 2.5, specifically, as the sum of the intersected areas of gap polygons retained above the 20 m^2 minimum threshold within each 1-ha grid cell, after border effect correction. Grid cells with no retained gap polygon were assigned a gap area of zero, reflecting closed-canopy conditions. For each forest type at both study sites, mean gap area per hectare was estimated together with its 95% confidence interval based on the standard error. Statistical differences in total gap area ($\text{m}^2 \text{ ha}^{-1}$) between GIL and MIXED forests were assessed at each height level (Figure 3) using the adaptive test procedure described in Section 2.9.

2.8. Calculation of Forest Gap Area/Basal Area Ratio

To evaluate the influence of large trees on canopy gap size distribution, we introduced the forest canopy gap area-to-basal area ratio (GAP/BA) and a fully remote-sensing-based equivalent, the forest canopy gap area-to-top-of-canopy height ratio (GAP/TCH). These ratios enable the comparison of gap structure across forests while accounting for equivalent levels of structural development, as canopy gap size distribution is expected to vary with stand development and biomass accumulation. Given the overall similarity in basal area between GIL and MIXED forests in the region [25], the GAP/BA ratio provides a consistent basis for comparing canopy gap characteristics under equivalent basal area conditions.

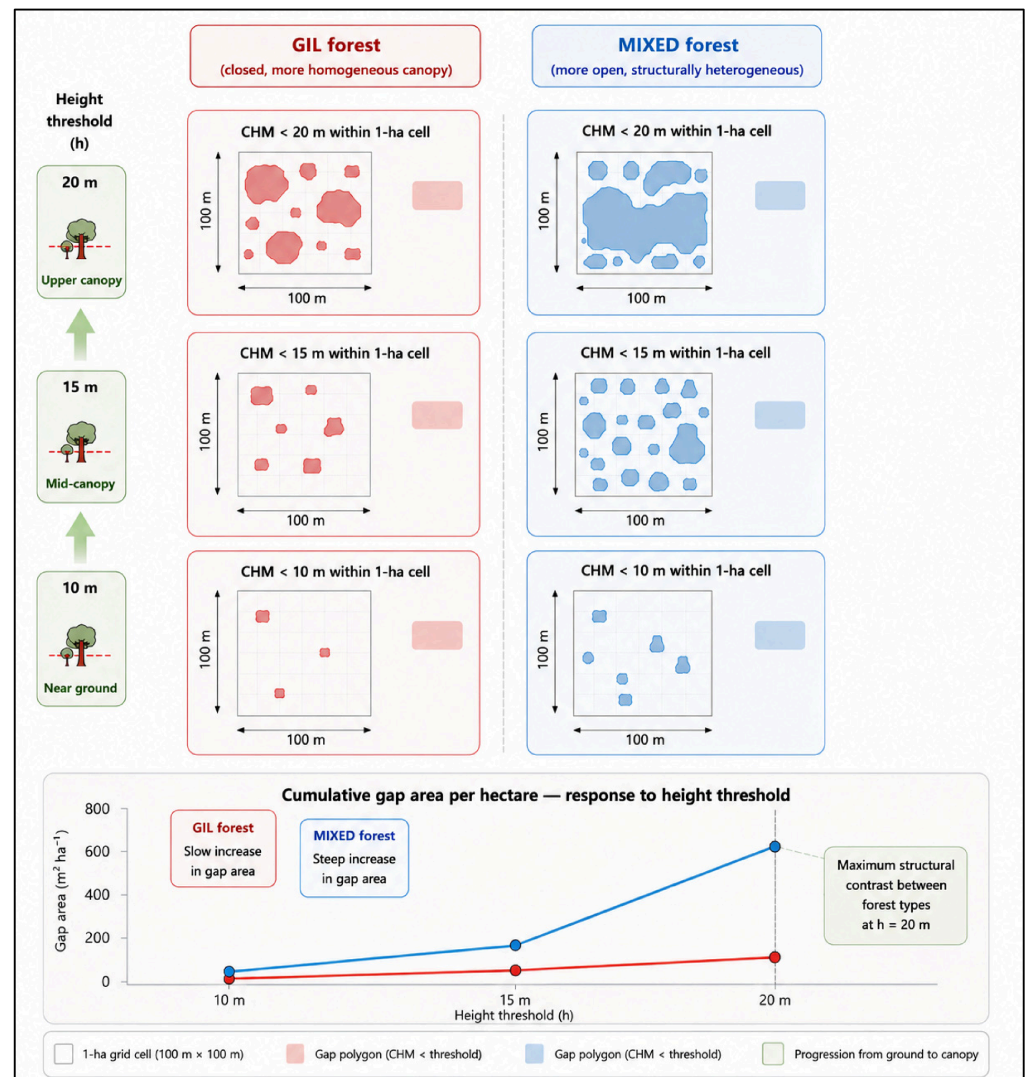


Figure 3. A conceptual diagram illustrates the multi-level CHM height threshold approach. The arrow indicates the fixed dimensions (length and width) of the aggregation grid cell used to calculate gap area, while the red dashed line represents the canopy height threshold used for gap detection. For each threshold (e.g., 10, 15, and 20 m), gap polygons (colored polygons) represent areas where CHM values fall below the threshold within a 1-ha grid cell of 100 m × 100 m. In GIL forests (red), gap polygon size and total gap area per hectare increase modestly across thresholds. In MIXED forests (blue), gap polygon size and cumulative gap area increase steeply, with polygons coalescing at higher thresholds. The summary chart (bottom) illustrates this divergence: GIL gap area increases slowly with canopy threshold, whereas MIXED gap area increases rapidly, yielding the largest structural contrast at $h = 20 \text{ m}$.

For each 1-ha grid cell, gap area (GAP) corresponds to the total gap area ($\text{m}^2 \text{ha}^{-1}$) computed as described in Section 2.5. Stand basal area (BA) was computed as the sum of the cross-sectional areas at breast height of all inventory trees within each plot.

The GAP/BA and GAP/TCH ratios were calculated by dividing GAP by BA and top-of-canopy height (TCH), respectively. Several TCH metrics were derived from the CHM, including mean, median, and percentile canopy height values. The relationship between GAP/BA and each candidate GAP/TCH metric was evaluated using the 13 field inventory plots, each contributing one observation per canopy height threshold, yielding 117 observations in total (13 plots × 12 height levels, after exclusion of observations with zero or undefined CHM values) as the unit of analysis for this regression. The TCH metric showing the strongest Pearson correlation with the field-based GAP/BA ratio across these 117 ob-

servations was subsequently retained to derive the remotely sensed GAP/TCH structural indicator used to map differences among old-growth forest types (Appendix A Table A2). To assess whether this in-sample performance reflected overfitting given the limited number of field plots, we additionally performed a leave-one-plot-out cross-validation (LOOCV): in each fold, all 12 height-level observations from one plot were withheld, and the regression was refitted on the remaining 12 plots, generating out-of-sample predictions for the held-out plot. Cross-validated performance metrics (R^2 , RMSE, Pearson r) closely matched the in-sample estimates, confirming that the relationship between GAP/BA and the retained GAP/TCH metric generalizes across plots (Appendix A Table A2). We also compared GAP/BA and GAP/TCH ratio distributions across the 12 height levels and both forest types at each study site. Statistical comparisons of GAP/BA and GAP/TCH between forest types were performed as described in Section 2.9.

2.9. Statistical Analysis

Statistical comparisons between GIL and MIXED forests were performed using an adaptive test procedure applied consistently across all analyses described in Sections 2.6–2.8. For each pairwise comparison, normality was first assessed using the Shapiro–Wilk test. When both groups met the normality assumption, a Student’s t -test was applied if variances were equal (Levene’s test, $p > 0.05$), or Welch’s t -test otherwise. When normality was not met in at least one group, a Wilcoxon rank-sum test was used. For the analyses of vertical gap area and the GAP/BA or GAP/TCH ratios (Sections 2.7 and 2.8), this procedure was applied independently at each of the 12 canopy height levels and at each study site separately, yielding site-specific significance profiles across the vertical canopy profile. For the stem density and basal area comparisons by DBH class (Section 2.6), the procedure was applied independently within each DBH class.

Because each statistical analysis involved multiple simultaneous hypothesis tests, p -values were adjusted using the Benjamini–Hochberg false discovery rate (FDR) procedure within 7 sets of comparisons, as these addressed distinct hypotheses and response variables: (1) GIL vs. MIXED gap area comparisons by site across 24 combinations (2 sites $\times$ 12 height levels); (2) Lileko vs. Yangambi gap area comparisons by forest type across 24 combinations (2 forest types $\times$ 12 height levels); (3) GIL vs. MIXED GAP/TCH comparisons by site across 24 combinations (2 sites $\times$ 12 height levels); (4) GIL vs. MIXED GAP/TCH comparisons by forest type across 24 combinations (2 forest types $\times$ 12 height levels); (5) GIL vs. MIXED stem density comparisons across 4 DBH classes; (6) GIL vs. MIXED basal area comparisons across 4 DBH classes; and (7) the threshold sensitivity analysis, comprising 96 GIL vs. MIXED comparisons across two sites, twelve height levels, and four gap area thresholds (Appendix A). Corresponding figures display FDR-adjusted significance levels (ns, *, **, ***, **** corresponding to adjusted p -values ≥ 0.05 , <0.05 , <0.01 , <0.001 , and <0.0001 , respectively), unless otherwise stated. All statistical analyses were performed in R version 4.5 or later, and results are presented as mean $\pm$ standard error (SE) with 95% confidence intervals. All R scripts, field inventory data, LiDAR-derived gap and canopy height metrics used to produce the analyses and figures are available in Supplementary Materials (File S1).

3. Results

3.1. Evaluation of Monodominance in the Upper Canopy Layer

At the 1-ha plot scale, stem density was higher in mixed forests (440 ± 70.4 stems ha^{-1}) than in monodominant forests (355 ± 56.6 stems ha^{-1} ; t -test, $p = 0.04$). Basal area was similar between forest types (34.4 ± 4.63 m^2 ha^{-1} in mixed vs. 34.5 ± 4.19 m^2 ha^{-1} in monodominant; t -test, $p = 0.96$). In monodominant stands, *G. dewevrei* accounted for 22.1%

of stems and 62.8% of basal area. In mixed forests, *Cola griseiflora* had the highest stem abundance (12.6%), while *Scorodophloeus zenkeri* contributed the largest basal area (17.4%).

Across DBH classes, *G. dewevrei* tree species dominated all classes in monodominant stands. But in MIXED forests, lower strata were dominated by other species: *Cola griseiflora* in the sub-canopy (10–30 cm) and *Scorodophloeus zenkeri* in the intermediate layer (30–80 cm).

Across all DBH classes, stem density and basal area did not differ significantly between monodominant and mixed forests after Benjamini–Hochberg FDR correction (Figure 4A,B). Stem density in the >80 cm DBH class was numerically higher in monodominant forests (17.8 ± 7.3 stems ha^{-1}) than in mixed forests (10.1 ± 4.0 stems ha^{-1}), but this difference was not significant after Benjamini–Hochberg FDR correction (raw $p = 0.030$; adjusted $p = 0.120$; Figure 4A). However, the composition of this large-tree cohort differed markedly between forest types. In monodominant stands, *G. dewevrei* tree species accounted for approximately 16 of the 17.8 stems ha^{-1} (~90%), whereas in mixed forests it represented only about 1.2 of the 10.1 stems ha^{-1} (~12%), highlighting a strong compositional divergence despite comparable stand-level structural attributes.

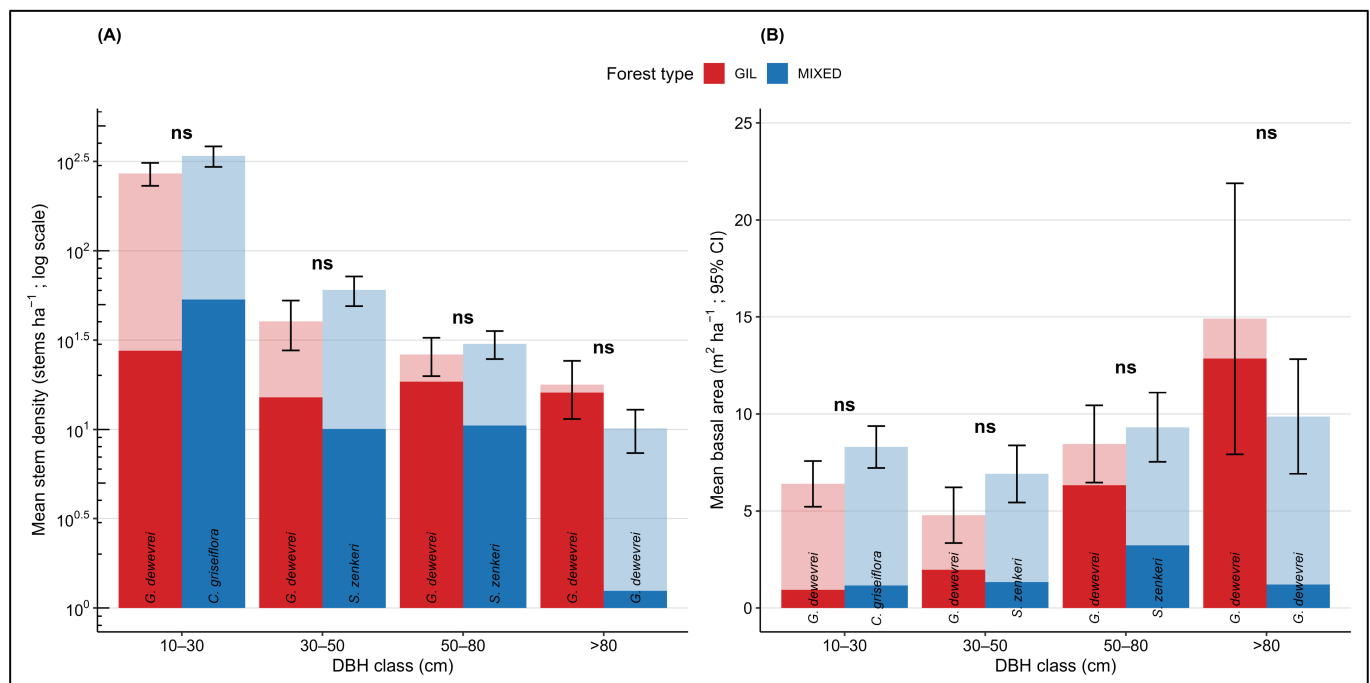


Figure 4. Distribution of stem density (A) and basal area (B) across DBH classes in monodominant *G. dewevrei* (GIL; red bars) and adjacent mixed (MIXED; blue bars) forests. Bars represent mean values within each DBH class, with dark segments indicating the contribution of the locally dominant species by basal area within each forest type and DBH class (italic labels). The dominant species is invariably *G. dewevrei* in GIL forests across all DBH classes, whereas in MIXED forests it varies by DBH class, consistent with the absence of a single structurally dominant species in mixed old-growth stands. Error bars denote 95% confidence intervals. Statistical comparisons between forest types within each DBH class were performed using an adaptive test selected based on normality (Shapiro–Wilk) and equality of variances (Levene): Student’s t -test when both conditions were met, Welch’s t -test when variances were unequal, and Wilcoxon rank-sum test otherwise. The Benjamini–Hochberg false discovery rate (BH-FDR) correction was applied separately within each panel (4 tests per panel). The significance levels shown are FDR-adjusted: ns = not significant.

