

## Anthropogenic disturbance regimes reduce biomass and alter floristic composition in montane forests of Kahuzi-Biega National Park, Eastern Democratic Republic of the Congo

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### ABSTRACT

Montane forests of Kahuzi-Biega National Park (PNKB), located in the Albertine Rift, represent a major reservoir of biodiversity and carbon, yet they are increasingly affected by anthropogenic disturbances despite their protected status. This study assessed how anthropogenic disturbances are spatially organized and how they affect forest structure, aboveground biomass, floristic diversity, and community composition in the high-altitude montane forests of PNKB. Specifically, we examined whether disturbances form non-random spatial regimes and whether their effects on floristic composition operate through both structural changes and direct ecological filtering. A total of 63 plots (0.25 ha each) were established along nine 1-km transects in the high-altitude zone, with seven plots per transect spaced approximately 100 m apart. Each transect represented a disturbance gradient ranging from more accessible areas to more remote locations. Disturbances were characterized using field-based indicators and analyzed through similarity indices and hierarchical clustering, while their effects were assessed using non-parametric tests and multivariate analyses (NMDS, PERMANOVA, dbRDA). Similarity analyses revealed a non-random organization of disturbances, dominated by the co-occurrence of logging, charcoal production, and agriculture. Disturbed plots exhibited significant reductions in tree density (−42%), basal area (−54%), and aboveground biomass (−51%; 53 vs 109 Mg ha<sup>−1</sup>,  $p < 0.001$ ). Species richness was lower ( $p = 0.047$ ), and floristic composition differed significantly among disturbance categories (PERMANOVA,  $p < 0.01$ ). Disturbances independently explained 10% of the variation in floristic composition, while the full model accounted for 31%, indicating both structural and directional effects on plant assemblages. These findings demonstrate that diffuse but cumulative disturbances can act as major structuring forces, capable of durably reshaping the ecological trajectory of tropical montane forests, even within protected areas.

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## 1. Introduction

The Albertine Rift mountain region is recognized as one of the world's major centers of biodiversity, hosting approximately 7500 plant and animal species, of which >1000 are endemic (Plumptre et al., 2003; Plumptre et al., 2007; Plumptre et al., 2015). It is identified as one of the 25 global biodiversity hotspots (Skarbek, 2008) and constitutes an important refuge for numerous rare and threatened species with restricted geographic ranges (Soh et al., 2019; Yaffar et al., 2023). Within this region, Kahuzi-Biega National Park (PNKB), located in eastern Democratic Republic of the Congo (DRC) and designated as a UNESCO World Heritage Site, represents a priority conservation area (the second most important site in the Albertine Rift) due to its exceptional species richness and the key role of its montane forests in carbon storage (Cuni-Sanchez et al., 2021; Plumptre et al., 2015). The park harbours a high proportion of endemic and threatened species, notably Grauer's gorilla (*Gorilla beringei graueri*) (Hart and Hall, 1996; Plumptre et al., 2015), and still preserves extensive forest blocks with high ecological integrity (Potapov et al., 2017).

Despite its protected status, PNKB is increasingly subjected to anthropogenic pressures, particularly in its peripheral and more accessible areas, generally located in the high-altitude zone (Cirezi et al., 2025a; UNESCO, 2024). Deforestation and forest degradation in PNKB result from a combination of direct drivers, including logging, charcoal production, agriculture, fire, and artisanal mining, largely driven by urban energy and resources demand (Ingram et al., 2011), as well as indirect drivers such as rapid population growth and persistent insecurity (Butsic et al., 2015; Draulans and Van Krunkelsven, 2002; Hosonuma et al., 2012; Spira et al., 2019). In contrast to large-scale industrial deforestation fronts in the Amazon and Southeast Asia (Buchadas et al., 2022; Skidmore et al., 2021; Vijay et al., 2016), forest degradation in the Congo Basin is often driven by small-scale, recurrent, and spatially diffuse disturbances (Mertz et al., 2012; Tyukavina et al., 2018). Although less visible, these disturbances can have substantial cumulative ecological effects, particularly in the PNKB landscape (Cirezi et al., 2025b).

These disturbances are likely to profoundly alter forest structure by reducing the density of large trees, basal area, and aboveground biomass, thereby compromising carbon storage (Baccini et al., 2017; Depecker et al., 2021; Dupuis et al., 2025; Fayolle et al., 2018). They also modify floristic composition by favouring disturbance-tolerant species at the expense of late-successional species, potentially leading to progressive homogenisation of plant assemblages (Cirimwami, 2021; Mangaza et al., 2022; Muhanguzi et al., 2007; Ouédraogo et al., 2011). Montane ecosystems are particularly sensitive to repeated disturbances because steep slopes, fragile soils, and strong environmental gradients can limit structural and floristic recovery (Cuni-Sanchez et al., 2016; Hall et al., 2011).

In the PNKB landscape, existing disturbance assessments have primarily relied on remote-sensing approaches, which are valuable for detecting broad forest-cover transitions but remain limited in capturing fine-scale, recurrent, and under-canopy disturbances such as selective logging, charcoal production, hunting signs, or small artisanal mining sites (Bullock et al., 2020; Cirezi et al., 2025a; Kabonyi et al., 2011). By using field-based indicators recorded at the plot level, our approach allows direct identification of disturbance types, their co-occurrence within plots, and their association with measured forest structure, aboveground biomass, taxonomic diversity, and floristic composition. This provides a more mechanistic assessment of how diffuse disturbances affect montane forest communities, complementing previous remote-sensing studies and addressing the lack of integrated field evidence in protected montane forests.

In protected montane forests, where disturbances are often diffuse, recurrent, and spatially heterogeneous, their structuring role in forest dynamics remains insufficiently quantified, although they are recognized as central processes influencing ecosystem structure, composition,

and functioning (Crausbay and Martin, 2016; Tweiten et al., 2014). In particular, it remains unclear whether these pressures constitute only localised alterations or represent forces capable of durably reshaping the ecological trajectory of plant communities. Understanding the cumulative, structural, and directional nature of these disturbances is essential for assessing the resilience of tropical montane ecosystems and the capacity of protected areas to maintain their ecological functions under persistent human pressures.

This study assessed the effects of anthropogenic disturbances on montane forests in PNKB. Specifically, we aimed to: (i) identify spatial patterns and disturbance regimes; (ii) quantify the effects of disturbances on forest structure, aboveground biomass, and floristic diversity; and (iii) determine whether changes in floristic composition are driven by structural degradation, direct ecological filtering, or both.

## 2. Materials and methods

### 2.1. Study area

Kahuzi-Biega National Park (PNKB) is located in eastern Democratic Republic of the Congo between North-Kivu, South-Kivu and Maniema provinces (Fig. 1a) covering approximately 6700 km<sup>2</sup> (Hall et al., 1997; Spira et al., 2018). The park exhibits a pronounced altitudinal gradient, ranging from approximately 600 m in the western lowlands to over 3300 m at Mount Kahuzi, encompassing both lowland GuineoCongolian forests and montane Afro-alpine ecosystems (ICCN-KBNP, 2010; Spira et al., 2019). The climate is tropical humid, with mean annual rainfall ranging between 1800 and 2000 mm and temperatures decreasing with increasing altitude (Balezi, 2012; Masumbuko, 2010).

The park is recognised as a key biodiversity area (IUCN, 2022) and was also designated as a Centre of Plant Diversity by IUCN and WWF in 1994, with at least 1178 plant species recorded in the high-altitude zone alone. It harbours 136 mammal species, including Grauer's gorilla (*Gorilla beringei graueri*), an endemic and critically endangered species, as well as 349 bird species (Fischer et al., 1993; Plumptre et al., 2003; IUCN, 2017; UNESCO, 2025). The high-altitude zone, recognised for its exceptional biodiversity, is highly exposed to anthropogenic pressures (Cirezi et al., 2025a; Plumptre et al., 2003) and was selected to assess the effects of disturbances on forest structure and floristic composition in montane forests (Fig. 1b).

