

Floristic and structural distinctness of monodominant *Gilbertiodendron dewevrei* forest in the western Congo Basin

Ellen Heimpel^{1,2}, Antje Ahrends¹, Kyle G. Dexter², Jefferson S. Hall³, Josérald Mamboueni⁴, Vincent P. Medjibe⁵, David Morgan⁶, Crickette Sanz^{7,8}, David J. Harris¹

- 1 Royal Botanic Garden Edinburgh, Edinburgh, UK
- 2 School of Geosciences, University of Edinburgh, Edinburgh, UK
- 3 Smithsonian Tropical Research Institute, Balboa, Ancon, Panama
- 4 Institut National de Recherche Forestière, Brazzaville, Congo
- 5 Gabon National Parks Agency, Libreville, Gabon
- 6 Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, USA
- 7 Department of Anthropology, Washington University in St. Louis, St. Louis, USA
- 8 Congo Program, Wildlife Conservation Society, Brazzaville, Congo

Corresponding author: Ellen Heimpel (ehempel@rbge.org.uk)

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Abstract

Background and aims – The forests of the Congo Basin contain high levels of biodiversity, and are globally important for carbon storage. In order to design effective conservation strategies, and to accurately model carbon stocks, a fine-scale understanding of the different forest types that make up this forest block is needed. Monodominant *Gilbertiodendron dewevrei* forest covers large areas of the Congo Basin, but it is currently unclear whether it is sufficiently distinct from adjacent mixed terre firme forest to warrant separate treatment for conservation planning and carbon calculations. This study aimed to compare the structure and diversity of monodominant and mixed forest, and ask whether there is a unique vascular plant community associated with *G. dewevrei* forest.

Material and methods – We utilised a combination of plot data and herbarium specimens collected in the Sangha Trinational (a network of protect areas in Cameroon, Central African Republic, and the Republic of Congo). Plot inventories were used to compare *G. dewevrei* forest and mixed forest for stem density, basal area, above ground biomass, stem size distribution, species diversity, and species composition. In addition, a database of 3,557 herbarium specimens was used to identify species of vascular plant that are associated with *G. dewevrei* forest.

Key results – *Gilbertiodendron dewevrei* forest is distinct in both structure and species composition from mixed forest. *Gilbertiodendron dewevrei* forest has a lower stem number (of trees ≥ 10 cm), but a greater proportion of larger trees (> 70 cm), suggesting higher carbon stocks. The species composition is distinct from mixed forest, with 56 species of vascular plant significantly associated with *G. dewevrei* forest.

Conclusion – Monodominant *G. dewevrei* forest in the Sangha Trinational is both compositionally and structurally distinct from mixed forest. We therefore recommend this forest type be considered separately from mixed forest for conservation planning and carbon stock calculations.

Keywords

carbon stocks, Congo Basin, conservation, floristic diversity, forest structure, *Gilbertiodendron dewevrei*, herbarium collections, monodominance, species composition

INTRODUCTION

Tropical forests contain the Earth's highest levels of terrestrial biodiversity, and are often central in biodiversity conservation discourse (Sullivan et al. 2017). To effectively prioritise conservation efforts, it is necessary to understand the different vegetation types that make up this broad habitat. Some fundamental differences between the three main tropical forest areas (Africa, Americas, and Asia) have been documented, in terms of both biodiversity (e.g. Slik et al. 2015) and structural attributes (e.g. Lewis et al. 2013). However, within the continental groups, forests vary substantially in both composition and structure (e.g. Thenkabail et al. 2003; Fayolle et al. 2014; Réjou-Méchain et al. 2021). A finer-scale understanding of differences in species composition of different forest types is important if the aim of conservation is to mitigate climate change and prevent species extinction.