Basal area increased with DBH in both forest types (Figure 4B). Monodominant forests exhibited slightly lower basal area in the 10–30 cm DBH class than mixed forests (6.40 ± 1.35 vs. 8.30 ± 1.56 $\text{m}^2 \text{ha}^{-1}$), although this difference was not significant after FDR correction (raw $p = 0.046$; adjusted $p = 0.184$). Likewise, upper-

canopy basal area (>80 cm DBH) did not differ significantly between forest types (14.90 ± 7.97 vs. 9.87 ± 4.26 m² ha⁻¹; raw $p = 0.160$; adjusted $p = 0.215$). Nevertheless, the species contributing to this basal area contrasted sharply. In monodominant forests, *G. dewevrei* tree species represented approximately 12.85 m² ha⁻¹ (~86%) of the upper-canopy basal area, compared with only 1.20 m² ha⁻¹ (~12%) in mixed forests. Thus, similar stand-level basal area can arise from fundamentally different species composition and canopy organization.

Individual-based rarefaction curves ordered by decreasing tree height also reveal a strong and consistent divergence between GIL and MIXED forests in upper canopy species diversity (Figure 5). In GIL forest plots, empirical curves systematically fall below the theoretical random expectation from the first sampled individuals onward, indicating that the tallest trees are disproportionately dominated by a single species, *G. dewevrei*, rather than being drawn randomly from the local species pool. At a standardized sample of 50 upper-canopy individuals ($\approx$ DBH > 40 cm), GIL plots accumulate only 5–15 species, compared to 15–35 species in MIXED forests (Figure 5). This contrast persists across the full sampling range, with cumulative species richness reaching 35–65 species at 300 individuals in GIL forests versus 60–80 species at equivalent sample sizes in MIXED forests. In mixed forests, empirical curves closely track or exceed the theoretical expectation from the outset, confirming a more equitable distribution of species across height strata and the absence of upper-canopy monopolization by any single species. The marked gap between empirical and theoretical curves in GIL forests therefore constitutes a direct statistical signature of the non-random vertical stratification driven by *G. dewevrei* dominance, corroborating the LiDAR-derived gap metrics and confirming that structural differences between forest types are most pronounced in the upper canopy layers.

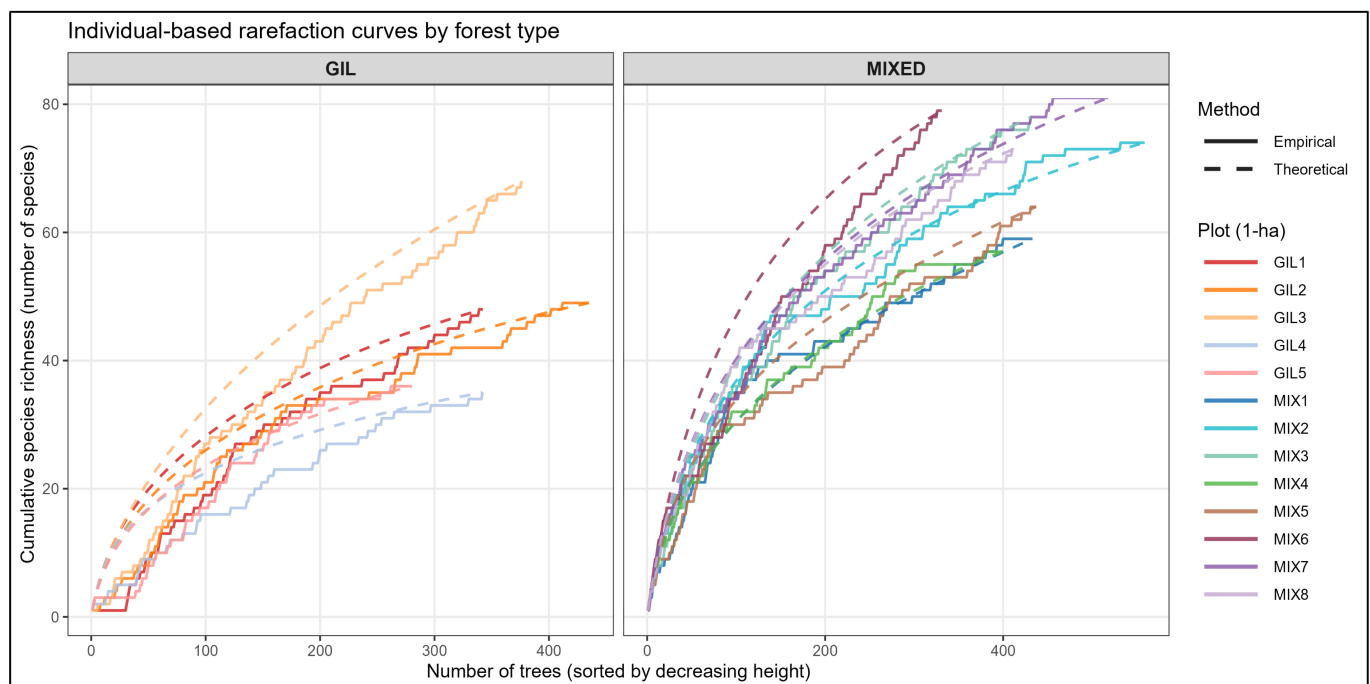


Figure 5. Specific richness accumulation as a function of the number of stems per decrease in height between GIL and MIXED forests. All empirical curves lie below the theoretical curves, suggesting low floristic richness. Among the 50 tallest trees ($\approx$ DBH > 40 cm), only ~13 species are recorded in monodominant plots, compared with ~25 in mixed forests.

3.2. Vertical Distribution of Gap Area Across Forest Types

Gap area per hectare was consistently lower in GIL than in MIXED forests across the vertical canopy profile at Lileko, with the contrast increasing toward the upper canopy (Figure 6C). Differences were significant at every height threshold from 10 to 20 m and remained so after Benjamini–Hochberg FDR correction (adjusted $p < 0.001$ throughout, reaching adjusted $p < 0.0001$ above 13 m). At Yangambi, GIL forests showed the same overall trend of lower gap area than MIXED forests, but none of the comparisons remained significant after FDR correction. Although the raw p -values at 19 m ($p = 0.046$) and 20 m ($p = 0.028$) suggested marginal differences, these became non-significant after adjustment (adjusted $p = 0.085$ and 0.056 , respectively). Consequently, no significant differences in vertical gap profiles were detected between GIL and MIXED forests at Yangambi after accounting for multiple comparisons.

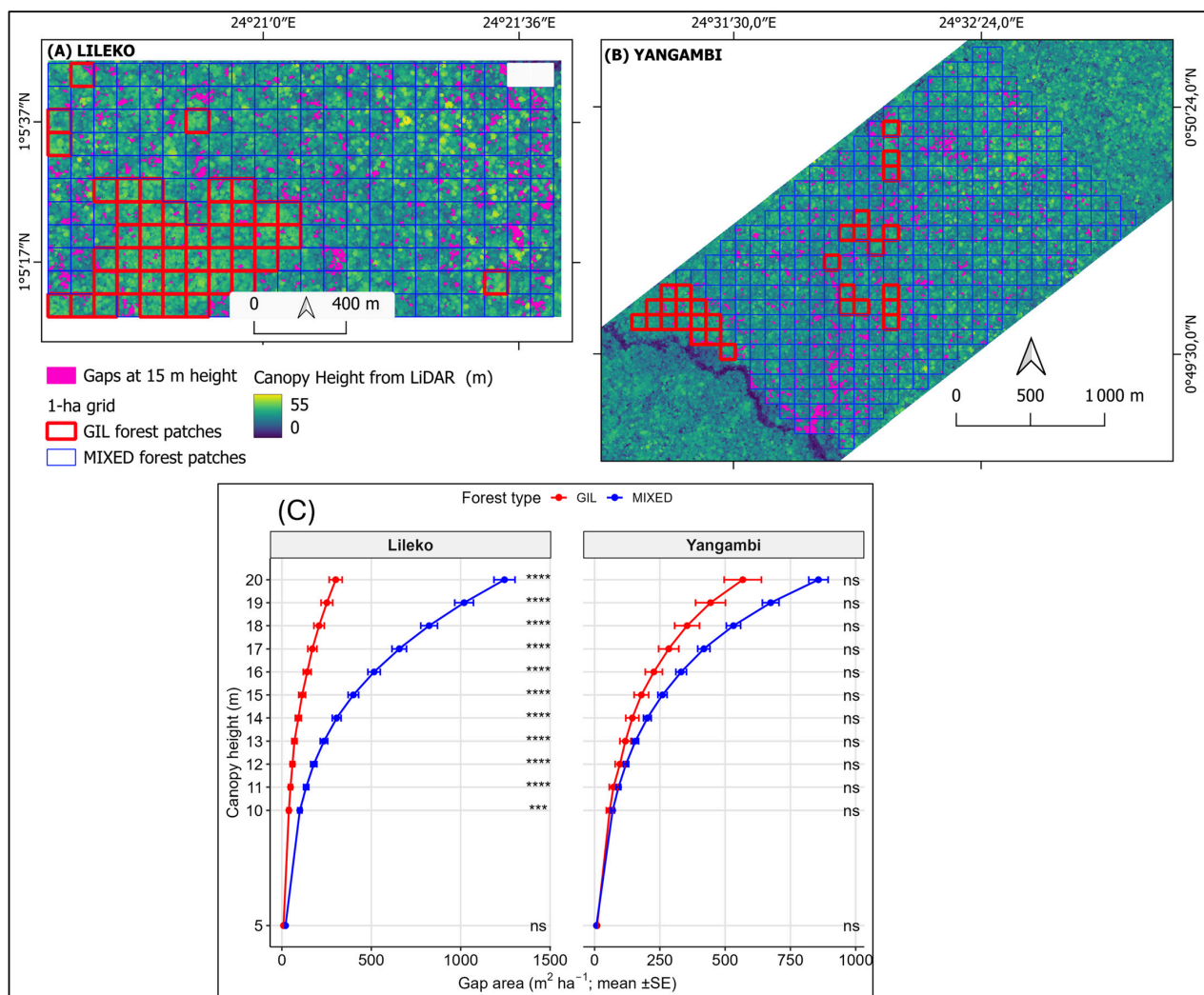


Figure 6. Spatial distribution and vertical profiles of canopy gaps in monodominant *G. dewevrei* (GIL) and adjacent mixed (MIXED) forests at the two study sites. Panels (A,B) show canopy gaps detected at the 15 m height threshold within 1-ha grid cells classified as GIL (red) or MIXED (blue) forests at Lileko and Yangambi, respectively. (C) Mean gap area (m² ha⁻¹) across 12 canopy height thresholds (5 m and every meter from 10 to 20 m) for GIL (red) and MIXED (blue) forests at each site. Error bars indicate ± 1 standard error (SE). Significance levels correspond to Benjamini–Hochberg false discovery rate (FDR)-adjusted p -values (p_{adj}) for the GIL–MIXED comparison at each height threshold: ns = not significant, *** $p_{adj} < 0.001$, **** $p_{adj} < 0.0001$.

In GIL forests, the mean canopy opening area per hectare measured between 10 and 20 m ranged from 39.11 (95% CI: 19.84–58.39) to 300.96 (95% CI: 229.44–372.49) at Lileko, and from 58.00 (95% CI: 32.50–83.50) $\text{m}^2 \text{ha}^{-1}$ to 567.56 (95% CI: 427.63–707.48) $\text{m}^2 \text{ha}^{-1}$ at Yangambi. In MIXED forests, the corresponding values ranged from 100.41 (95% CI: 77.31–123.51) to 1244.97 (95% CI: 1129.48–1360.45) $\text{m}^2 \text{ha}^{-1}$ at Lileko, and from 69.10 (95% CI: 55.28–82.93) to 857.40 (95% CI: 784.73–930.07) $\text{m}^2 \text{ha}^{-1}$ at Yangambi.

3.3. Vertical Distribution of Ratio Between Gap Area and Stand Structural Attributes

The GAP/BA is significantly correlated to several remotely derived metrics (Pearson $r > 0.90$). The median canopy height (TCH_median) exhibited the highest Pearson correlation with the field-based GAP/BA ratio (Figure 7, $R^2 = 0.99$, Pearson $r = 1.00$) and was therefore retained as the primary TCH metric for the GAP/TCH ratio calculation (Appendix A Table A2). The GAP/TCH ratio is consequently a good substitute for the GAP/BA ratio and can be calculated on the entire surveyed LiDAR extent without the need for field inventories.