### 2.2. Sampling design, disturbance assessment and dendrometric inventory

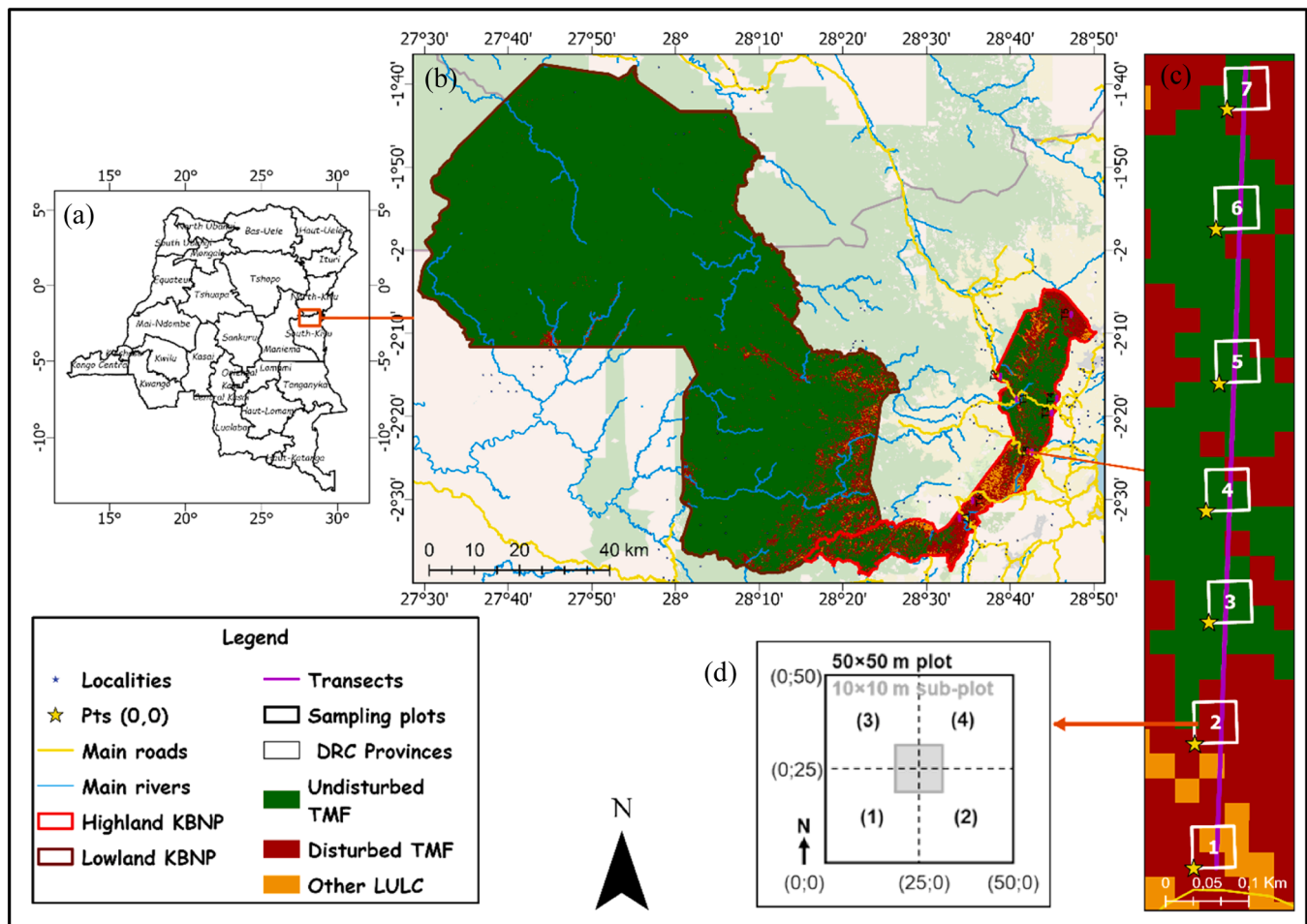
#### 2.2.1. Sampling design

A linear transect-based sampling design was implemented to capture a gradient of disturbance, ranging from forest edges and accessible areas (i.e. zones close to roads, access tracks, villages and park boundaries) to less accessible interior forest sectors (Fig. 1b). Transect locations were defined prior to fieldwork based on (i) transition zones between disturbed and undisturbed forests identified through remote sensing over the 1990–2024 period, (ii) accessibility (roads, trails, villages), and (iii) previous studies highlighting disturbance hotspots within PNKB (Cirezi et al., 2025a; Malhi et al., 2013; Vancutsem et al., 2021). This stratification aimed to capture contrasting levels of human pressure without a priori assumptions regarding the final disturbance status of the plots.

Nine transects were established, each comprising seven square plots of 0.25 ha (50 × 50 m), spaced approximately 100 m apart (Fig. 1c), giving a total of 63 sampled plots. Based on field-recorded disturbance indicators, 42 plots were classified as disturbed and 21 as undisturbed. Each plot was labelled, georeferenced, oriented to the north, and recorded using a GPS in tracking mode during field surveys.

#### 2.2.2. Disturbance inventory

Anthropogenic disturbances were recorded in each plot based on visible field indicators (Table 1), as identified and characterized in



**Fig. 1.** Study area and sampling design in Kahuzi-Biega National Park (PNKB), eastern Democratic Republic of the Congo. (a) Location of Kahuzi-Biega National Park (PNKB) across the provinces of North Kivu, South Kivu, and Maniema in eastern Democratic Republic of the Congo (DRC). (b) Distribution of disturbed and undisturbed tropical moist forests (TMF and UTMF) from 1990 to 2024 in PNKB (adapted from [Vancutsem et al., 2021](#)), and spatial distribution of sampled transects located along disturbance boundaries in the high-altitude zone. The sampled plots were located between 1920 and 2400 m of altitude. (c) Arrangement of sampling plots along transects, including starting points of sampling (pt s(0,0)). (d) Layout of sampling plots.

previous studies ([Gardner et al., 2009](#); [Mangaza et al., 2022](#); [Rakotondraso, 2012](#)). Data were recorded in binary form (presence/absence) for each disturbance indicator. Plots were subsequently classified as disturbed or undisturbed based on the presence or absence of observed disturbance factors.

In addition to the binary classification of plots as disturbed or undisturbed, disturbance richness was calculated for each plot as the total number of disturbance types recorded. This cumulative disturbance score was used to represent the intensity of multiple co-occurring pressures and to avoid reducing disturbance effects to a simple presence/absence contrast.

### 2.2.3. Dendrometric inventory

Within each plot, all trees with a diameter at breast height (DBH)  $\geq 10$  cm were located, measured, and identified, following standard protocols used in tropical forest inventories ([Chave et al., 2005](#); [Cuni-Sanchez et al., 2016](#); [Phillips et al., 2002](#)). Each plot was subdivided into four subplots according to the design shown in [Fig. 1d](#). Within each subplot, all trees meeting the DBH threshold were measured and identified.

Each tree was assigned a unique identifier (tree ID) and its position recorded using local coordinates (x, y) relative to a reference origin point (0,0). Diameter was measured at 1.30 m above ground level (or 30–50 cm above any deformation) using a diameter tape. For multi-stemmed individuals, each stem with DBH  $\geq 10$  cm was measured

separately, with the point of measurement (POM) recorded.

Tree height was measured using a laser hypsometer Forestry Pro II for a subsample of 837 trees out of 3120 individuals. The subsample was stratified by plot and diameter class, with one tree selected per 10 cm DBH class in each plot whenever possible. This procedure ensured that height measurements covered the full range of tree sizes and both disturbed and undisturbed plots. Species were identified in the field by an experienced team of botanists. Unidentified individuals were collected as botanical specimens, labelled, and later identified at the CRSN Lwiro herbarium based on plot reference and tree number.

Before conducting the dendrometric analyses, several data harmonization steps were performed. Species names were checked and standardized using the [African Plant Database](#). Wood density values were then assigned to each taxon using the tropical African wood density database, accessed through the Biomass package in RStudio ([Chave et al., 2009](#); [Flores and Coomes, 2010](#); [Réjou-Méchain et al., 2017](#)).

When species-level wood density values were unavailable, the corresponding genus-level mean was used. For taxa identified only to genus or family level, the mean wood density of the respective taxonomic group was assigned following [Flores and Coomes \(2010\)](#). When no taxon-specific value was available, the overall mean wood density from the database was used.

**Table 1**

Illustration of selected disturbance factors and their corresponding field indicators recorded in sampled plots in the high-altitude zone of Kahuzi-Biega National Park. (Adapted from (Gardner et al., 2009; Rakotondraso, 2012). Legend: A: Cuted and abandoned tree trunk located in the Transect 5, Plot 4, Lat:  $-2.129940^{\circ}$ , Long:  $28.78809^{\circ}$ ; B: Charcoal kiln and filled charcoal bag located in the Transect 5, Plot 1, Lat:  $-2.132899^{\circ}$ , Long:  $28.78814^{\circ}$ ; C: Bean field located in the Transect 6, Plot 6, Lat:  $-2.504027^{\circ}$ , Long:  $28.591778^{\circ}$ ; D: Burn marks on a tree located in the Transect 5, Plot 1, Lat:  $-2.132899^{\circ}$ , Long:  $28.78814^{\circ}$ ; E: Small settlement within the park located in the Transect 5, Plot 6, Lat:  $-2.125860^{\circ}$ , Long:  $28.788306^{\circ}$ ; F: Stone quarry located in the Transect 8, Plot 5, Lat:  $-2.132988^{\circ}$ , Long:  $28.78809^{\circ}$ ; G: National Road 2 crossing the park located in the Transect 2, Plot 3, Lat:  $-2.254418^{\circ}$ , Long:  $28.646843^{\circ}$ ; H: Game trap located in the Transect 2, Plot 4, Lat:  $-2.251664^{\circ}$ , Long:  $28.647525^{\circ}$ ; Photos: Nadège Cirezi.

| No | Disturbance factor             | Indicators                                                                    | Illustration                                                                          |
|----|--------------------------------|-------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|
| 1  | <b>Logging</b>                 | Presence of stumps (with or without regrowth); presence of felled tree trunks |    |
| 2  | <b>Charcoal production</b>     | Presence of charcoal kilns or other signs of carbonisation                    |    |
| 3  | <b>Agriculture</b>             | Presence of cultivated fields; presence of fallow land                        |   |
| 4  | <b>Vegetation fires</b>        | Presence of fire traces (burn marks on trees, charred trunks)                 |  |
| 5  | <b>Settlements / campfires</b> | Presence of houses, huts, tents, or campfires                                 |  |

(continued on next page)

Table 1 (continued)

| No | Disturbance factor           | Indicators                                                      | Illustration                                                                         |
|----|------------------------------|-----------------------------------------------------------------|--------------------------------------------------------------------------------------|
| 6  | Mining                       | Presence of small-scale mining sites and artisanal mining camps |   |
| 7  | Accessibility (roads/trails) | Presence of roads, tracks, or collection paths                  |   |
| 8  | Hunting                      | Presence of traps; presence of firearm cartridges               |  |

2.3. Data analysis

Given that plots were arranged along transects, analyses accounted for potential spatial dependence. Transects were established across ecologically contrasting areas, and plots were regularly spaced to capture landscape gradients rather than replicate the same micro-site. Accordingly, parameters were analysed at the landscape scale rather than as strictly independent fine-scale observations. Analyses were conducted using the R (4.4.2 version) packages *vegan* (Oksanen et al., 2020), *iNEXT* (Hsieh et al., 2016), *ggplot2* (Wickham, 2016), and *dplyr* (Dimitris et al., 2023), as well as the Python libraries *pandas* (McKinney, 2010), *scipy*, *statsmodels* (Seabold and Perktold, 2010), and *scikit-bio*.