In addition, tropical forests contain 40–50% of the carbon stored in terrestrial vegetation (Pan et al. 2011; Feldpausch et al. 2012), with accurate quantification of these stocks underpinning policies to mitigate CO₂ emissions such as IPCC recommendations and the UN-REDD+ program (Gibbs et al. 2007). However, there are still large uncertainties associated with tropical forest carbon stock estimations (Panzou et al. 2021). This is partly because the variation in biomass amongst different types of tropical forest is poorly quantified, particularly in Africa. When reporting carbon stored in vegetation, most central African countries rely on default IPCC values, which can be substantially different from reality (White et al. 2021). For example, Cuni-Sanchez et al. (2021) found that in montane forests near the edge of the Congo Basin, measured carbon storage values were 67% higher than the IPCC default values for these forests in Africa. Increasing knowledge of structural variation of different tropical forest types will help improve the accuracy of carbon stock models.

Central Africa is home to 30,423 plant species (Raven et al. 2020), and contains some of the most extensive tropical forests globally (UNESCO 1978; Justice et al. 2001; Hansen et al. 2013). These forests are recognised as a global conservation priority because of their high biodiversity, and extensive areas of intact, undisturbed, forest (Mittermeier et al. 1998; Brooks et al. 2006; Dargie et al. 2017; Grantham et al. 2020). However, plant diversity within Central African forests is increasingly being threatened by deforestation and degradation, with a preliminary assessment of 22,036 vascular plant species in tropical Africa revealing that 33% are threatened with extinction (Stévant et al. 2019). Shapiro et al. (2023) highlight the biggest cause of this as expanding small-scale agriculture, and associated roads and settlements. This is a complex issue, root causes of which include poverty, land tenure insecurity, weak legal frameworks, and lack of modern technologies and agricultural inputs (e.g. Tegegne et al. 2016). In addition, a recent pattern of decreased rainfall and higher temperatures reflect global

climatic changes. Ensuring that the Congo Basin forests are able to adapt to these changes, and protecting their plant diversity, requires coordinated conservation efforts, including addressing the many underlying social and political causes of deforestation and forest degradation, which simple fortress conservation may not solve.

A forest type that has gone almost unnoticed in conservation discourse in the Central African tropics is monodominant *Gilbertiodendron dewevrei* forest. These are forest stands in which 50–90% of the trees ≥ 10 cm in diameter belong to a single species: *Gilbertiodendron dewevrei*. *Gilbertiodendron dewevrei* forest is found across Nigeria, Cameroon, Central African Republic, Gabon, the Republic of Congo, and the Democratic Republic of Congo (DRC) (Gérard 1960). It occurs interspersed within mixed terre firme forest and stands range in size from patches of several trees to areas of hundreds of square kilometres (Gérard 1960; Letouzey 1968, 1985; Hart et al. 1989; Hart 1990). *Gilbertiodendron dewevrei* forest is found largely alongside rivers and streams (Blake and Fay 1997; Fayolle et al. 2014; Kearsley et al. 2017), but also in dry upland sites (Letouzey 1983; Barbier et al. 2017; Hall et al. 2020).

While substantial research has examined how *G. dewevrei* can achieve this remarkable level of dominance, there has been limited work looking at this forest as a vegetation type, and whether it is sufficiently distinct from adjacent mixed terre firme forest to merit separate treatment in conservation planning and carbon calculations. This has resulted in *G. dewevrei* forest being lumped with mixed species forest for conservation, or largely being ignored due to its perceived lower tree species diversity. For example, Grantham et al. (2020) identified 64 different forest ecosystems across Central Africa, but did not include any mention of *G. dewevrei* forest.

Most research into *G. dewevrei* forest has focused on the factors enabling this species to dominate stands. Barbier et al. (2017) conducted multivariate analysis on plot inventories from Cameroon and DRC, finding no correlation of *G. dewevrei* dominance with climate or pedagogical variables. Katembo et al. (2020) in forests east of Kisangani found that variation in abundance of three dominant species, including *G. dewevrei*, occur independently of topographical or pedagogical variables. This study also found strong correlations between the dominance in the canopy and in the lower strata, suggesting this as indicative of multiple stable states induced by endogenous feedbacks. Substantial research has been conducted into traits specific to *G. dewevrei* allowing it to achieve high levels of dominance. Torti et al. (2001) concluded that the monodominance of *G. dewevrei* was due to a suite of adult traits of this species allowing it to modify the understory environment, inhibiting recruitment of other species. These include forming a dense canopy, which shades the understorey, and creating a deep layer of leaf litter that decomposes slowly, hindering seed germination and seedling