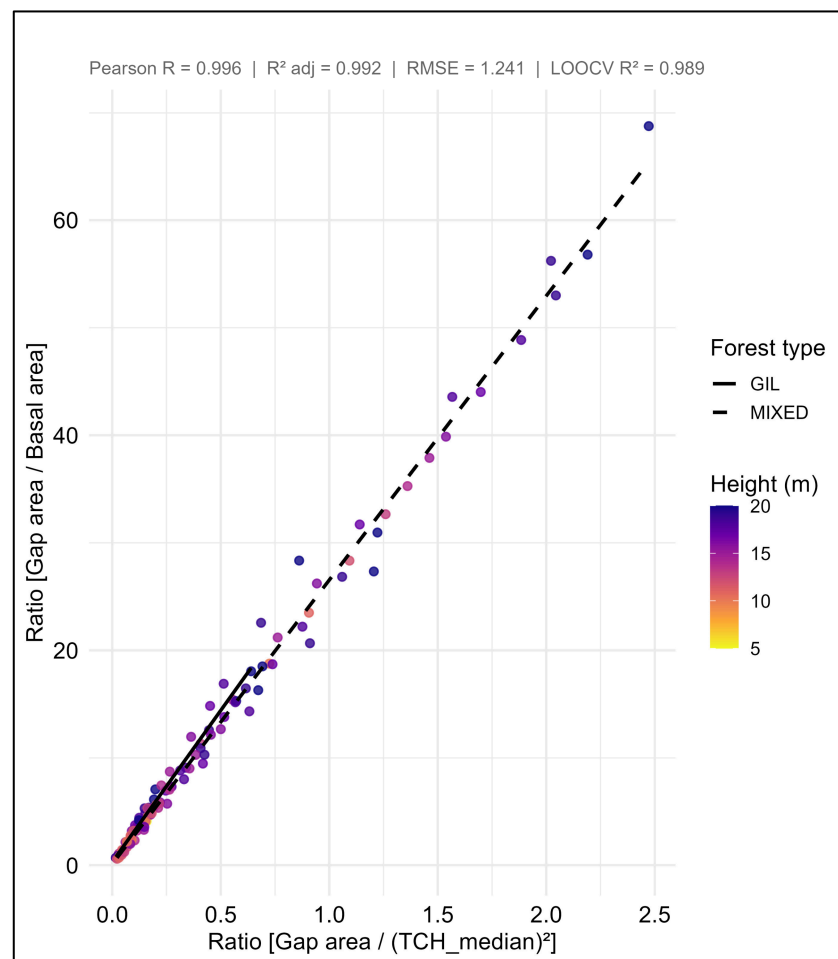


Figure 7. Relationship between the field-based gap area-to-basal area ratio (GAP/BA) and the LiDAR-derived gap area-to-squared median top-of-canopy height ratio [GAP/(TCH_{median})²]. Gap area ($\text{m}^2 \text{ha}^{-1}$) was quantified across 12 canopy height levels (5 m and every meter from 10 to 20 m), yielding $n = 117$ observations (13 field plots $\times$ 12 height levels). Points are colored by canopy height level (5–20 m); regression lines are shown separately for monodominant *G. dewevrei* (GIL; solid line) and mixed (MIXED; dashed line) forests. In-sample evaluation and leave-one-plot-out cross-validation (LOOCV) were applied.

Upscaling the GAP/TCH ratio across the entire surveyed area reveals more consistent contrast patterns between the two forest types throughout the vertical canopy profile at both study sites. Similar to absolute gap area, the GAP/TCH ratio per hectare was consistently lower in GIL forests than in mixed forests across all height levels, with differences becoming more pronounced at greater canopy heights (Figure 8C,D).

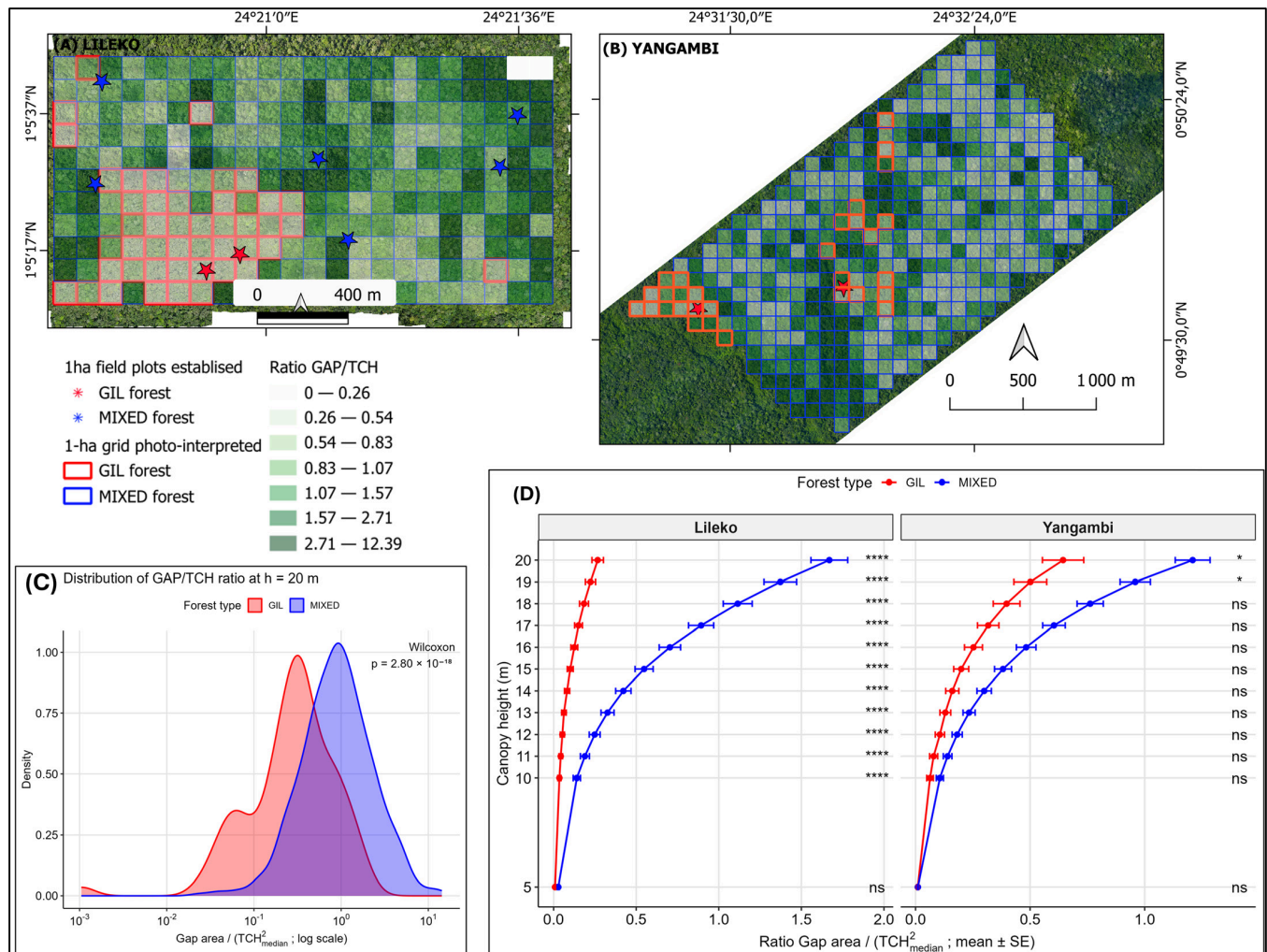


Figure 8. Spatial distribution and vertical profiles of the GAP/TCH structural ratio at the Lileko (A) and Yangambi (B) study sites. GAP represents gap area ($m^2 ha^{-1}$) derived from gaps detected at a canopy height of 20 m, and TCH corresponds to the squared top-of-canopy height per hectare. Panels (A,B) show the continuous spatial distribution of the GAP/TCH ratio at a canopy height of 20 m across each site, independent of forest-type classification. (C) Distribution of GAP/TCH values in monodominant *G. dewevrei* (GIL; red area) and adjacent mixed (MIXED; blue area) forests across both sites at a canopy height of 20 m. (D) Vertical profile of the GAP/TCH ratio, with GAP quantified across 12 canopy height levels (5 m and every meter from 10 to 20 m), in GIL (red lines) and MIXED (blue lines) forests at both study sites. Horizontal error bars represent standard errors (SE). Significance levels correspond to Benjamini–Hochberg false discovery rate (FDR)-adjusted p -values (p_{adj}) for the GIL–MIXED comparison at each height threshold: ns = not significant, * $p_{adj} < 0.05$, *** $p_{adj} < 0.0001$.

At Lileko, the GAP/TCH ratio was consistently and significantly lower in GIL than in MIXED forests across the full 10–20 m canopy range, with all differences remaining highly significant after B-H FDR adjustment ($p_{adj} < 0.0001$ at all heights). At Yangambi, the same trend was observed but was vertically constrained: significant differences after correction were restricted to the upper canopy (19–20 m; $p_{adj} = 0.033$ and 0.020), while intermediate

strata lost significance after B-H FDR adjustment, and no differences were detected below 18 m. Overall, the GAP/TCH ratio strongly enhances the separation between forest types. It is systematically lower in GIL forests (0.04–0.64) than in MIXED forests (0.11–1.67), highlighting clear structural contrasts across sites and canopy heights. Spatially, this divergence is particularly evident at a canopy height of 20 m (Figure 8C,D), especially at Lileko (Figure 8A), where forest-type domains are distinctly separated, consistent with the statistical results.

4. Discussion

4.1. *G. dewevrei* Largely Structures and Dominates the Upper Canopy Layer

Our results confirm that structural differences between GIL and MIXED forests are substantial but site-dependent, as noted in previous Central African studies [25]. At Yangambi, basal area did not differ significantly between GIL and MIXED forests (34.5 ± 4.19 vs. 34.4 ± 4.63 m² ha⁻¹; *t*-test, $p = 0.96$), consistent with [28,29]. Stem density, however, was higher in mixed forests (440 ± 70.4 stems ha⁻¹) than in GIL forests (355 ± 56.6 stems ha⁻¹; *t*-test, $p = 0.04$), reflecting a moderate reduction in tree abundance in GIL stands, similar to patterns observed in the Sangha Trinational region [22], but contrasting with other Central African regions where stem density differences are negligible [25,28].

Across all DBH classes, stem density and basal area did not differ significantly between monodominant and mixed forests after Benjamini–Hochberg FDR correction (Figure 4A,B). But, in terms of stem density by tree species, in monodominant forests, *G. dewevrei* dominates the upper canopy, accounting for ~86% of upper-canopy basal area and nearly 90% of large trees (DBH > 80 cm), corroborating the importance of *G. dewevrei* for forest biomass [24] and reduced species richness, with only ~13 species among the 50 tallest trees (DBH > 40 cm) compared to ~25 in mixed forests (Figure 5). This indicates a non-random vertical distribution and strong vertical stratification driven by a single dominant species. These patterns confirm previous observations in Central African forests, where monodominant species are scarce in lower layers but dominate the upper canopy [27,59].

Overall, these findings emphasize that GIL forests at Yangambi are structurally characterized by a higher degree of disproportionate dominance of *G. dewevrei* in the upper canopy, while plot-level basal area remains similar to adjacent mixed forests. Vertical stratification analyses and canopy-focused indicators are therefore essential for detecting the specific structural signature of monodominant tropical forests and for understanding how single-species dominance shapes biomass and forest composition across different Central African regions.

4.2. Vertical Canopy Gap Structure Contrasts Within Tropical Old-Growth Forests

To our knowledge, this study is the first to use airborne LiDAR to explicitly quantify vertical variation in canopy gap size distributions between contrasting old-growth forest types in Central Africa, despite the ecological and biogeochemical importance of these forests. By accounting for the vertical organization of canopy openings across multiple height strata, our analysis reveals clear and consistent differences in canopy gap dynamics between monodominant *G. dewevrei* (GIL) and mixed (MIXED) forests. Across the vertical canopy profile, gap area per hectare was consistently lower in GIL forests. These differences were particularly strong and statistically significant at Lileko (Figure 6). At Yangambi, the same directional pattern was observed, but none of the GIL–MIXED contrasts in gap area reached statistical significance after Benjamini–Hochberg FDR adjustment, including at $h = 19$ and 20 m, where raw *p*-values were marginally significant before adjustment ($p = 0.046$ and 0.028 , respectively) but did not survive adjustment for multiple comparisons ($p_{\text{adj}} = 0.085$ and 0.056 , both ns; Figure 6C). This absence of a statistically robust structural

contrast at Yangambi in gap area terms, highlighting, the influence of site-specific differences in canopy structure and stand developmental stage on forest-type differentiation.

Gap areas detected across the vertical canopy profile in both forest types are broadly consistent with earlier ground-based treefall gap surveys in the Ituri forests of the eastern Congo Basin. Hart et al. [30] reported total canopy area opened of 84–199 m² ha^{−1} in monodominant *G. dewevrei* forest and 166–433 m² ha^{−1} in adjacent mixed forest—values that fall within the lower range of our LiDAR-derived gap area profiles, corresponding to canopy height thresholds of 10–12 m at Lileko and 10–15 m at Yangambi. This correspondence suggests that ground-based surveys primarily capture openings in the lower and middle canopy strata where tree crowns are visible from the ground, whereas our multi-level LiDAR approach additionally resolves gap structure in the upper canopy ($h = 15\text{--}20\text{ m}$), where the largest and most ecologically consequential openings accumulate. Consistent with Hart et al. [30], neither study documents significant GIL–MIXED differences at low canopy height levels ($h \leq 10\text{ m}$ at Yangambi; $h = 5\text{ m}$ at both sites), suggesting that the absence of detectable structural contrasts in earlier ground-based studies reflects both the methodological limitation of single-stratum gap detection and the genuine reduction of structural divergence at lower canopy strata. By integrating gap detection across 12 consecutive canopy height levels from 5 to 20 m, our approach reveals structural contrasts that are more expressed in the upper canopy and would remain undetected by conventional ground-based or single-height LiDAR approaches, making the results more directly comparable with those of recent LiDAR-based studies in Amazonian forests [10,52,53,60].