All analyses were conducted at the plot level, except disturbance frequencies, which were summarized at the transect level. Prior to group comparisons, normality and homogeneity of variance were assessed using Shapiro–Wilk and Levene tests, respectively. Because several structural and diversity variables did not meet parametric assumptions, non-parametric Mann–Whitney U tests were used to compare disturbed and undisturbed plots. Results of assumption tests are provided in **Appendix 1**.

2.3.1. Identification of disturbance regimes

To assess spatial heterogeneity and identify potential disturbance hotspots, relative frequencies were calculated as the proportion of affected plots per transect (Musavandalo et al., 2025). Beyond this aggregated description, non-random disturbance regimes were examined at the plot level using a binary presence/absence matrix (plot × disturbance type), where a disturbance type was coded as present when at least one corresponding field indicator was observed.

Dissimilarity among plots was quantified using Jaccard distance, which is appropriate for binary data and excludes joint absences.

Agglomerative hierarchical clustering with average linkage was then applied to identify groups of plots sharing similar disturbance combinations (Chung et al., 2019). The robustness of the three-cluster solution was assessed using average silhouette width and ecological interpretability of the resulting groups. The  $k = 3$  partition provided the most meaningful separation of disturbance regimes, distinguishing weakly disturbed plots, plots dominated by poaching/mining signals, and plots affected by active forest degradation (Legendre and Legendre, 2012; McCune et al., 2002).

2.3.2. Effects of disturbances on forest structure and diversity

Forest structure was quantified per 0.25 ha plot and standardized to a per-hectare basis. Structural variables included stem density (trees ha<sup>-1</sup>), basal area (m<sup>2</sup> ha<sup>-1</sup>), Lorey’s height (m), and mean wood density (g cm<sup>-3</sup>). Basal area was calculated from DBH for each tree and summed at the plot level. Lorey’s height was computed as a basal-area-weighted mean height.

Aboveground biomass was estimated at the tree level using the pan-tropical allometric model of Chave et al. (2014), incorporating DBH, wood density, and tree height. Tree height was measured for a sub-sample of individuals using a laser hypsometer; for trees without measured height, predicted values from local height–diameter models were used. Candidate height–diameter models were fitted following (Fayolle et al., 2018), and compared only when based on the same dataset, response scale, and likelihood basis. The final model was selected using comparable AIC values, residual standard error, and biological plausibility(Appendix 2).

Taxonomic diversity was evaluated at the plot level using observed species richness (Sobs), Fisher’s alpha, Shannon index (H’), Simpson index (1 – D), and Pielou’s evenness index (J) (Magurran, 2021). Species dominance was estimated from the proportion of stems per species,

and the five most abundant taxa were identified separately for disturbed and undisturbed plots (Mangaza et al., 2022).

Species accumulation curves were generated with iNEXT using 999 permutations to assess sampling completeness (Hsieh et al., 2016). Floristic composition was analysed using NMDS based on Bray–Curtis dissimilarity (Legendre and Legendre, 2012), and differences between disturbance categories were tested using PERMANOVA with explained variance reported as  $R^2$  (Oksanen et al., 2020). Multivariate significance was assessed using permutation-based procedures, which do not require strict normality assumptions.

### 2.3.3. Indirect and direct effects on floristic composition

Relationships between structural attributes and diversity indices were quantified using Spearman rank correlations, with false discovery rate correction applied for multiple (Benjamini and Hochberg, 1995). To distinguish indirect and direct pathways of disturbance effects, floristic composition was further examined using distance-based redundancy analysis (dbRDA), with structural variables, disturbance indicators, and a cumulative disturbance index included as explanatory variables. The cumulative disturbance index was defined as the number of disturbance types recorded per plot and represented additive pressure intensity, following approaches used in montane systems (Ensslin et al., 2015). Model significance and individual terms were tested using

permutation-based ANOVA with 999 permutations (Legendre and Anderson, 1999).

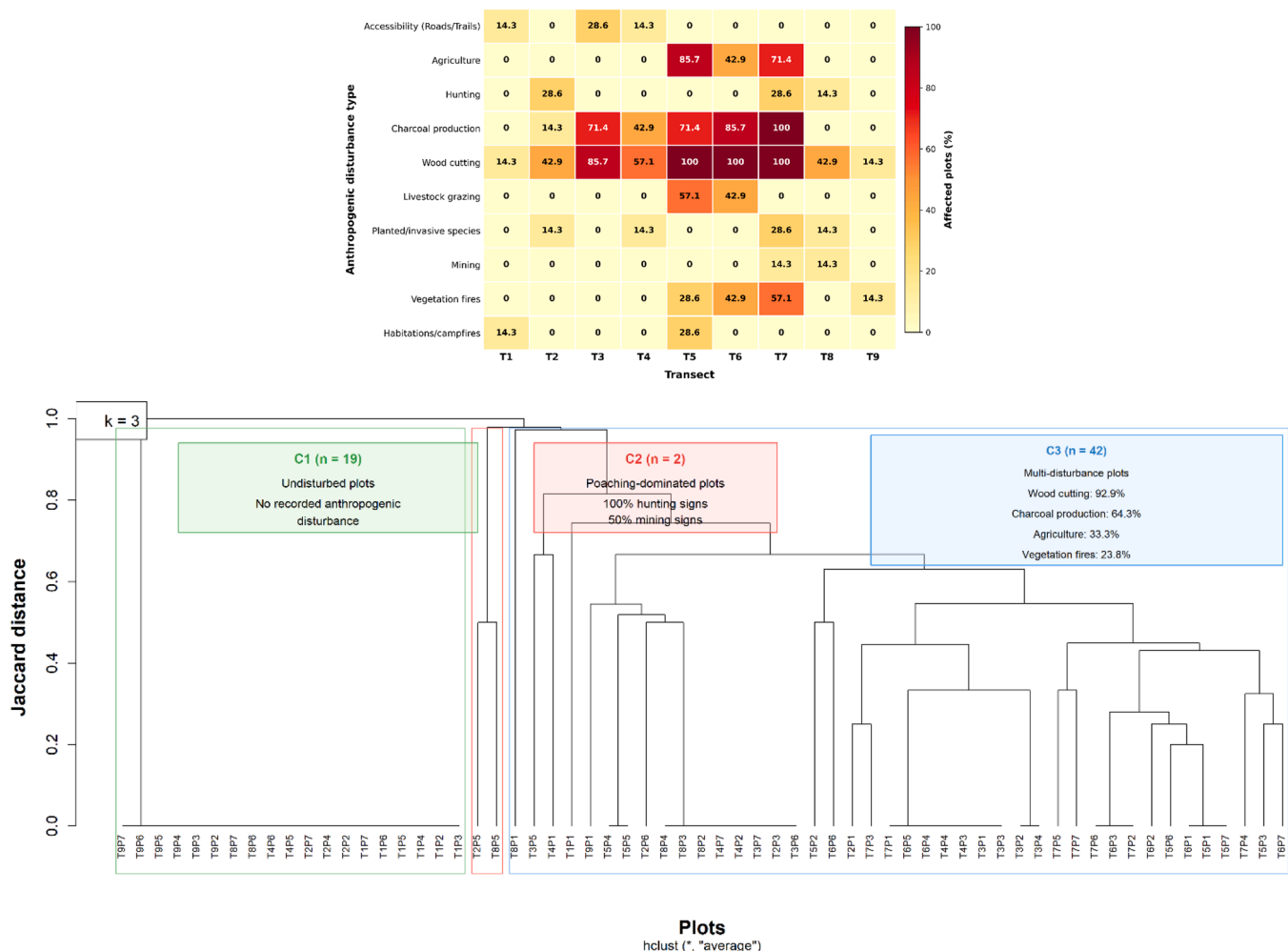
## 3. Results

### 3.1. Spatial heterogeneity and anthropogenic disturbance regimes

Relative frequencies by transect indicate that logging, charcoal production, and agriculture constitute the dominant pressures, whereas fires, grazing, and accessibility occur more locally (Fig. 2a). This distribution highlights a high degree of spatial heterogeneity in disturbances across the study area.

Hierarchical clustering based on Jaccard dissimilarity among plots revealed three distinct disturbance regimes. The first cluster comprises plots that are weakly or not disturbed, characterised by the near absence of anthropogenic indicators. The second corresponds to a specific regime dominated by poaching (100% of plots) and, to a lesser extent, artisanal mining (50%), with no notable co-occurrence with other pressures. The third represents an active forest degradation regime, characterised by a strong co-occurrence of logging (92.9%), charcoal production (64.3%), agriculture (33.3%), and fires (23.8%).

The cumulative disturbance index varied strongly among transects, confirming that disturbance intensity was not captured by the



**Fig. 2.** a. Heatmap of relative frequencies (%) of anthropogenic disturbances by transect (T1–T9) in Kahuzi-Biega National Park (PNKB). Values in each cell represent the percentage of plots exhibiting a given disturbance within each transect, and colour intensity reflects the frequency of these disturbances. b. Dendrogram resulting from hierarchical clustering of plots based on Jaccard distance, illustrating the non-random structuring of anthropogenic disturbances in the high-altitude zone of Kahuzi-Biega National Park (PNKB). Plots were grouped according to the similarity of their disturbance combinations (presence/absence). The vertical axis represents Jaccard dissimilarity between plots. Three main clusters can be distinguished, corresponding to contrasting disturbance regimes.

disturbed/undisturbed classification alone (Appendix 3). The highest mean CDI values were observed in T7 (26.14), T6 (25.14), and T4 (23.71), whereas the lowest values occurred in T1 (0.71), T8 (1.71), and T9 (1.71). Maximum CDI values also indicated localized hotspots of cumulative pressure, particularly in T4 (96), T7 (44), T6 (41), and T3 (27). The disturbance types contributing most to cumulative intensity were wood cutting, vegetation fires, charcoal production, livestock grazing, and agriculture. These results indicate that disturbance regimes represent gradients of cumulative pressure rather than a simple binary contrast between disturbed and undisturbed plots.