establishment, and leading to lower nutrient turnover. Peh et al. (2011) present a mechanistic model for *G. dewevrei* monodominance that includes feedbacks among traits and with the environment. These include adult traits to modify the understory; traits which enable *G. dewevrei* seedlings to persist in this inhospitable environment (e.g. large seeds, shade tolerance, and mast fruiting), and a lack of endogenous and exogenous disturbance. Hall et al. (2020) reframed this model to one of resource acquisition, showing that *G. dewevrei* forest occurs on infertile soils and providing evidence for the role of EM fungi in allowing *G. dewevrei* to directly acquire nitrogen and phosphorus from soil organic matter. They also show that seedlings of *G. dewevrei* survive and grow well under a wide variety of light environments, providing a competitive advantage to recruit and release at different light levels. Hall et al. (2020) conclude that these factors combine to allow *G. dewevrei* to be competitively superior at acquiring and retaining resources. In addition, Tovar et al. (2019) found that *G. dewevrei* has persisted in one location in the Sangha Trinational for at least 2,700 years, in the absence of major disturbance, suggesting that lack of disturbance may also be an important contributing factor to *G. dewevrei* monodominance.

In addition to the presence or absence of *G. dewevrei*, some differences have been found between *G. dewevrei* forest and mixed terre firme forest in terms of structure and species diversity. A lower tree species richness and diversity has been found in *G. dewevrei* compared to mixed forest in the Sangha Trinational (Hall et al. 2020). This has also been shown by Hart et al. (1989) and Glick et al. (2021) in the Ituri region (eastern DRC), by Djuikouo et al. (2010, 2014) and Peh et al. (2014) in the Dja Biosphere reserve (Cameroon), and by Kearsley et al. (2017) in Yangambi (central DRC). Katembo et al. (2020) found that monodominance in the Cuvette Centrale (east of Kisangani, DRC) was associated with low richness of both rare and abundant tree species. However, published data on species composition is rare. The consensus from the literature is that the floristic composition of the two forest types is similar, except for the presence or absence of *G. dewevrei*. For example, Hart (1990) and Hart et al. (1996) reported that monodominant forest patches have the same overall species composition as adjacent mixed forest, and that mixed forest species are not excluded. This was also reported by Djuikouo et al. (2010), when examining monodominant *G. dewevrei* forests in the Dja Reserve (Cameroon). However, this does not fit with observations of *G. dewevrei* forest in the Sangha Trinational, where certain species have been identified that are more common in *G. dewevrei* forest, and some which have only been seen in this forest type (Harris 2002).

Differences in stand structure have also been observed between monodominant *G. dewevrei* and mixed terre firme species forest, although findings are less consistent than for species richness and diversity. Within the Sangha Trinational, Hall et al. (2020) reported lower

stem numbers in monodominant forest than plots in one stand of mixed forest, but not the other two mixed forest stands sampled, and found no difference in basal area. A lower stem number has also been reported by Hart et al. (1989) in the Ituri forest (eastern DRC), and Djuikouo et al. (2014) and Glick et al. (2021) in the Dja Biosphere Reserve (Cameroon), whilst Djuikouo et al. (2010) found no significant difference in stem number between *G. dewevrei* forests and heterogeneous terre firme forests. Hart et al. (1989) and Harris (2002) observed that the structure of *G. dewevrei* forest is much more homogenous than that of mixed forest, with a more or less continuous canopy of *G. dewevrei* crowns. In the Dja Biosphere Reserve, Djuikouo et al. (2010) found higher above ground biomass (AGB) in *G. dewevrei* forest, which was also seen in the Ituri forest (Makana et al. 2011; Glick et al. 2021). Makana et al. (2011) concluded that 25% more biomass was stored in *G. dewevrei* forest than mixed forest in the Ituri region of DRC, and a spread of *G. dewevrei* would significantly increase carbon stored in the Congo Basin forests. Aboveground biomass of *G. dewevrei* forest has yet to be investigated in the Sangha Trinational.