Our findings are consistent with the multi-height LiDAR analysis of Kellner and Asner [10], who showed that canopy gap size–frequency distributions follow similar scaling relationships across canopy strata. We extend this perspective to Central African forests by demonstrating that vertical gap profiles not only capture general canopy organization but also discriminate between monodominant and mixed forest types. Our results show that canopy openness increased with canopy height threshold, reflecting the hierarchical structure of tropical forest canopies. However, canopy openness in the Yangambi landscape remained substantially lower than values reported for Amazonian forests. At the 10 m height threshold commonly used in LiDAR gap studies [52–54], gap areas ranged from 39–100 m² ha^{−1} in our study, compared with averages of 411 m² ha^{−1} across the Brazilian Amazon [52] and 120–549 m² ha^{−1} in the Ducke and Tapajós forests [53]. This pattern was consistent across all minimum gap-area thresholds tested (Appendix A Figure A2), indicating that the more continuous canopy cover observed in Central African old-growth forests is robust to methodological choices. These results are consistent with broader evidence that Congo Basin forests experience lower disturbance rates, longer biomass residence times, and greater aboveground biomass than their Amazonian counterparts [14,61]. In this context, the relatively closed canopies documented here, particularly in *G. dewevrei* forests, suggest a disturbance regime dominated by smaller and less frequent canopy openings and highlight the value of LiDAR-derived vertical gap profiles for characterizing forest structural dynamics at landscape scales.

Differences in canopy openness between Lileko and Yangambi suggest that GIL forests represent different stages of structural development. At Lileko, lower gap areas coincide with a greater abundance of large *G. dewevrei* trees, with the >80 cm DBH class exhibiting the highest stem density (20.0 stems ha^{−1}; Appendix A Figure A3) and extensive, continuous monodominant patches (Figure 8A). This inverted size distribution is consistent with a mature canopy in which *G. dewevrei* has attained structural dominance, resulting in a closed upper canopy architecture typical of late-stage monodominant stands, as described in Central African forest dynamics studies [21,25,30]. Such dominance by large emergent individuals is commonly associated with canopy stabilization, reduced gap formation

rates, and lower small-stem recruitment under closed-canopy conditions in old-growth tropical forests [6].

In contrast, Yangambi GIL forests are dominated by smaller stems (10–30 cm DBH: 38.7 stems ha^{-1}), suggesting active recruitment and a less advanced stage of canopy development consistent with earlier or intermediate phases of monodominant stand development reported for *Gilbertiodendron*-dominated forests under expansion or aggradation dynamics [21,30,62]. Because, by definition, *G. dewevrei* is largely absent from MIXED plots (Figure 4), we compared these species-level patterns (Appendix A Figure A3) with total community stem density (Appendix A Figure A4). The latter was broadly similar between sites in both forest types (Appendix A Figure A4), indicating that the inter-site contrast (Appendix A Figure A5) is likely driven primarily by the population structure of *G. dewevrei* rather than by differences in overall stand density. Given the limited number of plots, this comparison is presented as descriptive evidence, and further sampling incorporating topographic and edaphic covariates will be required to test this interpretation formally.

This developmental interpretation is further supported by landscape configuration. At Yangambi, the GIL forests occur as smaller and more fragmented patches embedded within a mixed-forest matrix (Figures 1 and 8B), a landscape configuration that may plausibly reflect both an earlier developmental stage and the topo-edaphic heterogeneity documented in the Yangambi landscape. Such spatial organization is consistent with previous studies suggesting that *G. dewevrei* forests undergo progressive expansion from topographically favorable sites and may coexist at different developmental stages within the same landscape [28,59,63,64]. Accordingly, the weaker GIL–MIXED structural contrast observed at Yangambi, where LiDAR-derived gap metrics largely overlap throughout the vertical profile, likely reflects greater structural heterogeneity and a lower degree of canopy differentiation between forest types than at Lileko (Figure 6C).

These findings also highlight the added value of vertically resolved structural metrics for forest typology mapping. Although recent deep-learning approaches using Sentinel-2 imagery have improved the regional discrimination of GIL and mixed forests [23,48], their performance remains constrained by the limited spectral separability of these forest types and by sensitivity to atmospheric correction. The LiDAR-derived structural indicators developed here therefore provide complementary information that is particularly valuable for identifying small and fragmented monodominant stands that remain difficult to map reliably using optical imagery alone.

4.3. A LiDAR-Based Integrative Canopy–Stand Indicator of Structural Functioning Differences Between Monodominant and Mixed Forests

At the plot or stand level, previous studies have generally reported no significant differences between GIL and MIXED forests in parameters such as stem density, basal area, aboveground biomass, and floristic richness [25–29]. This absence of a significant contrast is consistent with our own findings at the community level across DBH classes (Figure 4A,B), where neither stem density nor basal area differed significantly between GIL and MIXED forests in any DBH class after correction for multiple comparisons, even though *G. dewevrei* accounted for a disproportionate share of stems and basal area within GIL stands specifically. In this study, we introduced a new integrative indicator that combines canopy openness with stand wood volume: the gap area to basal area ratio (GAP/BA). Unlike conventional stand metrics, this indicator revealed clearer structural contrasts between forest types, with GIL forests consistently exhibiting lower GAP/BA values than mixed forests (Figure 7).

Because GAP/BA standardizes canopy openings by basal area, this result indicates that for comparable levels of stand wood volume, GIL forests tend to maintain smaller canopy openings than mixed forests. This pattern is consistent with our observations of

lower absolute gap areas in GIL forests across most height levels, particularly at Lileko, and suggests a denser and more continuous upper canopy in monodominant stands rather than differences in total biomass. The added value of this normalization is evident at Yangambi, where absolute gap area does not differ significantly between GIL and MIXED forests after correction for multiple comparisons, whereas the height-normalized GAP/TCH ratio retains significant differences in the upper canopy. This suggests that standardizing canopy openness by canopy structural development improves the detection of genuine forest-type contrasts in landscapes characterized by high developmental-stage variability.

To extend this integrative approach beyond field plots, we examined whether the GAP/BA ratio could be approximated using fully remote-sensing-based metrics. We found very strong correlations (Pearson's $r > 0.90$) between GAP/BA and several gap-area-to-top-of-canopy height (GAP/TCH) metrics, particularly GAP/TCH_p25, GAP/TCH_mean, and GAP/TCH_median (Appendix A Table A2). Among these, GAP/TCH_median showed the strongest correlation with field-based GAP/BA ($R^2_{\text{adj}} = 0.992$, Pearson $r = 0.996$, $n = 117$ observations) and was therefore retained as the primary remote-sensing-based structural indicator used throughout this study (Figure 7). A leave-one-plot-out cross-validation confirmed that this relationship generalizes across plots rather than reflecting overfitting to the limited number of field plots available (Appendix A Table A2). This indicates that GAP/TCH remote-sensing-based indicators capture essentially the same structural contrast as GAP/BA, while removing the dependency on ground-based basal area measurements.

When applied across the entire surveyed landscape, GAP/TCH_median revealed clearer and more spatially continuous contrasts between GIL and mixed forests throughout the vertical canopy profile (Figure 8). Similar to absolute gap area, GAP/TCH values were consistently lower in GIL forests than in MIXED forests, with differences becoming more pronounced at greater canopy heights. However, the canopy height at which differences became statistically significant varied between sites: above 10 m at Lileko, and only at 19 and 20 m at Yangambi (Figure 8D). This site-dependent pattern mirrors the structural differences already observed in gap area alone and highlights the importance of considering local canopy structure when interpreting these indicators (Section 4.2).

The spatial distribution of GAP/TCH values across both study sites further reinforces confidence in the structural coherence of the forest type classification. At Lileko, lower GAP/TCH values are consistently collocated with GIL-classified grid cells (Figure 8A), and GAP/TCH distributions differ highly significantly between forest types across both sites combined (Wilcoxon rank-sum, $p = 2.80 \times 10^{-18}$; Figure 8C). This structural segregation, derived from a metric entirely independent of the RGB imagery used for visual delineation, illustrates the potential of GAP/TCH as a complement to spectral approaches for old-growth forest type discrimination [23,48], a particularly relevant property in the Congo Basin where spectral separability between GIL and adjacent mixed forests remains a persistent challenge for automated mapping approaches.

Integrating canopy gap information with TCH yields a robust and spatially explicit indicator that closely reflects field-based GAP/BA patterns (Figure 7), strengthening forest classification and providing an operational framework for monitoring structural and functional diversity using LiDAR data alone. Extending this approach to spaceborne structural products such as GEDI waveform LiDAR or the NASA-ISRO Synthetic Aperture Radar (NISAR) and BIOMASS missions is not expected to be a direct transfer. However, these products operate at coarser spatial resolution than the 1 m resolution CHM used to detect individual canopy gaps in the present study. The GEDI acquires discrete, non-contiguous footprints of approximately 25 m diameter along orbital tracks rather than continuous spatial coverage [65], BIOMASS provides continuous coverage but at a nominal resolution

of 200 m for its aboveground biomass and forest height products (50 m for its forest disturbance product) [66], and NISAR's L-band radar resolution ranges from approximately 3 to 48 m depending on acquisition mode, and none of these products natively resolves individual canopy gaps at the scale analyzed here. Following the calibration strategy demonstrated by Lang et al. [36] and Wan et al. [37] for canopy height mapping, high-resolution airborne or UAV LiDAR reference sites, including the Yangambi 2023 UAV LiDAR dataset used in the present study, could be used to calibrate coarser satellite-derived structural products. A comparable empirical calibration approach, tailored to the resolution and sensing characteristics of each spaceborne product, would likely be required to adapt the GAP/TCH indicator for regional-scale monitoring. This represents a necessary methodological step for future work rather than an immediate capability of the current framework, and is particularly relevant in Central African forests, where extensive ground-based inventories are logistically challenging to implement over large and remote areas [67].

4.4. Implications for the Forest Dynamics Process and Species Interactions

The lower GAP/BA and GAP/TCH values observed in GIL forests reinforce the broader structural pattern identified earlier in this study: monodominant forests tend to exhibit more closed and homogeneous canopies than adjacent mixed forests, particularly in the upper strata (Figures 4–6). Rather than necessarily indicating lower disturbance rates, this pattern suggests that, at equivalent basal area levels, canopy openness in GIL forests is lower on average than in mixed forests and is therefore likely to have a more limited structural impact on GIL forest stands.

These patterns are consistent with previous observations that tropical monodominant forests often exhibit reduced disturbance regimes and relatively stable canopy structures [15,18]. They also have implications for theories of gap size–frequency distribution [10,50] and for the links between canopy structure and forest dynamics (growth, mortality, and recruitment) [1,4]. The smaller area and lower frequency of gaps in GIL forests suggest a more diffuse disturbance regime, dominated by isolated treefall events and rapid canopy closure that primarily favors recruitment under the closed canopy. In contrast, the larger and more frequent gaps in mixed forests indicate a more heterogeneous disturbance regime, generating a wider range of light environments and thereby creating greater opportunities for species with contrasting life-history strategies, particularly pioneers [68]. By incorporating the vertical dimension of canopy gaps, our results reinforce the view that canopy structure is not merely a consequence of demographic processes but also plays an active role in shaping growth, mortality, and regeneration trajectories at both stand and landscape scales.

In this context, our findings complement functional-ecological evidence from Central African GIL forests. GIL stands are characterized by strong environmental filtering and reduced functional diversity, associated with specific hydraulic and nutrient-use traits and ectomycorrhizal associations [28]. Such trait-based constraints likely interact with the more closed and homogeneous canopy structure that we document here, jointly reinforcing a disturbance regime dominated by small, infrequent gaps and limiting opportunities for light-demanding pioneer species [68], even though the direction and magnitude of these interactions remain to be established experimentally.

These findings are also consistent with the ecological mechanism of intraspecific facilitation [69], whereby dense aggregations of conspecific trees promote crown interconnection, canopy continuity, and persistence of dominant individuals in the upper strata. In this regard, our results are compatible with the hypothesis that low-diversity tropical forests would be maintained through a combination of low adult mortality, dense litter accumulation that limits the establishment of other species, and positive interactions among

conspecific individuals that may contribute to canopy closure and structural homogeneity [15,26,30]. However, while our LiDAR-derived canopy gap metrics provide robust evidence of contrasting canopy architectures and disturbance regimes, they do not directly reveal the underlying ecological interactions among trees. Direct empirical support for facilitation mechanisms would require targeted experimental manipulations (e.g., controlled canopy openings or litter removal) or long-term monitoring of gap closure, tree mortality, and recruitment dynamics to establish causal links between canopy structure and species interactions.

4.5. Limitations and Future Research Directions

While this study provides the first LiDAR-based quantification of vertical gap size distributions across contrasting old-growth forest types in Central Africa, several limitations point toward promising avenues for future research.