### 3.2. Structural simplification and floristic reorganisation

Disturbed plots exhibit marked structural simplification compared to undisturbed plots (Table 2). Stem density and basal area are significantly reduced ( $p \leq 0.001$ ), resulting in an approximately 50% decrease in aboveground biomass ( $p < 0.001$ ). In contrast, mean stand height and average wood density do not differ significantly between forest conditions ( $p > 0.05$ ), indicating that disturbances primarily affect tree abundance and space occupation rather than average functional traits. At the plot scale, species richness is significantly lower in disturbed plots ( $p < 0.05$ ). However, diversity indices incorporating evenness (Shannon, Simpson, Pielou) show no significant differences, suggesting a reduction in the number of species without major changes in relative abundance

**Table 2**

Mean values ( $\pm$  standard deviation) of forest structural attributes, aboveground biomass, and taxonomic diversity in disturbed and undisturbed plots of Kahuzi-Biega National Park (PNKB).  $p$ -values correspond to statistical comparisons between the two plot categories. Dominant species refer to the five taxa with the highest number of individuals in each forest condition.

| Forest structure indicators                                  | Disturbed plots   | Undisturbed plots | Mann–Whitney U ( $p$ -value) |
|--------------------------------------------------------------|-------------------|-------------------|------------------------------|
| Density (trees ha <sup>-1</sup> )                            | 167,5 $\pm$ 172,3 | 286,5 $\pm$ 137,8 | 0001**                       |
| Lorey's height (m)                                           | 14,7 $\pm$ 2,8    | 15,2 $\pm$ 2,2    | 0,379ns                      |
| Basal area (m <sup>2</sup> ha <sup>-1</sup> )                | 9,23 $\pm$ 10,0   | 20,2 $\pm$ 12,6   | <0001***                     |
| Aboveground biomass (Mg ha <sup>-1</sup> )                   | 53,1 $\pm$ 67,8   | 109,4 $\pm$ 82,7  | <0001***                     |
| Wood density (g cm <sup>-3</sup> )                           | 0529 $\pm$ 0068   | 0506 $\pm$ 0051   | 0,279ns                      |
| Taxonomic diversity indicators                               |                   |                   |                              |
| Species richness (S)                                         | 9,05 $\pm$ 7,20   | 11,74 $\pm$ 6,37  | 0047*                        |
| Singletons (unique species)                                  | 3,98 $\pm$ 2,87   | 3,53 $\pm$ 3,84   | 0,164ns                      |
| Doubletons                                                   | 1,29 $\pm$ 1,63   | 1,47 $\pm$ 1,22   | 0,285ns                      |
| Shannon diversity (H')                                       | 1,58 $\pm$ 0,66   | 1,89 $\pm$ 0,55   | 0,11ns                       |
| Simpson diversity (1-D)                                      | 0,69 $\pm$ 0,21   | 0,77 $\pm$ 0,14   | 0,141ns                      |
| Evenness (J)                                                 | 0,78 $\pm$ 0,23   | 0,80 $\pm$ 0,11   | 0,646ns                      |
| Top 5 dominant species (number of individuals)               |                   |                   |                              |
| <i>Agauria salicifolia</i> (Comm. ex Lam.) Hook. f. ex Oliv. | 148               | -                 |                              |
| <i>Hagenia abyssinica</i> J.F. Gmel.                         | 122               | -                 |                              |
| <i>Maesa lanceolata</i> Forssk.                              | 157               | -                 |                              |
| <i>Neobutonia macrocalix</i> Pax                             | 120               | -                 |                              |
| <i>Macaranga mildbraediana</i> Pax                           | 113               | 359               |                              |
| <i>Polyscias fulva</i> (Hiern) Harms                         | -                 | 88                |                              |
| <i>Syzygium guineense</i> (Willd.) DC.                       | -                 | 94                |                              |
| <i>Tabernaemontana</i> L.                                    | -                 | 82                |                              |

$p$ -values thresholds significance:  $p \geq 0.05$ ns: no statistical evidence of an effect,  $p < 0.05$ \*: moderate evidence,  $p < 0.01$ \*\* : Strong evidence,  $p < 0.001$ \*\*\*:very strong evidence.

distributions. Species accumulation curves (Fig. 3b) confirm this trend, with higher cumulative richness observed in undisturbed plots for a comparable sampling effort.

Floristic composition differed significantly between disturbed and undisturbed plots (PERMANOVA,  $p = 0.001$ ), but the proportion of explained variance was very low ( $R^2 = 0.015$ ). Accordingly, this result should be interpreted as evidence of a weak compositional signal rather than a clear separation between groups. The NMDS ordination based on Bray–Curtis dissimilarity showed only partial separation, with substantial overlap between disturbed and undisturbed plots (Fig. 3a). The relatively high stress value (0.295) further indicates that the two-dimensional ordination provides a limited representation of the multivariate floristic structure. Therefore, the NMDS should be interpreted as a visual summary of broad compositional tendencies rather than as strong evidence of distinct floristic assemblages.

### 3.3. Indirect and direct pathways of influence on floristic diversity

Spearman correlations indicate significant positive relationships between major structural variables (density, basal area, and aboveground biomass) and species richness, whereas relationships with evenness are weak or negative (Table 3).

Distance-based redundancy analysis (dbRDA) shows that anthropogenic disturbances explain a significant proportion of the variation in floristic composition independently of structural variables (adjusted  $R^2 \approx 0.10$ ;  $p < 0.01$ ). The global model explains approximately 31% of the total floristic variance, suggesting that disturbances act both indirectly, through modifications of forest structure, and directly, as an ecological filter influencing species assembly processes.

## 4. Discussion

### 4.1. Spatially structured disturbance regimes in a protected landscape

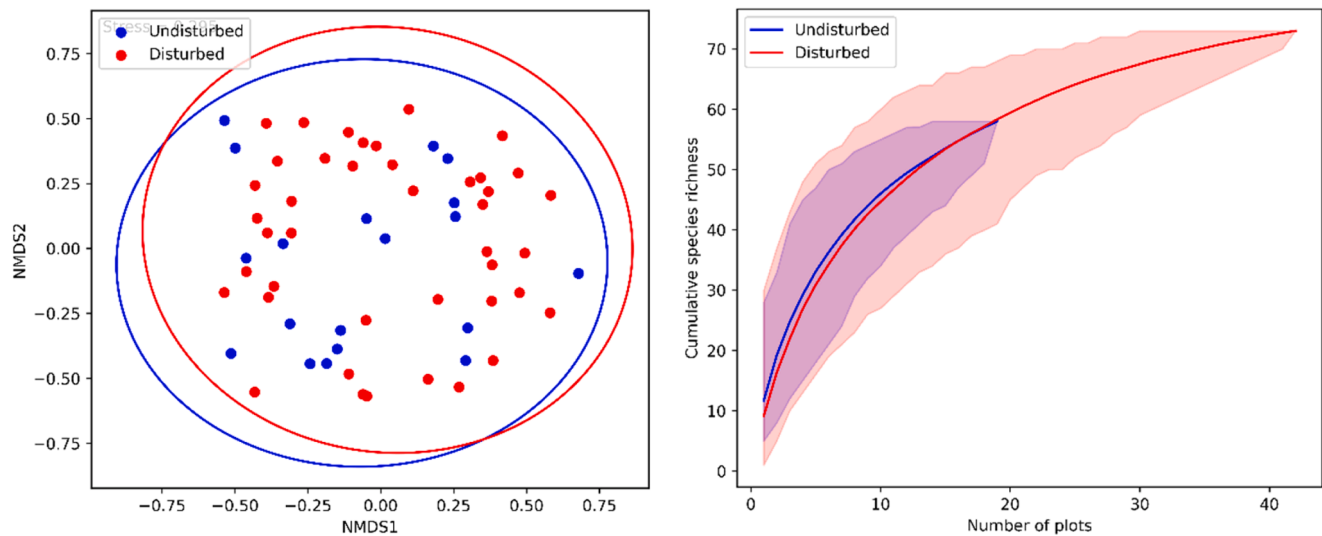
Anthropogenic disturbances observed in the montane zones of PNKB are neither uniformly nor independently distributed but are organised into non-random spatial regimes characterised by the recurrent co-occurrence of multiple pressures within the same plots. Such structuring has been documented in protected tropical forest landscapes, where human accessibility, energy demand, and agricultural encroachment may spatially aggregate even under formal conservation status (de Merode et al., 2004; Vancutsem et al., 2021). Similar patterns have also been reported in African montane protected areas and conservation landscapes where disturbance intensity increases along accessibility gradients (Cuni-Sanchez et al., 2016; Ensslin et al., 2015).

Within the same PNKB landscape, Cirezi et al. (2025b) showed, using remote sensing, that recent forest transitions follow recurrent configurations linked to gradients of accessibility and use intensity, suggesting cumulative effects of pressures rather than a sequence of isolated events. However, such structuring is not universal. In some protected landscapes with low human population density, disturbances tend to be more diffuse and opportunistic (Ahrends et al., 2010; Laurance et al., 2012), highlighting the importance of the socio-ecological context.

The combined use of Jaccard similarity and hierarchical clustering enables the identification of these disturbance regimes at a fine local scale by focusing on co-occurrence patterns rather than isolated frequencies (Chung et al., 2019; Mainali et al., 2017; McCune et al., 2002). These regimes should therefore be interpreted as dynamic configurations reflecting emerging ecological trajectories, a particularly concerning situation in a protected area where such pressures are expected to remain limited.

### 4.2. Structural simplification and directional ecological trajectories

The observed patterns indicate that anthropogenic disturbances are associated with progressive structural simplification, lower



**Fig. 3.** a. Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity of floristic assemblages in disturbed and undisturbed plots. Ellipses represent 95% confidence intervals around group centroids. The stress value (0.295) indicates a moderate representation of ecological distances in two-dimensional space. b. Species accumulation curves for disturbed (red) and undisturbed (blue) plots, showing cumulative species richness as a function of the number of sampled plots. Lines represent the mean derived from 999 random permutations, and shaded areas indicate 95% confidence intervals.