In this study, we use a combination of plot inventories and herbarium specimens to compare monodominant *G. dewevrei* forest with mixed terre firme forest in the Sangha Trinational in terms of forest structure and composition of vascular plants. Specifically, this study aims to: (1) Investigate differences in forest structural attributes between monodominant *G. dewevrei* and mixed terre firme forest, in particular AGB and stem size distributions. (2) Compare tree species richness, diversity, and equitability between monodominant *G. dewevrei* and mixed terre firme forest. (3) Use plot inventories to investigate differences in tree species composition between monodominant *G. dewevrei* and mixed terre firme forests, identifying indicator tree species for each forest type. (4) Use herbarium specimens to investigate differences in species composition of vascular plants between monodominant and mixed forest, identifying those species associated with *G. dewevrei* forest.

MATERIAL AND METHODS

Study area

This research was carried out in the Sangha Trinational ('Trinational de la Sangha' or 'TNS'), which is a network of protected areas in the north-west of the Congo River Basin, where Cameroon, the Central African Republic, and the Republic of Congo meet at the Sangha River (Fig. 1). It covers a total area of 746,309 hectares, including three national parks: the Nouabalé-Ndoki National Park (Republic of the Congo; 2°05'–3°03'N, 16°51'–16°56'E, 4238.7 km²), the Lobéké National Park (Cameroon; 2°05'–2°30'N, 15°33'–16°11'E, 2178.54 km²), and the Dzanga-Ndoki National Park (Central African Republic; 2°22'–3°08'N, 16°06'–16°55'E, 1143.26 km²), as well as a

forest reserve and buffer zones where logging, hunting, and the harvesting of some non-timber forest products is permitted (Dzanga Sangha Reserve, Central African Republic, 6865.54 km²). This region was classified by White (1983) as mixed moist semi-evergreen Guineo-Congolian rainforest. Harris (2002) identified five forest types in this area: mixed species terre firme forest, monodominant *Gilbertiodendron dewevrei* forest, streamside forest, *Raphia* swamp forest, and seasonally flooded forest along the Sangha River. Approximately 11% of the vegetation of the Sangha Trinational consists of monodominant *G. dewevrei* forest (Blake and Fay 1997; Laporte 2002; Hall et al. 2020). Annual rainfall within the Sangha Trinational ranges from 1,450 to over 1,600 mm, and it is wetter in the south and drier in the north (European Commission 2010; Hall et al. 2020). Soils within the region can be broadly classified as Ferralsols (both Xanthic and Orthic) and Orthic Luvisols (FAO/UNESCO 1977).

Data

Data collected consisted of (1) tree plot inventories and (2) herbarium specimens of vascular plants collected through general collecting.

Plot data collection

The plot data consists of two datasets, with a total of 93 plots. From 2000 to 2002, 82 plots of 30 m × 30 m were established in the Sangha Trinational, 17 in *G. dewevrei* forest and 65 in mixed terre firme forest. All 82 plots were in unlogged forest with no permanent villages or fields within 10 km of any plot. Plots were in blocks of 16–18, distributed across five sites (A, B, C, D, and E; Fig. 1). At each site, the 30 m × 30 m plots were laid out at 500 m intervals along four parallel 1.5 km transects as described by Hall et al. (2003). In November–December 2022, additional plots were set up in *G. dewevrei* forest within the Nouabalé-Ndoki National Park, at the Goulougo Triangle Ape Project (site F). These consist of nine plots 100 m × 20 m, and two further plots of 130 m × 20 m and 56.75 m × 40 m respectively.