First, the manual forest-type delineation approach used here, although cross-referenced against field inventory reference plots, remains subject to observer-dependent uncertainty. This uncertainty could be reduced in future studies through automated classification approaches combined with systematic post-classification ground validation. In particular, the present photo-interpretation was not followed by an independent ground-truthing campaign to reassess classified grid cells beyond the reference plot locations, and additional sources of uncertainty may arise from spectral overlap between GIL and MIXED canopies under closed-canopy conditions and mixed pixels at forest-type boundaries. Recent studies have demonstrated promising advances in deep learning-based forest typology mapping in Central Africa using Sentinel-2 imagery [23,48]. However, the low spectral separability between GIL and adjacent MIXED forests [23], combined with the sensitivity of classification accuracy to atmospheric and BRDF preprocessing [48], highlights the persistent limitations of optical imagery alone for reliably discriminating these forest types across diverse landscapes. Structural LiDAR-derived metrics, such as the GAP/TCH indicator developed here, could therefore provide valuable complementary information to improve automated forest-type classification by integrating canopy architecture beyond spectral properties, particularly for small and fragmented GIL patches that remain difficult to map reliably at regional scales.

Second, the Yangambi dataset combines field inventories conducted in 2012 with LiDAR data acquired in 2014, a two-year interval that is considered acceptable given the slow structural dynamics characteristic of old-growth tropical forests, where stand-level attributes such as basal area and stem density change at decadal rather than annual timescales. Furthermore, no higher-quality dataset acquired closer to 2023 is currently available that provides equivalent spatial coverage of all forest types across the Yangambi landscape. This is particularly critical for GIL forests at this site, which occur as small, scattered patches embedded within a mixed-forest matrix, a configuration that requires broad spatial coverage to achieve sufficient sample sizes for robust structural comparisons. The 2014 airborne LiDAR acquisition therefore remains the most comprehensive remote sensing resource available for capturing the structural diversity of these forest types at landscape scale in Yangambi. Nevertheless, future studies should prioritize temporally consistent multi-site acquisitions to further reduce uncertainty in structural comparisons and to disentangle developmental stage effects from site-specific environmental drivers such as soil conditions, topographic position, and disturbance history.

Third, the gap detection approach relies on a fixed minimum gap area threshold of 20 m² across all canopy height strata. This threshold does not correspond to a specific tree diameter and crown area relationship, as treefall gaps typically exceed the projected crown area of the fallen tree owing to collateral damage, crown breakage, and, occasionally,

multiple tree falls [49]. The 20 m² threshold used in this study should therefore be regarded as a conservative detection floor rather than a precise ecological size class. It is consistent with established practice in tropical treefall gap research, notably Brokaw's original definition of a minimum detectable gap (20–40 m²) at BCI [50]. It also falls within the lower range of naturally occurring treefall gaps reported from the same forest by Schnitzer & Carson [51], whose most frequent gap-size class was 25–75 m². Moreover, a 20 m² opening is broadly consistent with the projected crown area of a small canopy tree based on the Cameroon–Gabon crown allometry of Blanchard et al. [55].

Sensitivity analyses using thresholds of 10, 20, 25, and 50 m² at canopy heights of 10, 12, and 20 m, with Benjamini–Hochberg FDR correction, confirmed that GIL–MIXED structural contrasts in gap area and GAP/TCH were not sensitive to gap size threshold choice (Appendix A Figure A2). At Lileko, GIL–MIXED contrasts remained highly significant across all thresholds, whereas no significant contrasts were detected at Yangambi under any threshold. This consistent pattern supports the interpretation that the weaker structural differentiation at Yangambi reflects site-specific forest development rather than methodological sensitivity. Although the 20 m² threshold provides a robust basis for the present analyses, ecological interpretation of canopy gap size in Central African forests remains constrained by the limited availability of region-specific empirical relationships linking tree diameter, crown dimensions, and canopy gap formation. Future studies combining detailed field inventories with terrestrial laser scanning (TLS), UAV photogrammetry, and airborne LiDAR across contrasting forest types and developmental stages would help establish robust allometric and structural relationships adapted to African forests. Such datasets would improve our understanding of how individual tree architecture and treefall processes translate into canopy gap size and shape, thereby providing a stronger ecological basis for selecting gap detection thresholds and enhancing the interpretation of remotely sensed canopy gaps in studies of forest dynamics and forest degradation.

Fourth, the strength of the conclusions drawn in this study varies with the type and volume of underlying data. The GAP/TCH and gap area comparisons across forest types (Figures 6 and 8) are derived entirely from LiDAR at the 1-ha grid-cell level and are supported by a relatively large sample size ($n = 654$ cells: 233 at Lileko and 422 at Yangambi, excluding edge and ambiguous cells), providing robust statistical inference largely independent of the field inventory. In contrast, complementary interpretations, including the *G. dewevrei* size-class analysis underpinning the developmental-stage hypothesis (Section 4.2) and community-level stem density comparisons, rely on a much smaller plot-based inventory ($n = 5$ GIL and $n = 8$ MIXED plots overall, with as few as $n = 2$ –3 plots per site $\times$ forest-type combination). These analyses are therefore exploratory in nature and are presented as such throughout the present study, whereas the core LiDAR-derived structural results benefit from substantially stronger statistical support.

While the GAP/TCH indicator shows strong potential as a transferable structural metric, its calibration against spaceborne data remains to be validated. As discussed in Section 4.3, extending the GAP/TCH framework to satellite-based structural products such as GEDI, NISAR, and BIOMASS is unlikely to be directly transferable given their coarser spatial resolution relative to the 1 m CHM used here, and would instead require an empirical calibration approach tailored to each product, following the strategy demonstrated by Lang et al. [36] and Wan et al. [37] for canopy height mapping. This remains a necessary methodological step for future work rather than an immediate capability of the current framework.

Finally, extending the vertical gap profiling approach to other monodominant forest types in Central Africa [18,59], including forests dominated by *Aucoumea klaineana*, *Cynometra alexandri*, and *Julbernardia seretii* in addition to *Gilbertiodendron dewevrei*, would help

determine whether the structural patterns observed here are a general characteristic of monodominant forests or arise from dominant species-specific functional traits. Differences in crown architecture, shade tolerance, and regeneration strategies are likely to generate distinct vertical gap signatures and recovery trajectories across these monodominant systems. Such an extension will require, at minimum, harmonized forest-type mapping and high-resolution LiDAR-derived CHM for each system, while the ecological mechanisms underlying monodominance (e.g., feedback involving soil conditions, disturbance regimes, or biotic interactions) remain to be explicitly tested rather than assumed. Comparative analyses across these forest types would nevertheless provide a stronger basis for generalizing structural diagnostics of tropical monodominance across the Congo Basin.

5. Conclusions

This study tested three hypotheses regarding the vertical organization of canopy gaps in Central African old-growth forests, providing the first LiDAR-based quantification of vertical gap size distributions across contrasting forest types in the region. The results broadly supported all three hypotheses. Gap size distributions differed significantly between *G. dewevrei* (GIL) and mixed (MIXED) forests, with larger gaps consistently observed in MIX forests at canopy heights above 10 m (H1). Canopy openness remained systematically lower in GIL forests across all height strata, confirming the value of vertically stratified LiDAR metrics for forest type discrimination (H2). The GAP/BA and GAP/TCH ratios revealed stronger structural contrasts than conventional stand metrics, while their strong correlation indicates that canopy height can serve as a practical surrogate for basal area in large-scale assessments (H3).

However, structural differences were more pronounced at Lileko than at Yangambi, suggesting that the magnitude of GIL–MIXED divergence depends on forest developmental stage and topo-edaphic conditions. Overall, integrating canopy gap metrics with stand structure improves forest classification and provides an operational framework for monitoring structural and functional diversity in Central African rainforests. Combining airborne LiDAR with spaceborne observations from GEDI and forthcoming radar missions such as NISAR and BIOMASS could further enable regional-scale monitoring of canopy structure and disturbance dynamics across the Congo Basin.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/rs18142431/s1>. File S1: R scripts and processed data supporting the analyses and figures presented in this manuscript (field inventory data, LiDAR-derived gap area and canopy height metrics, forest-type delineation shapefiles, and all R scripts required to reproduce Figures 4–8, Appendix A Tables A1 and A2). The README file provides detailed information on the corresponding R scripts and their associated analyses.

Author Contributions: Conceptualization, T.B.N., J.-F.B. and J.B.; methodology, T.B.N., J.-F.B. and A.V.L.; software, T.B.N., A.V.L., A.P., Z.R., T.S.M. and T.C.; validation, J.-F.B. and J.B.; formal analysis, T.B.N. and J.-F.B.; investigation, T.B.N., A.V.L., T.d.H., W.H. and S.S.; resources, T.B.N., J.-F.B., W.H. and S.S.; data curation, T.B.N., A.V.L. and T.d.H.; writing—original draft preparation, T.B.N. and A.V.L.; writing—review and editing, T.B.N., A.V.L., J.B., T.d.H., A.P., T.S.M., Z.R. and T.C.; visualization, T.B.N., A.V.L., A.P., Z.R. and T.C.; supervision, J.-F.B.; project administration, T.B.N. and J.-F.B.; funding acquisition, T.B.N., A.V.L., J.-F.B. and W.H. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by AGRINATURA-EEIG/GEIE (European Alliance on Agricultural Knowledge for Development), ULIEGE, and the ERAIFT consortium through the European Union-funded project “Capacity building of biodiversity practitioners, scientists and policy makers for the sustainable management of protected areas and forest ecosystems in Africa: DCI-ENV 2020/416-397”; the FFRBA (fondation pour favoriser la recherche sur la biodiversité en Afrique

centrale) project; Fonds de la Recherche Scientifique–FNRS; and the CANOPi project, funded by FNRS under the EOS Call (grant number O.0026.22). Funding for previous forest inventory work in Yangambi was provided by the European Union (EU; project: EEC40 FORETS, supported by the XIth European Development Fund), the Belgian Directorate-General for Development Cooperation and Humanitarian Aid (DGD; projects: PilotMAB and PilotMABplus), the Belgian Science Policy Office (BELSPO; projects: I-1-D-6087–1/International Foundation for Science, SD/AR/01A/COBIMFO, BR/132/A1/AFRIFORD, BR/143/A3/HERBAXYLAREDD, FED-tWIN2019-prf-075-CongoFORCE, EF/211/TREE4FLUX, B2/223/P1/DAMOCO), the Belgian Climate Centre (BCC; CLOVER project), the Flemish Interuniversity Council (VLIR-UOS; projects: CD2018TEA459A103, FORMONCO II), and the Flemish Research Council (FWO; projects: G014123N COBARCHIVES, 3G0I3922 CANOPI).

Data Availability Statement: The Yangambi 2014 LiDAR dataset was originally acquired within the Carbon Map and Model (CM&M) project, implemented by the WWF and its partners and funded by the German development bank KfW and the German Federal Ministry for the Environment, Nature Conservation, and Nuclear Safety (BMU). Xu et al. [39]: <https://doi.org/10.1038/s41598-017-15050-z>; <https://osfac.net/fr/produits/monitoring-des-forets/facet-atlas/facet-congo/item/631-carte-de-biomasse-forestiere-de-la-rdc> (accessed on 3 June 2026). Field inventories from Yangambi (2012) are part of the Congo Basin integrated monitoring for forest carbon mitigation and biodiversity (COBIMFO) project [44]: <https://www.naturalsciences.be/en/science/research/biodiversity-in-a-changing-world/projects/cobimfo> (accessed on 3 June 2026). All R scripts, field inventory data, and LiDAR-derived gap and canopy height metrics used to generate the analyses and figures presented in this manuscript are available as Supplementary Material and can be downloaded at <https://www.mdpi.com/article/10.3390/rs18142431/s1> and are released under CC BY 4.0. Additional data will be made available by the authors upon request.

Acknowledgments: We would also like to thank SODEFOR (Société de développement forestier) (Tania Trindade, Raphaël Barbiche, Ricardo Neves and all field agents) for its collaboration and logistical support in the field, as well as INERA-YANGAMBI (Dieu-Merci Assumani, Bernard Bonyoma and all field agents) for its technical support. Finally, we thank Baudouin Michel and Emmanuel Heuse for administrative support.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Percentage of 1-ha grid cells containing at least one canopy gap at each height threshold (5–20 m), by forest type and study site. Denominators correspond to the total number of photo-interpreted grid cells per forest type: GIL ($n = 46$) and MIXED ($n = 187$) at Lileko (9 cells excluded from the analysis); GIL ($n = 30$) and MIXED ($n = 392$) at Yangambi. Values of 100% indicate that all cells of the corresponding type contained at least one gap at that height threshold.