**Table 3**  
Relationships between forest structural variables, anthropogenic disturbances, and floristic diversity indices (species richness, Shannon, Simpson [1–D], and evenness) across 63 plots in Kahuzi-Biega National Park (PNKB). Spearman correlation coefficients ( $\rho$ ) and associated p-values are reported for each diversity index. Results from the dbRDA are presented as F-values, p-values, and explained variance (adjusted  $R^2$ ). Dashes (–) indicate non-significant effects or variables not retained in the model.

| Term                                          | Richness                     | Shannon                     | Simpson (1-D)                | Evenness                     | F    | p-value                | Contribution (adj. $R^2$ ) |
|-----------------------------------------------|------------------------------|-----------------------------|------------------------------|------------------------------|------|------------------------|----------------------------|
| Density (trees ha <sup>-1</sup> )             | 0.742 ( $p < 0.001^{***}$ )  | 0.502 ( $p < 0.001^{***}$ ) | 0.375 ( $p = 0.0058^{**}$ )  | –0.399 ( $p = 0.0033^{**}$ ) | 3.21 | 0.002 <sup>**</sup>    | 0.08                       |
| Basal area (m <sup>2</sup> ha <sup>-1</sup> ) | 0.741 ( $p < 0.001^{***}$ )  | 0.539 ( $p < 0.001^{***}$ ) | 0.430 ( $p = 0.0016^{***}$ ) | –0.280 ( $p = 0.0519^*$ )    | 2.85 | 0.005 <sup>**</sup>    | 0.07                       |
| Lorey's height (m)                            | 0.151 ( $p = 0.3069$ ns)     | 0.177 ( $p = 0.2477$ ns)    | 0.203 ( $p = 0.1798$ ns)     | 0.163 ( $p = 0.2792$ ns)     | 1.11 | 0.31ns                 | –                          |
| AGB (Mg ha <sup>-1</sup> )                    | 0.717 ( $p < 0.0010^{***}$ ) | 0.518 ( $p < 0.001^{***}$ ) | 0.416 ( $p = 0.0021^{**}$ )  | –0.260 ( $p = 0.0718$ ns)    | 2.97 | 0.004 <sup>**</sup>    | 0.06                       |
| Mean wood density (g cm <sup>-3</sup> )       | 0.125 ( $p = 0.3890$ ns)     | 0.092 ( $p = 0.4819$ ns)    | 0.106 ( $p = 0.4392$ ns)     | 0.122 ( $p = 0.3890$ ns)     | 0.88 | 0.55 <sup>*</sup>      | –                          |
| Disturbance                                   |                              |                             |                              |                              | 4.56 | 0.001 <sup>***</sup>   | 0.1                        |
| Full model                                    |                              |                             |                              |                              |      | < 0.001 <sup>***</sup> | 0.31                       |

p-values thresholds significance:  $p \geq 0.05$ ns: no statistical evidence of an effect,  $p < 0.05^*$ : moderate evidence,  $p < 0.01^{**}$ : Strong evidence,  $p < 0.001^{***}$ :very strong evidence.

aboveground biomass stocks, and moderate changes in floristic diversity. In protected tropical forests and montane national parks, chronic disturbances such as selective logging, charcoal production, fire, and encroachment have often been associated with reduced forest structure and biomass, even where formal protection is in place (Ahrends et al., 2010; Barlow et al., 2016a; Laurance et al., 2012). Although our study did not directly quantify historical tree removal or size-specific extraction, the lower basal area and biomass observed in disturbed plots are consistent with patterns reported in protected forests subjected to recurrent human pressures.

In African montane forests located within protected areas or relatively low-disturbance conservation landscapes, aboveground biomass stocks are often reported within the range of ~150–300 Mg ha<sup>-1</sup>, with basal areas frequently exceeding 25–35 m<sup>2</sup> ha<sup>-1</sup> (Cuni-Sanchez et al., 2021; Imani et al., 2021). The values observed in PNKB, including in plots classified as undisturbed, fall within the lower part of these ranges. This may reflect the fact that “undisturbed” plots were defined based on the absence of visible disturbance indicators at the time of sampling, rather than on long-term historical intactness. Legacy effects of past disturbance, edge influence, local accessibility, smaller diameter structure, and site-specific edaphic or topographic constraints may therefore

contribute to the relatively low biomass observed. Direct comparisons should also be made with caution because biomass estimates vary with altitude, disturbance history, plot selection, DBH thresholds, and allometric models. In Central Africa, Fayolle et al. (2018) further emphasise that forest structure reflects both environmental constraints and legacy effects of past disturbances.

The relative stability of some mean functional attributes suggests that disturbances primarily affect tree abundance, basal occupation, and spatial distribution rather than the dominant traits of the remaining species. Similar decoupling between structural degradation and functional attributes has been reported in African montane forests, where recovery can be constrained by topographic and edaphic conditions (Cuni-Sanchez et al., 2016; Hall et al., 2011). Unlike lowland secondary forests, where species richness may temporarily increase through pioneer recruitment (Chazdon, 2014, 2008), patterns observed in PNKB suggest a gradual floristic homogenisation associated with cumulative and recurrent pressures (Balezi et al., 2023; Cirezi et al., 2025a) under constraining montane conditions (Obua et al., 2010).

The floristic signal should nevertheless be interpreted cautiously. Although PERMANOVA detected significant compositional differences between disturbed and undisturbed plots, the explained variance was

low, and the NMDS showed substantial overlap between groups. These results suggest a weak but directionally consistent floristic response to disturbance rather than a strong separation of distinct assemblages. Such patterns are common in ecological communities where multiple environmental and historical factors interact at fine spatial scales (Anderson, 2001; Legendre and Legendre, 2012). In tropical montane forests, topographic, microclimatic, and edaphic heterogeneity can further increase assemblage dispersion (Cuni-Sanchez et al., 2016; Hall et al., 2011).

The high variability among plots therefore likely reflects a mosaic of transformation stages rather than analytical inconsistency, consistent with models of heterogeneous secondary succession (Chazdon, 2014). The combined use of NMDS, PERMANOVA, and species accumulation curves provides complementary evidence on compositional tendencies and sampling completeness (Anderson, 2001; Bray and Curtis, 1957; Gotelli and Colwell, 2001; Kruskal, 1964). Overall, disturbances in PNKB appear less as abrupt collapse events than as a directional process of gradual structural and functional simplification, with a weaker but consistent floristic reorganisation.

#### 4.3. Structural mediation and ecological filtering in community dynamics

The analyses suggest that disturbances influence floristic diversity through a hierarchical mechanism, in which modifications of forest structure represent the primary pathway of impact, while a secondary direct effect on composition persists. This structural mediation is consistent with theoretical frameworks linking stand heterogeneity to local diversity (Chazdon, 2014; MacArthur and MacArthur, 1961), whereby reductions in vertical and horizontal complexity reconfigure microhabitats and biotic interactions.

Variance partitioning indicates that the global model explains a substantial proportion of floristic variability, whereas the independent effect of disturbances remains moderate. Such levels are common in community ecology, where species composition reflects the interaction of multiple environmental, historical, and biotic drivers operating across spatial scales (Borcard et al., 1992; Legendre and Anderson, 1999b). In tropical forests, it is rare for a single factor to account for a dominant share of floristic variance given the high structural complexity and micro-environmental heterogeneity (Chazdon, 2014; Condit et al., 2002).

The persistence of a detectable independent effect of disturbances after accounting for structural variables suggests that disturbances act not only indirectly through stand transformation but also as autonomous ecological drivers influencing community composition. Although moderate, this effect reflects a direct ecological filtering process favouring disturbance-tolerant species at the expense of more sensitive taxa. Under more intense disturbance regimes, such filtering may lead to rapid transitions towards alternative states (Barlow et al., 2016a). In the PNKB, however, the observed patterns rather indicate a gradual transformation, where structural mediation dominates without fully excluding a direct effect. The combined use of non-metric ordination, multivariate testing, and variance partitioning allows these mechanisms to be disentangled, avoiding purely descriptive interpretations of observed differences. Overall, disturbances emerge as interdependent forces progressively reshaping community composition through a combination of indirect and direct effects, embedded within a directional ecological trajectory rather than an abrupt regime shift.

From a management perspective, these results suggest that conservation strategies in PNKB should not focus solely on preventing large-scale deforestation but also on limiting diffuse and recurrent disturbances within apparently forested areas. The spatial structuring of

disturbance regimes highlights the importance of monitoring accessibility corridors and cumulative pressure hotspots. Integrating field-based ecological monitoring with remote-sensing approaches could improve early detection of degradation processes and help prioritize restoration and protection efforts in montane forest sectors exposed to repeated human use.

## 5. Conclusion

Anthropogenic disturbances in the montane forests of Kahuzi-Biega National Park are organised into spatially structured regimes and are associated with progressive structural simplification, lower above-ground biomass, and moderate but directionally consistent floristic reorganisation. Rather than indicating an abrupt shift between distinct forest communities, the results suggest a gradual ecological trajectory in which floristic changes are associated primarily with changes in stand structure, while a weaker direct ecological filtering effect may also contribute to community reorganisation.

These findings highlight that formal protection alone may not prevent internal forest degradation when diffuse, recurrent pressures remain active within accessible montane forest sectors. From a management perspective, conservation strategies in PNKB should therefore address not only large-scale forest loss but also cumulative small-scale disturbances, particularly along accessibility corridors and disturbance hotspots.

Although the observed patterns are consistent across the sampled landscape, this study is limited by its cross-sectional design, the absence of direct temporal monitoring, reliance on allometric biomass estimations, and potential spatial dependence linked to the transect-based sampling design. Future research combining repeated field inventories, fine-scale spatial data, functional traits, and hierarchical or explicitly spatial models would help clarify disturbance thresholds and assess the resilience of montane forests under cumulative anthropogenic pressures.