Within each plot, diameters were measured, and species identified for all trees ≥ 10 cm diameter at breast height (dbh). Diameters were measured at 1.3 m above the ground, except for trees with buttresses, which were measured 50 cm above the buttress. All identifications were made using one list of names (Harris and Wortley 2008), and species are organised within families as recognised by APG II taxonomy. Voucher specimens were made of each species and unidentified trees for later identification and are stored, mostly unmounted, at the Royal Botanic Garden Edinburgh and the Republic of Congo's National Herbarium in Brazzaville.

Structural analysis

All structural analyses were calculated on stem-level data; including multi-stemmed trees as separate stems (2% of

trees were multi-stemmed). Stem number and basal area were calculated for each plot, and then scaled up to per hectare measurements to allow for comparison. The basal area of each plot was calculated as the sum of all stems' basal area. AGB was calculated using regional allometric equations developed and tested by Fayolle et al. (2018) for Congo Basin forests. Regional model 12 was selected, as this was found to achieve the highest accuracy where height measurements were absent.

$$AGB_{est} = \exp[0.046 + 1.156 \times \log(WSG) + 1.123 \times \log(D) + 0.436 \times (\log(D))^2 - 0.045 \times (\log(D))^3]$$

Wood density was derived from tree species identity using the global wood density (GWD) database as a reference (Chave et al. 2009; Zanne et al. 2009; Réjou-Méchain et al. 2017). This was carried out using the `getWoodDensity` function from the R package `BIOMASS` v.2.1.8 (Réjou-Méchain et al. 2017). For trees only identified to genus level, the average wood density for the genus was used. For unidentified trees, those only identified to family level, or for genera missing from the reference database, the stand-level average wood density was used. Trees identified to family level were assigned stand-level average as taxon-average approach has been found to give relatively poor estimates above the genus level (Flores and Coomes 2011). AGB was then calculated at individual tree level using the above equation, and the AGB for each plot was calculated as the sum of all stems' AGB.

AGB was also calculated using the pantropical generalized allometric model eqn 4 (Chave et al. 2014), with heights estimated using the region-specific model proposed by Feldpausch et al. (2012), for the Central African region. This was carried out using the R package `BIOMASS` v.2.1.8 (Réjou-Méchain et al. 2017). Very similar results were found with the two methods, therefore we chose to only present the regional method, as it has been found to show a smaller bias for Congo Basin forests (Fayolle et al. 2018).

Significance of differences between structural features (stem number, BA, and AGB) of the two forest types were determined using Welch two-sample t-tests (Welch 1938), after verification of assumptions of normality. A Bartlett test was run to compare variance of each structural feature within each forest type (Snedecor and Cochran 1989). Density plots of dbh were also constructed to allow visual comparisons of stem size distribution between monodominant and mixed forest.

To verify plots of different size were not adding a signal in the analysis, analysis of per ha structural attributes was repeated comparing the different sized *G. dewevrei* plots (the 30 m × 30 m plots and the 100 m × 40 m plots). To address imbalance in number of plots between each forest type, analysis was also carried out comparing monodominant *G. dewevrei* plots to a randomly selected equal number of mixed forest plots, for each structural

metric. This was repeated 100 times and the mean p values reported.

Species richness, diversity, and equitability

All diversity and species composition analyses were calculated on individual tree-level data. Data were restricted to trees identified to species level (92.9% of individual trees).

We compared species richness, diversity, and equitability of the two forest types. To account for differing plot sizes, each plot was randomly subsampled (to 20 stems). This was done 100 times, and each time we calculated the species richness (total number of species) of trees with stems ≥ 10 cm dbh of each plot. Species diversity was calculated using the Shannon-Wiener Index (H') (Shannon 1948):

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

where S is the total number of species in the plot, p_i is the proportional abundance of the i^{th} species and \ln is the natural logarithm. Estimated abundance evenness for each plot was calculated using the Shannon Equitability Index (EH'), which is the ratio of H' to the log

transformed species richness (Smith and Wilson 1996). All measures were calculated using the R package *vegan* v.2.6-2 (Oksanen et al. 2022). A mean value for each metric across the 100 repeated subsamples was taken. Significance in differences between the two forest types for species richness, species diversity, and species evenness were tested using Welch two-sample t -tests (Welch 1938). These analyses were also repeated after removal of stems of *G. dewevrei* from the data prior to rarefaction.