Site	Forest Type (n)	5	10	11	12	13	14	15	16	17	18	19	20
Lileko	GIL ($n = 46$)	19.6%	43.5%	52.2%	60.9%	63.0%	73.9%	80.4%	84.8%	84.8%	93.5%	93.5%	97.8%
	MIXED ($n = 187$)	28.9%	74.9%	86.6%	90.9%	95.2%	97.9%	98.9%	100.0%	100.0%	100.0%	100.0%	100.0%
	Total ($n = 233$)	27.0%	68.7%	79.8%	85.0%	88.8%	93.1%	95.3%	97.0%	97.0%	98.7%	98.7%	99.6%
Yangambi	GIL ($n = 30$)	23.3%	53.3%	56.7%	73.3%	80.0%	83.3%	93.3%	93.3%	96.7%	96.7%	96.7%	96.7%
	MIXED ($n = 392$)	15.1%	60.2%	68.1%	76.5%	82.7%	89.3%	92.9%	96.2%	97.4%	98.7%	99.5%	100.0%
	Total ($n = 422$)	15.6%	59.7%	67.3%	76.3%	82.5%	88.9%	92.9%	96.0%	97.4%	98.6%	99.3%	99.8%

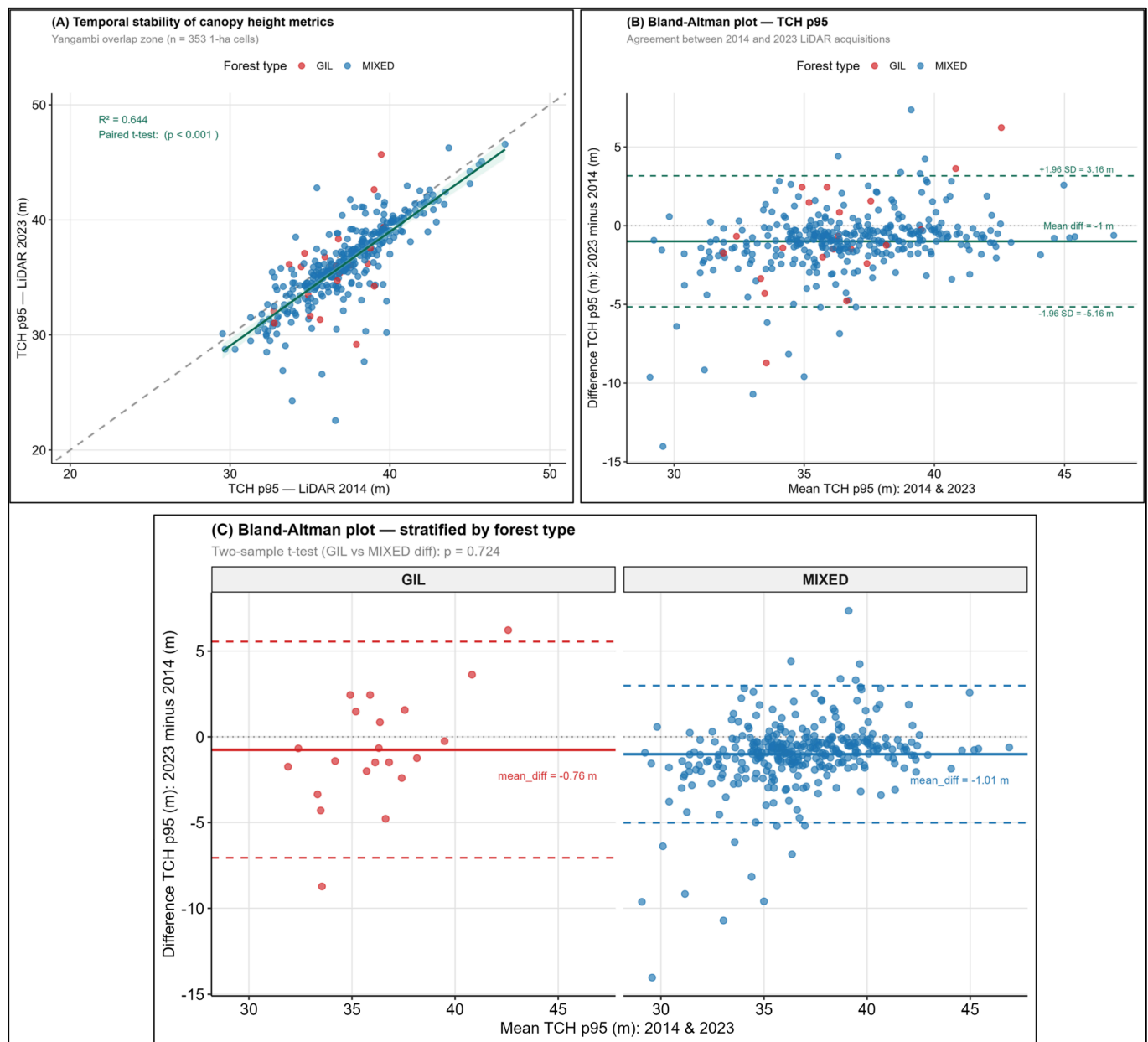


Figure A1. Temporal stability of LiDAR-derived canopy height metrics between the 2014 airborne LiDAR acquisition and the 2023 UAV-LiDAR acquisition within the area of spatial overlap at the Yangambi study site ($n = 353$ 1-ha grid cells). The 2023 UAV-LiDAR dataset was previously used by Wan et al. [37] as independent validation data for satellite-derived canopy height estimates. (A) Relationship between top-of-canopy height (TCH p95) derived from the two LiDAR acquisitions. The green line shows the linear regression ($R^2 = 0.644$; paired t -test: $p < 0.001$), and the gray dashed line represents the 1:1 relationship. (B) Bland–Altman plot showing agreement between acquisitions, with the mean difference (-1.0 m; green solid line) and the 95% limits of agreement (-5.16 to $+3.16$ m; green dashed lines). The small mean bias and limits of agreement within approximately ± 5 m indicate good structural comparability despite the nine-year interval between acquisitions. (C) Forest-type-stratified Bland–Altman analysis. Mean differences were similar for GIL ($n = 30$; -0.8 m; red solid line; 95% limits of agreement: -6.6 to $+5.0$ m) and MIXED forests ($n = 323$; -1.0 m; blue solid line; 95% limits of agreement: -5.0 to $+3.0$ m). No significant difference was detected between forest types (two-sample t -test: $t = 0.358$, $df = 21$, $p = 0.724$), indicating that temporal variability is non-differential with respect to forest type and is therefore unlikely to bias the GIL–MIXED structural comparisons presented in this study.

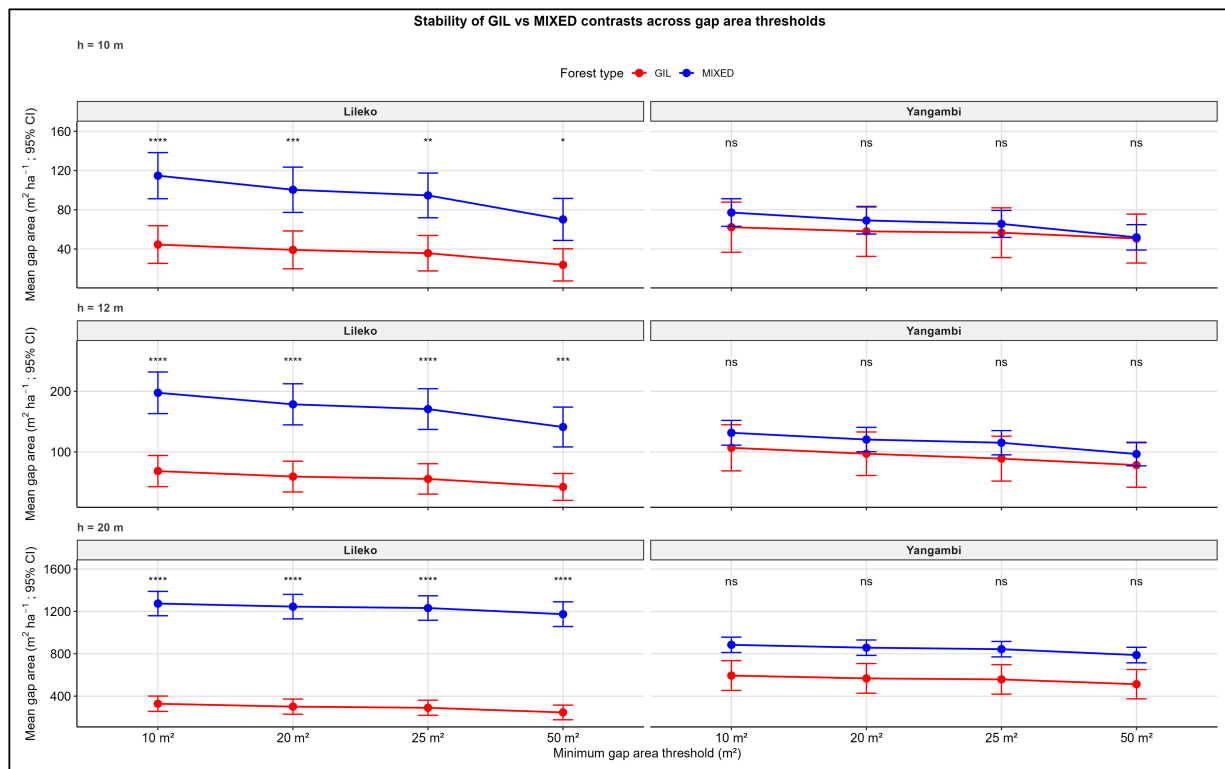


Figure A2. Stability of GIL vs. MIXED forest type contrasts in mean gap area per hectare across four minimum gap area thresholds (10, 20, 25, and 50 m²), shown at three canopy height levels. The h = 10 m is included for comparison with Amazonian forest studies, where this threshold is commonly used (Dalagnol et al. [52]; Hunter et al. [53]). Each panel shows the mean gap area ($\pm$ 95% CI) for GIL (red) and MIXED (blue) forest types at Lileko (left) and Yangambi (right). Each panel has an independent y-axis scale. Statistical comparisons between forest types were performed independently at each site, height level, and threshold using an adaptive test selected based on normality (Shapiro–Wilk) and equality of variances (Levene): Student’s *t*-test when both conditions were met, Welch’s *t*-test when variances were unequal, and Wilcoxon rank-sum test otherwise. Benjamini–Hochberg false discovery rate (FDR) correction was applied within the set of 96 test combinations (2 sites $\times$ 12 height levels $\times$ 4 thresholds; Section 2.9). The significance levels shown are FDR-adjusted: ns = not significant, * $p_{\text{adj}} < 0.05$, ** $p_{\text{adj}} < 0.01$, *** $p_{\text{adj}} < 0.001$, **** $p_{\text{adj}} < 0.0001$.

Table A2. Values of the criteria used to evaluate the quality of the relationships between the GAP/BA and GAP/TCH ratio metrics with gap area estimated above a canopy height of 15 m (CHM; TCH: top-of-canopy height; p25–p75–p95: 25th, 75th and 25th percentiles; cv: coefficient of variation; med: median; sd: standard deviation; LOOCV: leave-one-out cross-validation method) based on the following: number of plots = 13; number of observations = 117; LOOCV $R^2 = 0.99$; LOOCV RMSE = 1.47; and LOOCV Pearson $r = 0.99$.

Variable	R2	adjR2	AIC	RMSE	Pearson r
ratio_GAP_CHM_med	0.99	0.99	388.55	1.24	1.00
ratio_GAP_CHM_mean	0.98	0.98	510.33	2.09	0.99
ratio_GAP_CHM_p25	0.98	0.98	510.46	2.09	0.99
ratio_GAP_CHM_p75	0.98	0.98	513.86	2.12	0.99
ratio_GAP_CHM_p95	0.96	0.96	582.99	2.85	0.98
ratio_GAP_CHM_cv	0.92	0.91	666.28	4.07	0.96
ratio_GAP_CHM_max	0.91	0.91	670.86	4.15	0.95
ratio_GAP_CHM_sd	0.74	0.74	796.54	7.10	0.86
ratio_GAP_CHM_min	0.00	−0.01	954.72	13.95	0.02

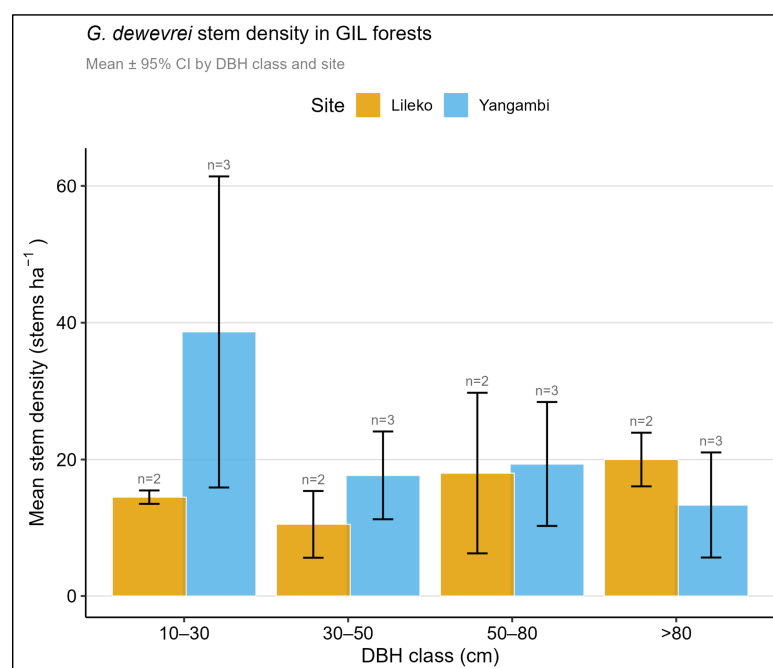


Figure A3. Mean stem density of *Gilbertiodendron dewevrei* trees (stems ha⁻¹) by DBH class in GIL monodominant forests at Lileko (orange) and Yangambi (blue). Error bars represent 95% confidence intervals. Sample sizes (n = number of field inventory plots per site and DBH class) are indicated above each bar.