## CRedit authorship contribution statement

**Nadège Cizungu Cirezi:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Pyame Balemirwe Mushagalusa:** Formal analysis, Methodology, Writing – review & editing. **Lisette Mangaza:** Conceptualization, Data curation, Methodology, Writing – review & editing. **Lea Mukubu Pika:** Formal analysis, Visualization, Writing – review & editing. **Roselande Jesuka:** Formal analysis, Validation, Writing – review & editing. **Alphonse Zihahirwa Balezi:** Conceptualization, Investigation, Supervision, Writing – review & editing. **Katcho Karume:** Conceptualization, Writing – review & editing. **Raymond Sinsi Lum-buenamo:** Conceptualization, Supervision, Writing – review & editing. **Olivia Lovanirina Rakotondrasoa:** Formal analysis, Validation, Writing – review & editing. **Jean-François Bastin:** Conceptualization, Supervision, Validation, Visualization, Writing – review & editing. **Adeline Fayolle:** Conceptualization, Methodology, Validation, Writing – review & editing. **Jan Bogaert:** Methodology, Supervision, Validation, Visualization, Writing – review & editing.

## Declaration of competing interest

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

## Appendices

**Table A1**

Results of normality and homogeneity of variance tests for selected structural variables prior to group comparisons.

| Variable   | Shapiro p | Levene p | Decision       |
|------------|-----------|----------|----------------|
| Basal area | <0.05     | 0.03     | non-parametric |
| AGB        | <0.001    | 0.02     | non-parametric |

Shapiro–Wilk and Levene tests were used to assess normality and homogeneity of variance, respectively. Variables that did not meet parametric assumptions were analysed using non-parametric tests (Mann–Whitney U test). AGB = aboveground biomass.

**Table A2**

Height–diameter candidate models tested for tree height estimation in Kahuzi-Biega National Park (PNKB). Models were fitted using the same dataset but are presented separately according to the response scale: original tree height (H) and log-transformed height [log(H)]. For each model, the table reports the Akaike Information Criterion (AIC), model parameters (a, b, c), residual standard error (RSE), and sample size (n). AIC values should only be compared among models fitted on the same response scale and likelihood basis. The final model was selected based on comparable AIC values, residual standard error, and biological plausibility for subsequent biomass estimation.

| Height–diameter model comparison                 |                                                         |                |        |        |        |          |     |     |
|--------------------------------------------------|---------------------------------------------------------|----------------|--------|--------|--------|----------|-----|-----|
| A. Models fitted on original height scale        |                                                         |                |        |        |        |          |     |     |
| model                                            | model name                                              | response scale | AIC    | a      | b      | c        | RSE | n   |
| m01                                              | Linear                                                  | H              | 8409.7 | 9.63   | 0.167  |          |     | 837 |
| m02                                              | Log-linear                                              | H              | 8406.2 | −8.98  | 7.4    |          |     | 837 |
| m03.1                                            | Power law, using nls fitting                            | H              | 8407.2 | 3.71   | 0.419  |          |     | 837 |
| m04                                              | Second-order polynomial, $H \sim D$                     | H              | 8408.4 | 5.38   | 0.401  | −0.00198 |     | 837 |
| m05                                              | Second-order polynomial of log-linear, $H \sim \log(D)$ | H              | 8407.8 | −28.62 | 19.47  | −1.804   |     | 837 |
| m06.1                                            | Second-order log-log polynomial, using nls fitting      | H              | 8407.6 | −1.564 | 2.069  | −0.2295  |     | 837 |
| m07                                              | Asymptotic, 3-parameter exponential                     | H              | 8407.6 | 22.5   | 24.8   | 0.0489   |     | 837 |
| m08                                              | Asymptotic, Gompertz                                    | H              | 8407.4 | 21.7   | 2.22   | 0.0734   |     | 837 |
| m09                                              | Asymptotic, Weibull                                     | H              | 8407.5 | 21.7   | 0.0245 | 1.213    |     | 837 |
| m10                                              | Asymptotic, Michaelis–Menten                            | H              | 8405.9 | 30.6   | 26.6   |          |     | 837 |
| B. Models fitted on log-transformed height scale |                                                         |                |        |        |        |          |     |     |
| model                                            | model name                                              | response scale | AIC    | a      | b      | c        | RSE | n   |
| m03                                              | Power law, linear after log-transformation              | log(H)         | 765.9  | 1.12   | 0.433  |          |     | 837 |
| m06                                              | Second-order log-log polynomial, $\log(H) \sim \log(D)$ | log(H)         | 765.1  | 0.545  | 0.784  | −0.0523  |     | 837 |

\*for non-linear model (nls fitting) I used parameter values of published models as start value.

**Table A3**

Variation in cumulative disturbance intensity index (CDI) across transects in the montane forests of Kahuzi-Biega National Park. The cumulative disturbance index (CDI) represents the additive intensity of anthropogenic disturbances recorded per plot based on the number and co-occurrence of disturbance indicators. For each transect, the table reports the number of sampled plots (n\_plots), total CDI, mean disturbance intensity, standard deviation (SD), and minimum and maximum CDI values observed among plots.

| transect_no | n_plots | total_CDI | mean_CDI | sd_CDI | min_CDI | max_CDI |
|-------------|---------|-----------|----------|--------|---------|---------|
| 1           | 7       | 5,00      | 0,71     | 1,89   | 0,00    | 5,00    |
| 2           | 7       | 21,00     | 3,00     | 5,00   | 0,00    | 14,00   |
| 3           | 7       | 90,00     | 12,86    | 8,90   | 1,00    | 27,00   |
| 4           | 7       | 166,00    | 23,71    | 33,52  | 0,00    | 96,00   |
| 5           | 7       | 66,00     | 9,43     | 3,87   | 5,00    | 15,00   |
| 6           | 7       | 176,00    | 25,14    | 11,82  | 12,00   | 41,00   |
| 7           | 7       | 183,00    | 26,14    | 9,74   | 15,00   | 44,00   |
| 8           | 7       | 12,00     | 1,71     | 1,80   | 0,00    | 5,00    |
| 9           | 7       | 12,00     | 1,71     | 4,54   | 0,00    | 12,00   |

## Data availability

The datasets generated during and/or analyzed during the study are available from the corresponding author on reasonable request.

## References

- Ahrends, A., Burgess, N.D., Milledge, S.A.H., Bulling, M.T., Fisher, B., Smart, J.C.R., Clarke, G.P., Mhoro, B.E., Lewis, S.L., 2010. Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. *Proc. Natl. Acad. Sci. USA* 107, 14556–14561. <https://doi.org/10.1073/pnas.0914471107>.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* 26, 32–46.
- Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., Houghton, R.A., 2017. Tropical forests are a net carbon source based on aboveground measurements