Species composition

We used a Detrended Correspondence Analysis (DCA) and Non-metric Multidimensional Scaling (NMDS) to assess the variation in species composition between *G. dewevrei* and mixed terre firme forest plots. Ordinations were run on site-species matrices, containing the number of each of the 230 species in each of the 93 plots. The NMDS was run with four dimensions, with Bray-Curtis dissimilarity as the optimal measure of ecological distance and a well-established, asymmetric coefficient (Legendre and De Cáceres 2013). The DCA analysis was run with 26 segments, and a rescaling of axes with four iterations. Two ordination techniques were used to strengthen our conclusions, as they each have different advantages and limitations. DCA is well suited for analysis of non-linear gradients, but its approach for dealing with non-linearity is brute-force, which can sometimes introduce new distortions. In addition, a DCA is implicitly based

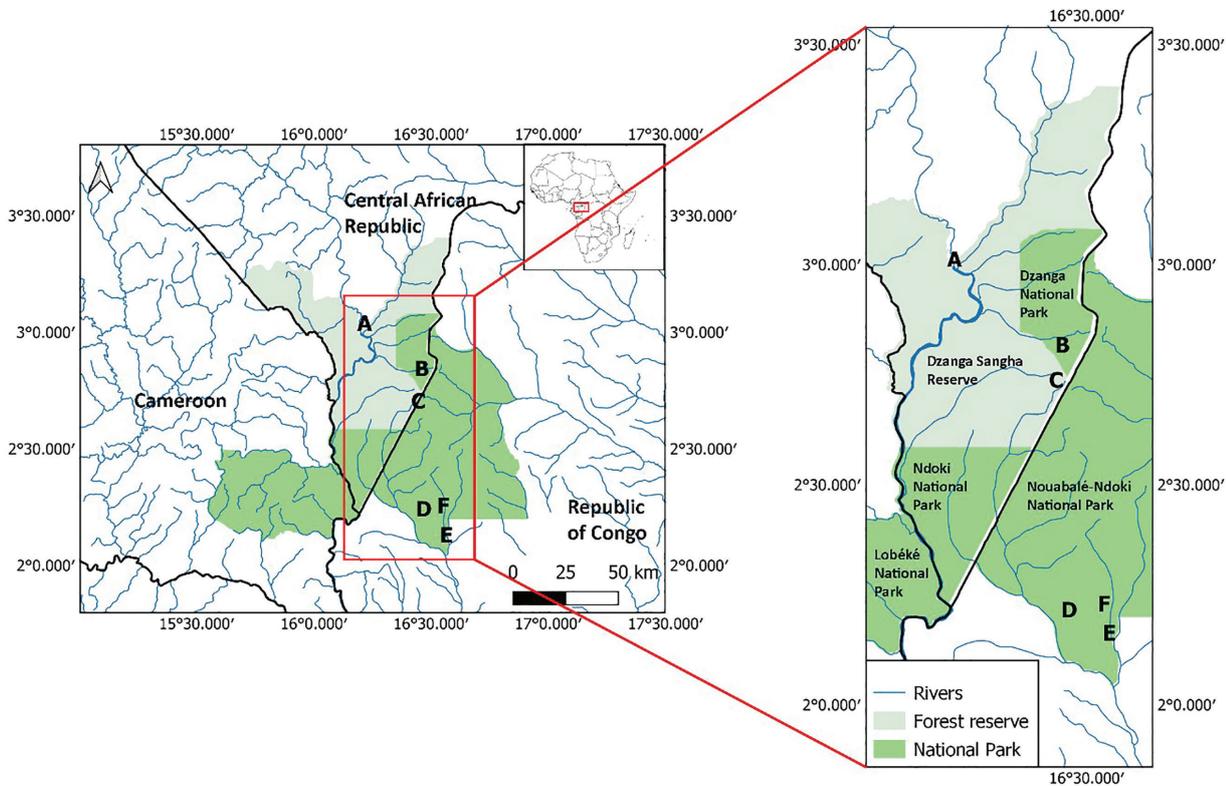


Figure 1. Map showing the location of the Sangha Trinational within the African continent, and the position of the plot sites. Letters represent sites where the plots were located. Sites A, C, D, and E are mixed terre firme forest plots, and sites B and F are *Gilbertiodendron dewevrei* plots. Created using QGIS v.3.22.

on chi-square distances, which can emphasise the contribution of rare species. NMDS based on a Bray-Curtis, on the other hand, imposes minimal distortions on the data, but assumes monotonic relationships and so may be affected by non-linearity in the data. Analysis of similarities (ANOSIM) was used to test the compositional differentiation of the vegetation types in the NMDS and DCA.

These ordination and ANOSIM analyses have been used in a number of studies examining the species composition of different vegetation types (Borcard et al. 2011; Legendre and Legendre 2012). Ordination and ANOSIM analyses were carried out using the R package *vegan* v.2.6-2 (Oksanen et al. 2022). The ANOSIM analysis was also carried out on the mixed terre firme

plots alone, repeatedly (100 times), while comparing a randomly selected 50% of plots to the other 50%, to provide a control.

We then performed an indicator species analysis to test whether there was a subset of species showing an association with each forest type. An Indicator Value (IV) is derived, with high IV values representing greater affinity of a given species towards a certain vegetation type. Analysis was carried out using the R package *indicpecies* v.1.7.12 function *R.g.* (De Cáceres and Legendre 2009).

Herbarium specimen dataset

We conducted analysis on a dataset of herbarium specimens of vascular plants collected in the Sangha