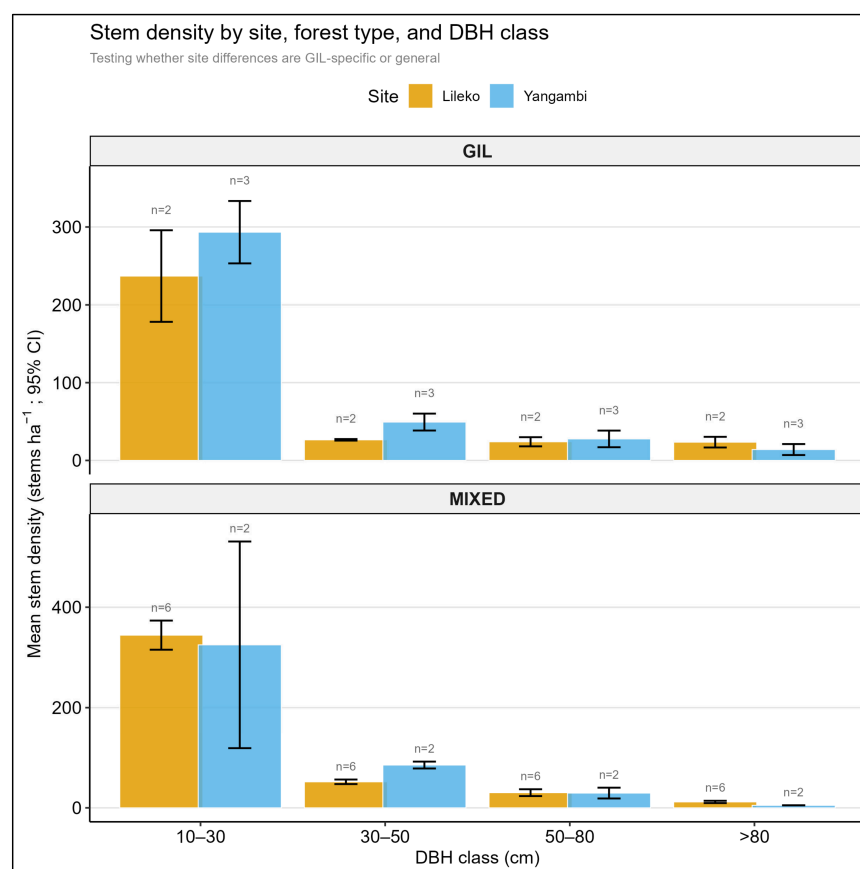


Figure A4. Mean total community stem density (all species combined, stems ha⁻¹) by DBH class, site, and forest type. The panels show data for GIL (top) and MIXED (bottom) forest plots; bars represent Lileko (orange) and Yangambi (blue). Error bars represent 95% confidence intervals.

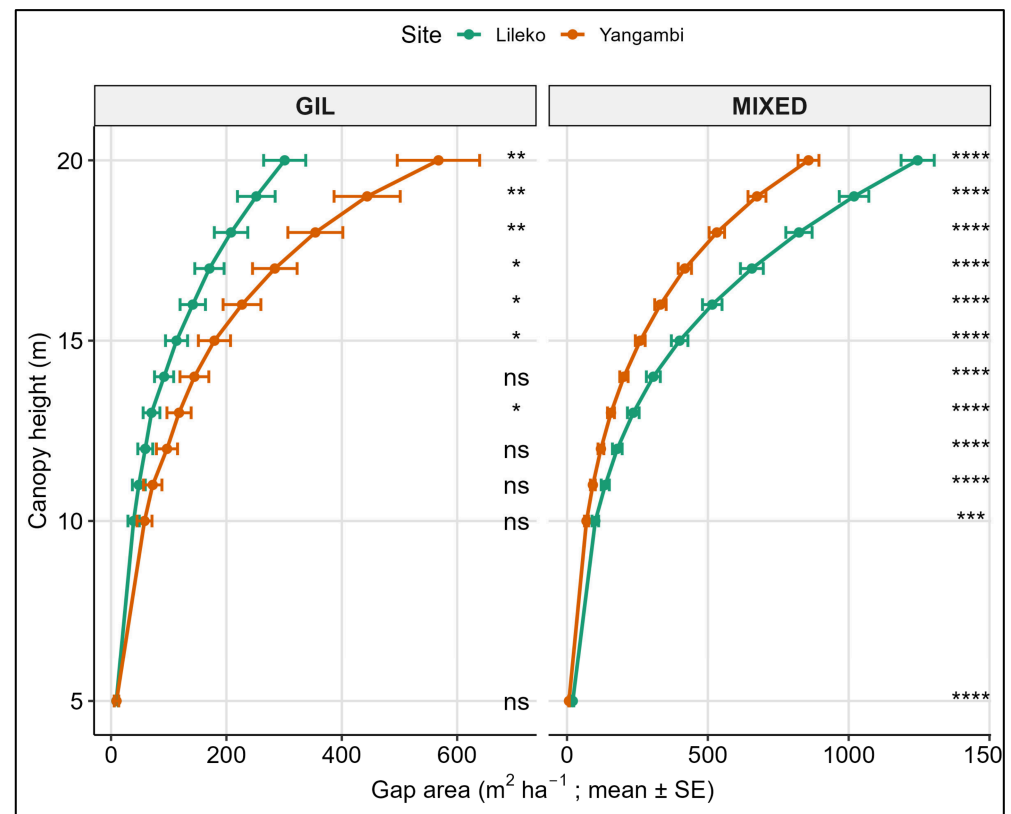


Figure A5. Gap area (m²/ha) distribution at various canopy heights in *Gilbertiodendron dewevrei* monodominant forests and adjacent mixed primary forests at the study sites of Lileko and Yangambi within the landscape of the Yangambi Biosphere Reserve. The significance levels shown are FDR-adjusted: ns = not significant, * $p_{\text{adj}} < 0.05$, ** $p_{\text{adj}} < 0.01$, *** $p_{\text{adj}} < 0.001$, **** $p_{\text{adj}} < 0.0001$.

References

1. Brokaw, N.V.L. Gap-Phase Regeneration in a Tropical. *Ecology* **1985**, *66*, 682–687. [\[CrossRef\]](#)
2. Muscolo, A.; Bagnato, S.; Sidari, M.; Mercurio, R. A Review of the Roles of Forest Canopy Gaps. *J. For. Res.* **2014**, *25*, 725–736. [\[CrossRef\]](#)
3. Shapiro, A.; D’Annunzio, R.; Desclée, B.; Jungers, Q.; Kondjo, H.K.; Iyanga, J.M.; Gangyo, F.I.; Nana, T.; Obame, C.V.; Milandou, C.; et al. Small Scale Agriculture Continues to Drive Deforestation and Degradation in Fragmented Forests in the Congo Basin (2015–2020). *Land Use Policy* **2023**, *134*, 106922. [\[CrossRef\]](#)
4. Wright, S.J.; Muller-Landau, H.C.; Condit, R.; Hubbell, S.P. Gap-Dependent Recruitment, Realized Vital Rates, and Size Distributions of Tropical Trees. *Ecology* **2003**, *84*, 3174–3185. [\[CrossRef\]](#)
5. Hallé, F.; Oldeman, R.A.A.; Tomlinson, P.B. *Tropical Trees and Forests: An Architectural Analysis*; Springer: Berlin/Heidelberg, Germany, 1978.
6. Van Der Meer, R.J.; Bongers, E. Formation and Closure of Canopy Gaps in the Rain Forest at Nouragues, French Guiana. *Vegetatio* **1996**, *126*, 167–179. [\[CrossRef\]](#)
7. Brokaw, N.V.L. Gap-Phase Regeneration of Three Pioneer Tree Species in a Tropical Forest. *J. Ecol.* **1987**, *75*, 9–19. [\[CrossRef\]](#)
8. Denslow, J.S. Tropical Rainforest Gaps and Tree Species Diversity. *Ann. Rev. Ecol. Syst.* **1987**, *18*, 431–451. [\[CrossRef\]](#)
9. Winstanley, P.; Dalagnol, R.; Mendiratta, S.; Braga, D.; Galvão, L.S.; Bispo, P.d.C. Post-Logging Canopy Gap Dynamics and Forest Regeneration Assessed Using Airborne LiDAR Time Series in the Brazilian Amazon with Attribution to Gap Types and Origins. *Remote Sens.* **2024**, *16*, 2319. [\[CrossRef\]](#)
10. Kellner, J.R.; Asner, G.P. Convergent Structural Responses of Tropical Forests to Diverse Disturbance Regimes. *Ecol. Lett.* **2009**, *12*, 887–897. [\[CrossRef\]](#) [\[PubMed\]](#)
11. Drake, J.B.; Dubayah, R.O.; Clark, D.B.; Knox, R.G.; Blair, B.J.; Hofton, M.A.; Chazdon, R.L.; Weishapel, J.F.; Prince, S.D. Estimation of Tropical Forest Structural Characteristics Using Large-Footprint Lidar. *Remote Sens. Environ.* **2002**, *79*, 305–319. [\[CrossRef\]](#)
12. Besisa Nguba, T.; Bogaert, J.; Makana, J.R.; Mate Mweru, J.P.; Sambieni, K.R.; Bwazani Balandi, J.; Mumbere Musavandalo, C.; Bastin, J.F. Assessing Forest Degradation in the Congo Basin: The Need to Broaden the Focus from Logging to Small-Scale Agriculture (A Systematic Review). *Forests* **2025**, *16*, 953. [\[CrossRef\]](#)

13. Richards, W.P. The Tropical Rain Forest. *Sci. Am.* **1973**, *229*, 58–68. [\[CrossRef\]](#)
14. Lewis, S.L.; Sonké, B.; Sunderland, T.; Begne, S.K.; Lopez-Gonzalez, G.; van der Heijden, G.M.F.; Phillips, O.L.; Affum-Baffoe, K.; Baker, T.R.; Banin, L.; et al. Above-Ground Biomass and Structure of 260 African Tropical Forests. *Philos. Trans. R. Soc. B Biol. Sci.* **2013**, *368*, 20120295. [\[CrossRef\]](#) [\[PubMed\]](#)
15. Connell, J.H.; Lowman, M.D. Low-Diversity Tropical Rain Forests: Some Possible Mechanisms for Their Existence. *Am. Nat.* **1989**, *134*, 88–119. [\[CrossRef\]](#)
16. Anbarashan, M.; Parthasarathy, N. Tree Diversity of Tropical Dry Evergreen Forests Dominated by Single or Mixed Species on the Coromandel Coast of India. *Trop. Ecol.* **2013**, *54*, 179–190.
17. Degagne, R.S.; Henkel, T.W.; Steinberg, S.J.; Fox, L. Identifying Dicycme Corymbosa Monodominant Forests in Guyana Using Satellite Imagery. *Biotropica* **2009**, *41*, 7–15. [\[CrossRef\]](#)
18. Peh, K.S.-H.; Lewis, S.L.; Lloyd, J. Mechanisms of Monodominance in Diverse Tropical Tree-Dominated Systems. *J. Ecol.* **2011**, *99*, 891–898. [\[CrossRef\]](#)
19. Fuhr, M.; Nasi, R.; Delegue, M.-A. Vegetation Structure, Floristic Composition and Growth Characteristics of Aucoumea Klaineana Pierre Stands as Influenced by Stand Age and Thinning. *For. Ecol. Manag.* **2001**, *140*, 117–132. [\[CrossRef\]](#)
20. Bastin, J.F.; Barbier, N.; Coutron, P.; Adams, B.; Shapiro, A.; Bogaert, J.; De Cannière, C. Aboveground Biomass Mapping of African Forest Mosaics Using Canopy Texture Analysis: Toward a Regional Approach. *Ecol. Appl.* **2014**, *24*, 1984–2001. [\[CrossRef\]](#) [\[PubMed\]](#)
21. Torti, S.D.; Coley, P.D.; Kursar, T.A. Causes and Consequences of Monodominance in Tropical Lowland Forests. *Am. Nat.* **2001**, *157*, 141–153. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Heimpel, E.; Ahrends, A.; Dexter, K.G.; Hall, J.S.; Mamboueni, J.; Medjibe, V.P.; Morgan, D.; Sanz, C.; Harris, D.J. Floristic and Structural Distinctness of Monodominant Gilbertiodendron Dewevrei Forest in the Western Congo Basin. *Plant Ecol. Evol.* **2024**, *157*, 55–74. [\[CrossRef\]](#)
23. Heimpel, E.; Harris, D.J.; Mamboueni, J.; Morgan, D.; Sanz, C.; Ahrends, A. Mapping of Monodominant Gilbertiodendron Dewevrei Forest Across the Western Congo Basin Using Sentinel-2 Imagery. *Remote Sens.* **2025**, *17*, 1639. [\[CrossRef\]](#)
24. Bastin, J.F.; Barbier, N.; Réjou-Méchain, M.; Fayolle, A.; Gourlet-Fleury, S.; Maniatis, D.; De Haulleville, T.; Baya, F.; Beeckman, H.; Beina, D.; et al. Seeing Central African Forests through Their Largest Trees. *Sci. Rep.* **2015**, *5*, 13156. [\[CrossRef\]](#) [\[PubMed\]](#)
25. Kearsley, E.; De Haulleville, T.; Hufkens, K.; Kidimbu, A.; Toirambe, B.; Baert, G.; Huygens, D.; Kebede, Y.; Defourny, P.; Bogaert, J.; et al. Conventional Tree Height-Diameter Relationships Significantly Overestimate Aboveground Carbon Stocks in the Central Congo Basin. *Nat. Commun.* **2013**, *4*, 2269. [\[CrossRef\]](#) [\[PubMed\]](#)
26. Makana, J.; Ewango, C.N.; McMahon, S.M.; Thomas, S.C.; Hart, T.B.; Condit, R. Demography and Biomass Change in Monodominant and Mixed Old-Growth Forest of the Congo. *J. Trop. Ecol.* **2011**, *27*, 447–461. [\[CrossRef\]](#)
27. Djuikouo, M.N.K.; Peh, K.S.H.; Nguembou, C.K.; Doucet, J.L.; Lewis, S.L.; Sonké, B. Stand Structure and Species Co-Occurrence in Mixed and Monodominant Central African Tropical Forests. *J. Trop. Ecol.* **2014**, *30*, 447–455. [\[CrossRef\]](#)
28. Kearsley, E.; Verbeeck, H.; Hufkens, K.; Van de Perre, F.; Doetterl, S.; Baert, G.; Beeckman, H.; Boeckx, P.; Huygens, D. Functional Community Structure of African Monodominant Gilbertiodendron Dewevrei Forest Influenced by Local Environmental Filtering. *Ecol. Evol.* **2017**, *7*, 295–304. [\[CrossRef\]](#) [\[PubMed\]](#)
29. Cassart, B.; Angbonga Basia, A.; Titeux, H.; Andivia, E.; Ponette, Q. Contrasting Patterns of Carbon Sequestration between Gilbertiodendron Dewevrei Monodominant Forests and Scorodophloeus Zenkeri Mixed Forests in the Central Congo Basin. *Plant Soil* **2017**, *414*, 309–326. [\[CrossRef\]](#)
30. Hart, T.B.; Hart, J.A.; Murphy, P.G. Monodominant and Species-Rich Forests of the Humid Tropics: Causes for Their Co-Occurrence. *Source Am. Nat.* **1989**, *133*, 613–633. [\[CrossRef\]](#)
31. Peh, K.S.H.; Sonké, B.; Séné, O.; Djuikouo, M.N.K.; Nguembou, C.K.; Taedoumg, H.; Begne, S.K.; Lewis, S.L. Mixed-Forest Species Establishment in a Monodominant Forest in Central Africa: Implications for Tropical Forest Invasibility. *PLoS ONE* **2014**, *9*, e97585. [\[CrossRef\]](#) [\[PubMed\]](#)
32. Roussel, J.R.; Auty, D.; Coops, N.C.; Tompalski, P.; Goodbody, T.R.H.; Meador, A.S.; Bourdon, J.F.; de Boissieu, F.; Achim, A. LidR: An R Package for Analysis of Airborne Laser Scanning (ALS) Data. *Remote Sens. Environ.* **2020**, *251*, 112061. [\[CrossRef\]](#)
33. Silva, C.A.; Valbuena, R.; Pinagé, E.R.; Mohan, M.; de Almeida, D.R.A.; North Broadbent, E.; Jaafar, W.S.W.M.; de Almeida Papa, D.; Cardil, A.; Klauber, C. ForestGapR: An r Package for Forest Gap Analysis from Canopy Height Models. *Methods Ecol. Evol.* **2019**, *10*, 1347–1356. [\[CrossRef\]](#)
34. Dubayah, R.; Blair, J.B.; Goetz, S.; Fatoyinbo, L.; Hansen, M.; Healey, S.; Hofton, M.; Hurtt, G.; Kellner, J.; Luthcke, S.; et al. The Global Ecosystem Dynamics Investigation: High-Resolution Laser Ranging of the Earth's Forests and Topography. *Sci. Remote Sens.* **2020**, *1*, 100002. [\[CrossRef\]](#)
35. de Conto, T.; Armston, J.; Dubayah, R. Characterizing the Structural Complexity of the Earth's Forests with Spaceborne Lidar. *Nat. Commun.* **2024**, *15*, 8116. [\[CrossRef\]](#) [\[PubMed\]](#)