- of gain and loss. *Science* 358 (1979), 230–234. <https://doi.org/10.1126/science.aam5962>.
- Balezi, A.Z., 2012. Taxonomie et écologie des hymenochaetales dans les forêts de montagne de l'Est de la République Démocratique du Congo. Le Cas Du Parc National De Kahuzi-Biega (Thèse de Doctorat). Université Catholique de Louvain, Louvain.
- Balezi, Z.A., Kazige, S.N., Migabo, N.N., Bahindwa, B.N., 2023. Assessment of anthropogenic activities effect on the use of biological resources around the Kahuzi-Biega National Park highland's part (South-Kivu. DRC). *Ann. Sci. Sci. Appl.* 5.
- Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Thomson Jr, N.R.M., de Ferraz, S.F.B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., de Oliveira RC, Souza Jr., C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535, 144–147. <https://doi.org/10.1038/nature18326>.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B Stat. Methodol.* 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055. <https://doi.org/10.2307/1940179>.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the Upland Forest communities of Southern Wisconsin. *Ecol. Monogr.* 27, 325–349. <https://doi.org/10.2307/1942268>.
- Buchadas, A., Baumann, M., Meyfroidt, P., Kuemmerle, T., 2022. Uncovering major types of deforestation frontiers across the world's tropical dry woodlands. *Nat. Sustain.* 5, 619–627. <https://doi.org/10.1038/s41893-022-00886-9>.
- Bullock, E.L., Woodcock, C.E., Olofsson, P., 2020. Monitoring tropical forest degradation using spectral unmixing and Landsat time series analysis. *Remote Sens. Env.* 238, 110968. <https://doi.org/10.1016/j.rse.2018.11.011>.
- Butsic, V., Baumann, M., Shortland, A., Walker, S., Kuemmerle, T., 2015. Conservation and conflict in the Democratic Republic of Congo: the impacts of warfare. *Mining. And protected areas on deforestation. Biol. Conserv.* 191, 266–273. <https://doi.org/10.1016/j.biocon.2015.06.037>.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145 (1), 87–99. <https://doi.org/10.1007/s00442-005-0100-x>.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12 (4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrizar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Péliissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* 20, 3177–3190. <https://doi.org/10.1111/gcb.12629>.
- Chazdon, R.L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320 (1979), 1458–1460. <https://doi.org/10.1126/science.1155365>.
- Chazdon, R.L., 2014. Second Growth. University of Chicago Press. <https://doi.org/10.7208/chicago/9780226118109.001.0001>.
- Chung, N.C., Miasojedow, B., Startek, M., Gambin, A., 2019. Jaccard/Tanimoto similarity test and estimation methods for biological presence-absence data. *BMC Bioinform.* 20, 644. <https://doi.org/10.1186/s12859-019-3118-5>.
- Cirezi, N.C., Bastin, J.F., Mugumaarhahama, Y., Useni, Y.S., Karume, K., Lumbuenamo, R. S., Bogaert, J., 2025a. Analyzing drivers of tropical moist forest dynamics in the Kahuzi-Biega national park landscape. *Eastern Democratic Republic of Congo from 1990 to 2022*. *Land* 14, 49. <https://doi.org/10.3390/land14010049>.
- Cirezi, N.C., Mugumaarhahama, Y., Useni, Y.S., Bayumbasire, C.C., Karume, K., Lumbuenamo, R.S., Bastin, J.-F., Bogaert, J., 2025b. Spatial patterns and ecological drivers of tropical moist forest transitions in the Kahuzi Biega national park landscape eastern Democratic Republic of Congo. *Discov. For.* 1, 43. <https://doi.org/10.1007/s44415-025-00046-9>.
- Cirimwami B.T.L., 2021. Caractérisation Des Habitats Et Effets Des Facteurs Environnementaux Sur L'organisation De La Végétation Du Parc National De Kahuzi-Biega en République Démocratique du Congo National De Kahuzi-Biega en République Démocratique du Congo. Université de Kisangani. Kisangani.
- Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., Hubbell, S.P., 2002. Beta-diversity in tropical forest trees. *Science* 295 (1979), 666–669. <https://doi.org/10.1126/science.1066854>.
- Crausbay, S.D., Martin, P.H., 2016. Natural disturbance. Vegetation patterns and ecological dynamics in tropical montane forests. *J. Trop. Ecol.* 32, 384–403. <https://doi.org/10.1017/S0266467416000328>.
- Cuni-Sanchez, A., Sullivan, M.J.P., Platts, P.J., Lewis, S.L., Marchant, R., Imani, G., Hubau, W., Abiem, I., Adhikari, H., Albrecht, T., Altman, J., Amani, C., Aneseyee, A. B., Avitabile, V., Banin, L., Batumike, R., Bauters, M., Beeckman, H., Begne, S.K., Bennett, A.C., Bitariho, R., Boeckx, P., Bogaert, J., Bräuning, A., Bulonvu, F., Burgess, N.D., Calders, K., Chapman, C., Chapman, H., Comiskey, J., de Haulleville, T., Decuyper, M., DeVries, B., Dolezal, J., Droissart, V., Ewango, C., Feyera, S., Gebrekirstos, A., Gereau, R., Gilpin, M., Hakizimana, D., Hall, J., Hamilton, A., Hardy, O., Hart, T., Heiskanen, J., Hemp, A., Herold, M., Hiltner, U., Horak, D., Kamdem, M.-N., Kayijamahe, C., Kenfack, D., Kinyanjui, M.J., Klein, J., Lisingo, J., Lovett, J., Lung, M., Makana, J.-R., Malhi, Y., Marshall, A., Martin, E.H., Mitchard, E.T.A., Morel, A., Mukendi, J.T., Muller, T., Nchu, F., Nyirambangutse, B., Okello, J., Peh, K.S.-H., Pellikka, P., Phillips, O.L., Plumptre, A., Qie, L., Rovero, F., Sainge, M.N., Schmitt, C.B., Sedlacek, O., Ngute, A.S.K., Sheil, D., Sheleme, D., Simegn, T.Y., Simo-Droissart, M., Sonké, B., Soromessa, T., Sunderland, T., Svoboda, M., Taedoung, H., Taplin, J., Taylor, D., Thomas, S.C., Timberlake, J., Tuagben, D., Umunay, P., Uzabaho, E., Verbeeck, H., Vlemminck, J., Wallin, G., Wheeler, C., Willcock, S., Woods, J.T., Zibera, E., 2021. High aboveground carbon stock of African tropical montane forests. *Nature* 596, 536–542. <https://doi.org/10.1038/s41586-021-03728-4>.
- Cuni-Sanchez, A., White, L.J.T., Calders, K., Jeffery, K.J., Abernethy, K., Burt, A., Disney, M., Gilpin, M., Gomez-Dans, J.L., Lewis, S.L., 2016. African Savanna-forest boundary dynamics: a 20-year study. *PLoS. One* 11, e0156934. <https://doi.org/10.1371/journal.pone.0156934>.
- De Mero, E., Homewood, K., Cowlishaw, G., 2004. The value of bushmeat and other wild foods to rural households living in extreme poverty in Democratic Republic of Congo. *Biol. Conserv.* 118, 573–581. <https://doi.org/10.1016/j.biocon.2003.10.005>.
- Depecker J., Asimonyio A.J., Miteho R., Hatangi Y., Kambale J.L., Verleysen L., Stoffelen P., Janssens S.B., Dhed'a B., Vandeloof F., Honnay O., 2021. Effects of forest disturbance and regeneration on tree species composition and traits in DR Congo. <https://doi.org/10.1101/2021.10.11.463162>.
- Dimitris, G.T., Christina, D.N., George, S.A., 2023. A class of algorithms for solving LP problems by prioritizing the constraints. *Am. J. Oper. Res.* 13.
- Draulans, D., Van Krunkelsven, E., 2002. The impact of war on forest areas in the Democratic Republic of Congo. *Oryx*. <https://doi.org/10.1017/S0030605301000011>.
- Dupuis, C., Ligot, G., Bastin, J.-F., Lejeune, P., Doucet, J.-L., Rossi, V., Fayolle, A., 2025. Scaling up the assessment of logging's impact on forest structure in Central Africa using field and UAV data. *Environ. Res. Lett.* 20, 014018. <https://doi.org/10.1088/1748-9326/ad99ea>.
- Enslin, A., Rutten, G., Pommer, U., Zimmermann, R., Hemp, A., Fischer, M., 2015. Effects of elevation and land use on the biomass of trees. Shrubs and herbs at Mount Kilimanjaro. *Ecosph.* 6, 1–15. <https://doi.org/10.1890/ES14-00492.1>.
- Fayolle, A., Ngomanda, A., Mbsi, M., Barbier, N., Bocko, Y., Boyemba, F., Couteron, P., Fonton, N., Kamdem, N., Katembo, J., Kondoaule, H.J., Loumeto, J., Maïdou, H.M., Mankou, G., Mengui, T., Mofack, G.I., Moundounga, C., Moundounga, Q., Ngumibous, L., Nsue Nchama, N., Obiang, D., Ondo Meyer Asue, F., Picard, N., Rossi, V., Senguela, Y.-P., Sonké, B., Viard, L., Yongo, O.D., Zapfack, L., Medjibe, V.P., 2018. A regional allometry for the Congo basin forests based on the largest ever destructive sampling. *For. Ecol. Manag.* 430, 228–240. <https://doi.org/10.1016/j.foreco.2018.07.030>.
- Fischer, E., Dieterlen, F., Hinkel, H., Klug, U., Schnurr, J., Steinhauer-Burkart, B., 1993. Die Vegetation des Parc National De Kahuzi-Biega. *Zaire mit Beiträgen von, Sud-Kivu*.
- Flores, O., Coomes, D.A., 2010. Estimating the wood density of species for carbon stock assessments. *Methods Ecol. Evol.* 2 (2), 214–220. <https://doi.org/10.1111/j.2041-210x.2010.00068.x>.
- Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* 12, 561–582. <https://doi.org/10.1111/j.1461-0248.2009.01294.x>.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Hall, J.M., Gillespie, T.W., Mwanga, M., 2011. Comparison of agroforests and protected forests in the East Usambara mountains. *Tanzan. Env. Manage.* 48, 237–247. <https://doi.org/10.1007/s00267-010-9579-y>.
- Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. Plea for standard terminology: the habitat concept and a plea for standard terminology key words peer refereed. *Biological Sciences East Building. Wildlife Society Bulletin*.
- Hart, J.A., Hall, J.S., 1996. Status of Eastern Zaire's forest parks and reserves. *Biology*.
- Hosonuma, N., Herold, M., Veronique, D.S., De Fries, R.S., Brockhaus, M., Verchot, L., Angelsen, A., Romijn, E., 2012. An assessment of deforestation and forest degradation drivers in developing countries. *Environ. Res. Lett.* 7, 044009. <https://doi.org/10.1088/1748-9326/7/4/044009>.
- Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>.
- ICCN-KBNP, 2010. Plan Général De Gestion 2009-2019. Parc national de Kahuzi-Biega.
- Imani, G., Kalume, J., Marchant, R., Calders, K., Batumike, R., Bulonvu, F., Cuni-Sanchez, A., 2021. Tree diversity and carbon stocks in the Itombwe Mountains of eastern DR Congo. *Biotropica* 53, 1594–1605. <https://doi.org/10.1111/btp.13008>.
- Ingram V.J., Nasi R., Dubiez E., 2011. Woodfuel for urban centres in the Democratic Republic of Congo. <https://doi.org/10.13140/2.1.2159.7760>.
- IUCN, 2022. Guidelines for using a global standard for the identification of key biodiversity areas: version 1.2, 2022, International Union for Conservation of Nature (IUCN). <https://portals.iucn.org/library/node/49979>.
- Kabonyi, C., Salmon, M., Roche, E., 2011. Le Parc National de Kahuzi - Biega (R. D. Congo). *Patrimoine en péril? Le secteur «Haute Altitude». situation et perspectives. Geo Eco Trop.* 35, 1–8.
- Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29, 115–129. <https://doi.org/10.1007/BF02289694>.
- Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M.A., Edwards, D., Edwards, F., Farwig, N., Fashing, P.,

- Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R., McClearn, D., Mudappa, D., Nielsen, M.R., Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G., J., Arroyo, L., Ashton, M., Augel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C.A., Bunyavechewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K., Herbringer, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H., Klop, E., Knott, C., Koné, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Latte, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaïotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R., Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K. E., Sukumar, R., Surbeck, M., Tobler, M., Tschamtké, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Vereza, C., Volkmer de Castilho, C., Walther, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D.D., Wright, P., Xiankai, L., Yonzon, P., Zamzani, F., 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* 489, 290–294. <https://doi.org/10.1038/nature11318>.
- Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.* 69, 1. <https://doi.org/10.2307/2657192>.
- Legendre, P., Legendre, L., 2012. *Numerical ecology*. Els. Ed. ed. Els. B.V.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598. <https://doi.org/10.2307/1932254>.
- Magurran, A.E., 2021. Measuring biological diversity. *Curr. Biol.* 31, R1174–R1177. <https://doi.org/10.1016/j.cub.2021.07.049>.
- Mainali, K.P., Bewick, S., Thielen, P., Mehoke, T., Breitwieser, F.P., Paudel, S., Adhikari, A., Wolfe, J., Slud, E.V., Karig, D., Fagan, W.F., 2017. Statistical analysis of co-occurrence patterns in microbial presence-absence datasets. *PLoS. One* 12, e0187132. <https://doi.org/10.1371/journal.pone.0187132>.
- Malhi, Y., Adu-Bredu, S., Asare, R.A., Lewis, S.L., Mayaux, P., 2013. African rainforests: past, present and future. *Philos. Trans. R. Soc. B. Biol. Sci.* 368, 20120312. <https://doi.org/10.1098/rstb.2012.0312>.
- Mangaza, L., Makana, J.-R., Hubau, W., Sonwa, D., Batsi, G., Fayolle, A., 2022. Impacts du changement d'utilisation des terres sur la biomasse et la diversité dans le paysage forestier de la réserve de biosphère de Yangambi en République démocratique du Congo. *Bois For. Trop.* 59–71.
- Masumbuko, N., 2010. *Ecologie De Sericostachys scandens. Liane Envahissante Dans Les Forêts De Montagne Du Parc National De Kahuzi-Biega. République Démocratique Du Congo. Université Libre de Bruxelles*.
- McCune, B., Grace, J.B., Urban, D.L., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach. OR.
- McKinney W., 2010. Data structures for statistical computing in Python. pp. 56–61. <https://doi.org/10.25080/Majora-92bf1922-00a>.
- Mertz, O., Müller, D., Sikor, T., Hett, C., Heinemann, A., Castella, J.-C., Lestrelin, G., Ryan, C.M., Reay, D.S., Schmidt-Vogt, D., Danielsen, F., Theilade, I., Noordwijk, M., van Verchot, L.V., Burgess, N.D., Berry, N.J., Pham, T.T., Messerli, P., Xu, J., Fensholt, R., Hostert, P., Pflugmacher, D., Bruun, T.B., Neergaard, A., de Dons, K., Dewi, S., Rutishauser, E., Sun, Z., 2012. The forgotten D: challenges of addressing forest degradation in complex mosaic landscapes under REDD+. *Geogr. Tidsskr.-Dan. J. Geogr.* 112, 63–76. <https://doi.org/10.1080/00167223.2012.709678>.
- Muhanguzi, H.D.R., Obua, J., Oryem-Origa, H., 2007. The effect of human disturbance on tree species composition and demographic structure in Kalinzu forest reserve. *Uganda. Afr. J. Ecol.* 45, 2–10. <https://doi.org/10.1111/j.1365-2028.2007.00844.x>.
- Musavandalo, C.M., Essouman, P.F.E., Ndjadi, S.S., Balandi, J.B., Nguba, T.B., Sodalo, C., Mweru, J.-P.M., Sambieni, K.R., Bogaert, J., 2025. Anthropogenic disturbances in Northwestern Virunga Forest amid armed conflict. *Land* 14, 732. <https://doi.org/10.3390/land14040732>.
- Obua, J., Agea, J.G., Ogwal, J.J., 2010. Status of forests in Uganda. *Afr. J. Ecol.* 48, 853–859. <https://doi.org/10.1111/j.1365-2028.2010.01217.x>.
- Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGinn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E., Wagner H., 2020. *Vegan: community ecology package* (R package version 2.5-7).
- Ouédraogo, D.-Y., Beina, D., Picard, N., Mortier, F., Baya, F., Gourlet-Fleury, S., 2011. Thinning after selective logging facilitates floristic composition recovery in a tropical rain forest of Central Africa. *For. Ecol. Manage.* 262, 2176–2186. <https://doi.org/10.1016/j.foreco.2011.08.009>.
- Phillips, O.L., Malhi, Y., Vinceti, B., Baker, T., Lewis, S.L., Higuchi, N., Laurance, W.F., Vargas, P., Núñez Martínez, R., Vásquez Laurance, S., Ferreira, L.V., Stern, M., Brown, S., Grace, J., Vargas, P., Nunez Martinez, R.V., 2002. Changes in growth of tropical forests: evaluating potential biases. *Ecol. Appl.* 12, 576. <https://doi.org/10.2307/3060964>.
- Plumptre, A.J., Behangana, M., Davenport, T., Kahindo, C., Kityo, E., Ndomba, E., Nkuutu, D., Owunji, I., Ssegawa, P., Eilu, G., 2003. *Albertine Rift biodiversity*. WCS. Ed.
- Plumptre, A.J., Davenport, T.R.B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J.K., Pilgrim, J.D., Wilson, M., Languy, M., Moyer, D., 2007. The biodiversity of the Albertine Rift. *Biol. Conserv.* 134, 178–194. <https://doi.org/10.1016/j.biocon.2006.08.021>.
- Plumptre A.J., Nixon S., Critchlow R., Vieilledent G., Nishuli R., Kirkby A., Williamson E.A., Hall J.S., Kujirakwinja D., 2015. Status of Grauer's gorilla and chimpanzees in eastern Democratic Republic of Congo: historical and current distribution and abundance.
- Potapov P., Hansen M.C., Laestadius L., Turubanova S., Yaroshenko A., Thies C., Smith W., Zhuravleva I., Komarova A., Minnemeyer S., Esipova E., 2017. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013.
- Rakotondraso, O., 2012. *Ecologie spatiale et dynamique de la forêt de Tapia. Uapaca bojeri Baill. (1958). Habitat Du Vers à Soieborocera Cajani (Vinson. 1863). Dans La Zone D'arivonimamo II-Madagascar. Université d'Antananarivo*.
- Réjou-Méchain, M., Tanguy, A., Piponi, C., Chave, J., Hérault, B., 2017. Biomass: an r package for estimating above-ground biomass and its uncertainty in tropical forests. In: Goslee, S. (Ed.), *Methods Ecol. Evol.* 8 (9), 1163–1167. <https://doi.org/10.1111/2041-210x.12753>.
- Seabold S., Perktold J., 2010. Statsmodels: econometric and statistical modeling with Python. pp. 92–96. <https://doi.org/10.25080/Majora-92bf1922-011>.
- Skarbek, C., 2008. A review of endemic species in the Eastern Arc afro-montane region: importance. *Inferences. Conserv. Macalester Rev. Biogeogr.*
- Skidmore, M.E., Moffette, F., Rausch, L., Christie, M., Munger, J., Gibbs, H.K., 2021. Cattle ranchers and deforestation in the Brazilian Amazon: production. Location. And policies. *Glob. Environ. Chang.* 68, 102280. <https://doi.org/10.1016/j.gloenvcha.2021.102280>.
- Soh, M.C.K., Mitchell, N.J., Ridley, A.R., Butler, C.W., Puan, C.L., Peh, K.S.-H., 2019. Impacts of habitat degradation on tropical montane biodiversity and ecosystem services: a systematic map for identifying future research priorities. *Front. For. Glob. Chang.* 2. <https://doi.org/10.3389/ffgc.2019.00083>.
- Spira, C., Kirkby, A., Kujirakwinja, D., Plumptre, A.J., 2019. The socio-economics of artisanal mining and bushmeat hunting around protected areas: kahuzi-Biega national park and itombwe nature reserve. *Eastern Democratic Republic of Congo. Oryx* 53, 136–144. <https://doi.org/10.1017/S003060531600171X>.
- Spira, C., Mitamba, G., Kirkby, A., Katembo, J., Kiyani Kambale, C., Musikami, P., Dumbo, P., Byaombe, D., Plumptre, A.J., Maisels, F., 2018. Inventaire de la biodiversité dans le Parc National de Kahuzi-Biega. *Répub. Démocr. du Congo*.
- Tweiten, M.A., Hotchkiss, S.C., Vitousek, P.M., Kellner, J.R., Chadwick, O.A., Asner, G.P., 2014. Resilience against exotic species invasion in a tropical montane forest. *J. Veg. Sci.* 25, 734–749. <https://doi.org/10.1111/jvs.12112>.
- Tyukavina, A., Hansen, M.C., Potapov, P., Parker, D., Okpa, C., Stehman, S.V., Kommareddy, I., Turubanova, S., 2018. Congo Basin forest loss dominated by increasing smallholder clearing. *Sci. Adv.* 4. <https://doi.org/10.1126/sciadv.aat2993>.
- UICN. 2017. Rapport de la mission conjointe de suivi réactif Centre du patrimoine mondial/UICN au Parc National de Kahuzi-Biega.
- UNESCO, 2024. *State of conservation: Kahuzi-Biega national park [WWW Document]. URL State Conserv.* (accessed 6.7.25).
- UNESCO. 2025. *Kahuzi-Biega national park [WWW document]. https://whc.unesco.org/en/list/137* (accessed 11.2.25).
- Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L.E.O.C., Nasi, R., 2021. Long-term (1990-2019) monitoring of forest cover changes in the humid tropics. *Sci. Adv.* 7.
- Vijay, V., Pimm, S.L., Jenkins, C.N., Smith, S.J., 2016. The impacts of oil palm on recent deforestation and biodiversity loss. *PLoS. One* 11, e0159668. <https://doi.org/10.1371/journal.pone.0159668>.
- Wickham H., 2016. *Ggplot2: Elegant Graphics For Data Analysis*. Springer International Publishing. Cham. <https://doi.org/10.1007/978-3-319-24277-4>.
- Yaffar, D., Addo-Danso, S.D., Powers, J.S., Meier, I.C., 2023. Fundamental but underrepresented: root carbon stocks in African montane forests. *Front. For. Glob. Change* 6. <https://doi.org/10.3389/ffgc.2023.1273996>.