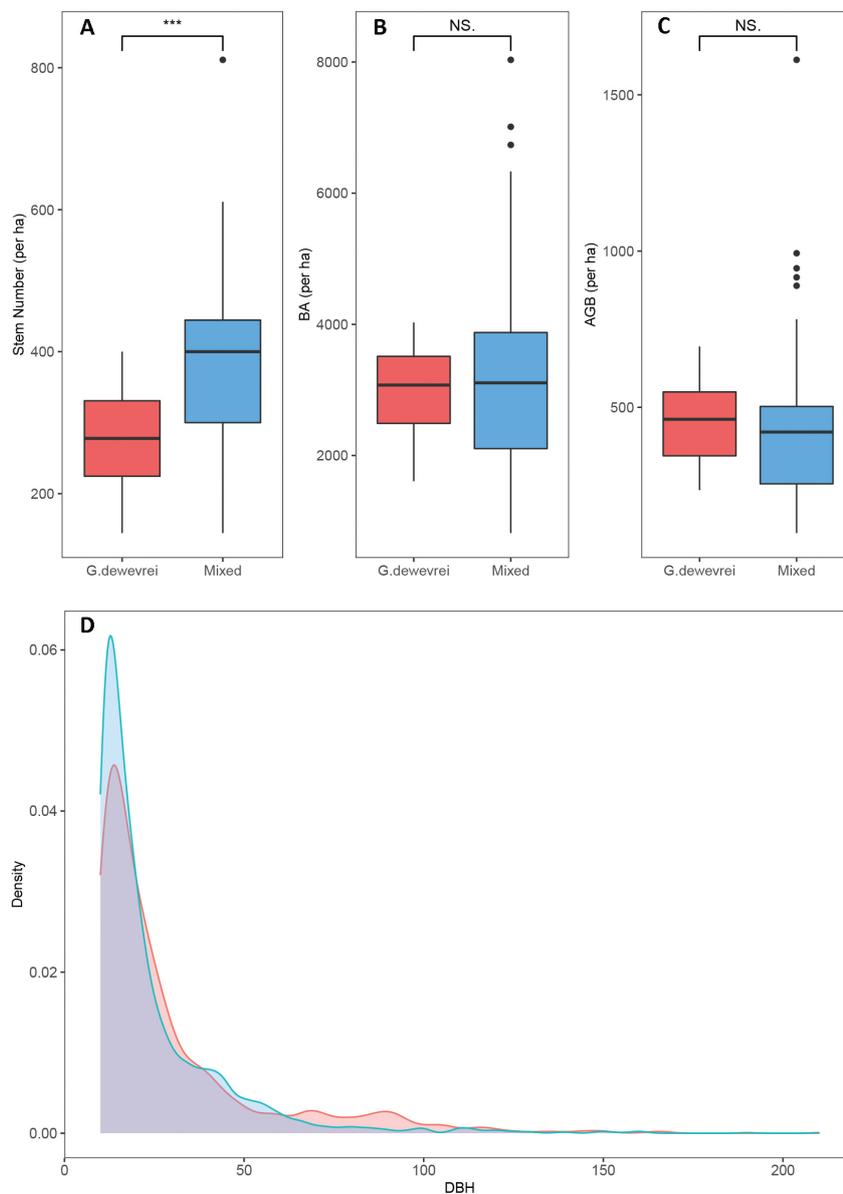


Figure 2. Structure of *Gilbertiodendron dewevrei* (red) and mixed terre firme (blue) plots. **A.** Stem number per hectare. **B.** Basal Area (BA) per hectare. **C.** Above Ground Biomass (AGB) per hectare. **D.** Density distribution of stem size. Whiskers on box plots represent 1.5 times the interquartile range plus or minus the first and third quartiles respectively. Values found beyond the whiskers are shown individually as points. Stars signify significance (***) represents $p < 0.001$ and NS indicates a lack of significant difference).

Trinational between 1987 and 2019. Plot vouchers were removed from the dataset, leaving only specimens collected through general collecting. General collecting, described by Harris (2002), was systematic and aimed at collecting specimens at different stages, in different habitats and at different localities. The aim was to collect all vascular plants whatever their life form, so the less commonly collected forms such as epiphytes and floating aquatics were also included with the more standard herbs, shrubs and trees. Specimens were collected and identified to species level by David J. Harris, with the help of other taxonomists. Species with less than five collections were removed from the dataset. Specimens were then classified from herbarium label data as either being collected from *G. dewevrei* forest or in other habitat types. A total of 10.2% of the specimens were collected in *G. dewevrei* forest.