36. Lang, N.; Jetz, W.; Schindler, K.; Wegner, J.D. A High-Resolution Canopy Height Model of the Earth. *Nat. Ecol. Evol.* **2023**, *7*, 1778–1789. [[CrossRef](#)] [[PubMed](#)]
37. Wan, L.; Ciaia, P.; de Truchis, A.; Sean, E.; Fischer, F.J.; Purnell, D.; Belouze, G.; Fayad, I.; Schwartz, M.; Xu, Y.; et al. Satellite-Based Mapping of Annual Canopy Height and Aboveground Biomass in African Dense Forests. *Front. Remote Sens.* **2025**, *6*, 1724950. [[CrossRef](#)]
38. Anser, G.P.; Anderson, C.B.; Martin, R.E.; Knapp, D.E.; Tupayachi, R.; Sinca, F.; Malhi, Y. Landscape-Scale Changes in Forest Structure and Functional Traits along Andes-to-Amazon Elevations Gradient. *Biogeosciences* **2014**, *11*, 843–856.
39. Xu, L.; Saatchi, S.S.; Shapiro, A.; Meyer, V.; Ferraz, A.; Yang, Y.; Bastin, J.F.; Banks, N.; Boeckx, P.; Verbeeck, H.; et al. Spatial Distribution of Carbon Stored in Forests of the Democratic Republic of Congo. *Sci. Rep.* **2017**, *7*, 15030. [[CrossRef](#)] [[PubMed](#)]
40. Likoko, B.; Mbifo, N.; Besango, L.; Totiwe, T.; Badjoko, D.; Likoko, A.; Botomo, A.; Litemandia, Y.; Posho, N.; Alongo, L.; et al. Climate Change for Yangambi Forest Region, DR Congo. *J. Aquat. Sci. Oceanogr.* **2019**, *1*, 1–10.
41. Kasongo Yakusu, E.; Van Acker, J.; Van de Vyver, H.; Bourland, N.; Mbifo Ndiapo, J.; Besango Likwela, T.; Lokonda Wa Kipifo, M.; Mbuya Kankolongo, A.; Van den Bulcke, J.; Beeckman, H.; et al. Ground-Based Climate Data Show Evidence of Warming and Intensification of the Seasonal Rainfall Cycle during the 1960–2020 Period in Yangambi, Central Congo Basin. *Clim. Change* **2023**, *176*, 142. [[CrossRef](#)]
42. Kearsley, E. Carbon Storage and Functional Diversity of Tropical Rainforest in the Congo Basin. Ph.D. Thesis, Ghent University, Ghent, Belgium, 2015.
43. d'Oliveira, M.V.N.; Reutebuch, S.E.; McGaughey, R.J.; Andersen, H.E. Estimating Forest Biomass and Identifying Low-Intensity Logging Areas Using Airborne Scanning Lidar in Antimary State Forest, Acre State, Western Brazilian Amazon. *Remote Sens. Environ.* **2012**, *124*, 479–491. [[CrossRef](#)]
44. Boeckx, P.; Steppe, K.; Verbeeck, H.; Beeckman, H.; Bogaert, J.; Defourny, P.; Dessein, S.; Verheyen, E.; Leirs, H. *Congo Basin Integrated Monitoring for Forest Carbon Mitigation and Biodiversity-COBIMFO. Final Report*; Belgian Science Policy: Brussels, Belgium, 2017.
45. Maitner, B. EnquistLab/RTNRS: CRAN Release 0.3.6 (v0.3.6). [Computer software]. *Zenodo* **2024**. [[CrossRef](#)]
46. Bénédet, F.; Gourlet-Fleury, S.; Allah-Barem, F.; Baya, F.; Beina, D.; Cornu, G.; Dimanche, L.; Dubiez, É.; Forni, É.; Freycon, V.; et al. 40 Years of Forest Dynamics and Tree Demography in an Intact Tropical Forest at M'Baïki in Central Africa. *Sci. Data* **2024**, *11*, 734. [[CrossRef](#)] [[PubMed](#)]
47. Clark, D.B.; Clark, D.A.; Oberbauer, S.F.; Kellner, J.R. Multidecadal Stability in Tropical Rain Forest Structure and Dynamics across an Old-Growth Landscape. *PLoS ONE* **2017**, *12*, e0183819. [[CrossRef](#)] [[PubMed](#)]
48. Viennois, G.; Tuleu, H.; Tresson, P.; Ploton, P.; Coutron, P.; Barbier, N. Sentinel-2 Forest Typology Mapping in Central Africa: Assessing Deep Learning and Image Preprocessing Effects. *Front. Remote Sens.* **2025**, *6*, 1682132. [[CrossRef](#)]
49. Denslow, J.S.; Ellison, A.M.; Sanford, R.E. Treefall Gap Size Effects on Above- and below-Ground Processes in a Tropical Wet Forest. *J. Ecol.* **1998**, *86*, 597–609. [[CrossRef](#)]
50. Brokaw, N.V.L. The Definition of Treefall Gap and Its Effect on Measures of Forest Dynamics. *Biotropica* **1982**, *14*, 158–160. [[CrossRef](#)]
51. Schnitzer, S.A.; Carson, W.P. Treefall Gaps and the Maintenance of Species Diversity in a Tropical forest. *Ecology* **2001**, *82*, 913–919. [[CrossRef](#)]
52. Dalagnol, R.; Wagner, F.H.; Galvão, L.S.; Streher, A.S.; Phillips, O.L.; Gloor, E.; Pugh, T.A.M.; Ometto, J.P.H.B.; Aragão, L.E.O.C. Large-Scale Variations in the Dynamics of Amazon Forest Canopy Gaps from Airborne Lidar Data and Opportunities for Tree Mortality Estimates. *Sci. Rep.* **2021**, *11*, 1388. [[CrossRef](#)] [[PubMed](#)]
53. Hunter, M.O.; Keller, M.; Morton, D.; Cook, B.; Lefsky, M.; Ducey, M.; Saleska, S.; De Oliveira, R.C.; Schietti, J.; Zang, R. Structural Dynamics of Tropical Moist Forest Gaps. *PLoS ONE* **2015**, *10*, e0132144. [[CrossRef](#)] [[PubMed](#)]
54. Reis, C.R.; Jackson, T.D.; Gorgens, E.B.; Dalagnol, R.; Jucker, T.; Nunes, M.H.; Ometto, J.P.; Aragão, L.E.O.C.; Rodriguez, L.C.E.; Coomes, D.A. Forest Disturbance and Growth Processes Are Reflected in the Geographical Distribution of Large Canopy Gaps across the Brazilian Amazon. *J. Ecol.* **2022**, *110*, 2971–2983. [[CrossRef](#)]
55. Blanchard, E.; Birnbaum, P.; Ibanez, T.; Boutreux, T.; Antin, C.; Ploton, P.; Vincent, G.; Pouteau, R.; Vandrot, H.; Hequet, V.; et al. Contrasted Allometries between Stem Diameter, Crown Area, and Tree Height in Five Tropical Biogeographic Areas. *Trees-Struct. Funct.* **2016**, *30*, 1953–1968. [[CrossRef](#)]
56. Hijmans, R. Terra: Spatial Data Analysis. R Package Version 1.8-54. 2025. Available online: <https://CRAN.R-project.org/package=terra> (accessed on 3 June 2026).
57. Pebesma, E. Simple Features for R: Standardized Support for Spatial Vector Data. *R J.* **2018**, *10*, 439–446. [[CrossRef](#)]
58. Colwell, R.K.; Chao, A.; Gotelli, N.J.; Lin, S.Y.; Mao, C.X.; Chazdon, R.L.; Longino, J.T. Models and Estimators Linking Individual-Based and Sample-Based Rarefaction, Extrapolation and Comparison of Assemblages. *J. Plant Ecol.* **2012**, *5*, 3–21. [[CrossRef](#)]
59. Katembo, J.M.; Libalah, M.B.; Boyemba, F.B.; Dauby, G.; Barbier, N. Multiple Stable Dominance States in the Congo Basin Forests. *Forests* **2020**, *11*, 553. [[CrossRef](#)]

60. Jucker, T.; Bongalov, B.; Burslem, D.F.R.P.; Nilus, R.; Dalponte, M.; Lewis, S.L.; Phillips, O.L.; Qie, L.; Coomes, D.A. Topography Shapes the Structure, Composition and Function of Tropical Forest Landscapes. *Ecol. Lett.* **2018**, *21*, 989–1000. [[CrossRef](#)] [[PubMed](#)]
61. Hubau, W.; Lewis, S.L.; Phillips, O.L.O.L.; Affum-Baffoe, K.K.; Beeckman, H.; Cuni-Sanchez, A.; Daniels, A.K.; Ewango, C.E.N.; Fauset, S.; Mukinzi, J.M.; et al. Asynchronous Carbon Sink Saturation in African and Amazonian Tropical Forests. *Nature* **2020**, *579*, 80–87. [[CrossRef](#)] [[PubMed](#)]
62. Glick, H.B.; Umunay, P.M.; Makana, J.R.; Thomas, S.C.; Reuning-Scherer, J.D.; Gregoire, T.G. Developmental Dynamics of Gilbertiodendron Dewevrei (Fabaceae) Drive Forest Structure and Biomass in the Eastern Congo Basin. *Forests* **2021**, *12*, 738. [[CrossRef](#)]
63. Glick, H.B.; Umunay, P.M.; Makana, J.R.; Tomlin, C.D.; Reuning-Scherer, J.D.; Gregoire, T.G. The Spatial Propagation and Increasing Dominance of Gilbertiodendron Dewevrei (Fabaceae) in the Eastern Congo Basin. *PLoS ONE* **2023**, *18*, e0275519. [[CrossRef](#)] [[PubMed](#)]
64. Maley, J.; Doumenge, C.; Giresse, P.; Mahé, G.; Philippon, N.; Hubau, W.; Lokonda, M.O.; Tshibamba, J.M.; Chepstow-Lusty, A. Late Holocene Forest Contraction and Fragmentation in Central Africa. *Quat. Res.* **2018**, *89*, 43–59. [[CrossRef](#)]
65. Burns, P.; Hakkenberg, C.R.; Goetz, S.J. Multi-Resolution Gridded Maps of Vegetation Structure from GEDI. *Sci. Data* **2024**, *11*, 881. [[CrossRef](#)] [[PubMed](#)]
66. Quegan, S.; Le Toan, T.; Chave, J.; Dall, J.; Exbrayat, J.F.; Minh, D.H.T.; Lomas, M.; D'Alessandro, M.M.; Paillou, P.; Papathanassiou, K.; et al. The European Space Agency BIOMASS Mission: Measuring Forest above-Ground Biomass from Space. *Remote Sens. Environ.* **2019**, *227*, 44–60. [[CrossRef](#)]
67. Picard, N. Dispositifs Permanents Pour Le Suivi Des Forêts En Afrique Centrale: Un État Des Lieux. *Cirad* **2007**, 1–38. Available online: <https://hal.science/cirad-00146347v1> (accessed on 3 June 2026).
68. Hubell, S.P.; Foster, R.B.; O'Brien, S.T.; Harms, K.E.; Condit, R.; Wechsler, B.; Wright, S.J.; Loo de Lao, S. Light Gap Disturbances Recruitment Limitation and Tree Diversity in a Neotropical Forest. *Science* **1999**, *283*, 554–557. [[CrossRef](#)] [[PubMed](#)]
69. Long, W.; Zang, R.; Ding, Y.; Huang, Y. Effects of Competition and Facilitation on Species Assemblage in Two Types of Tropical Cloud Forest. *PLoS ONE* **2013**, *8*, e60252. [[CrossRef](#)] [[PubMed](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.