We determined whether each species demonstrated a preference for *G. dewevrei* forest by comparing observed and expected frequencies using χ^2 tests. Observed frequencies were the counts of specimens collected in *G. dewevrei* forest or other habitat and expected frequencies were calculated under the assumption that 10.2% of specimens for each species would be collected in *G. dewevrei* forest, according to the collecting frequencies in *G. dewevrei* forest and other habitat types. Significant deviation from the expected frequencies was indicated

when $p < 0.05$. When χ^2 was significant, we assessed the source of significance by calculating post-hoc the Pearson standardised residual for *G. dewevrei* forest using the formula (observed - expected / $\sqrt{\text{expected}}$). A residual of greater than 1.95 indicated that the species had a significantly higher than expected proportion of specimens collected in *G. dewevrei* forest. This method was adapted from Cardoso et al. (2021), replacing stems with herbarium specimens.

All analyses were conducted in R v.4.2.1 (R Core Team 2022).

RESULTS

Comparison of structural attributes and floristic diversity of monodominant *G. dewevrei* and mixed terre firme forest using tree plot inventories

A total of 3,285 individual trees were measured across the 93 plots, 1,021 in *G. dewevrei* forest and 2,263 in mixed terre firme forest. 3,050 trees were identified to species level, 922 in *G. dewevrei* forest and 2,058 in mixed terre firme forest. These included trees from 46 families, 153 genera, and 232 species. The proportion of trees not identified to species level was higher in mixed forest (9.1%) than in *G. dewevrei* forest (2.8%).

Forest structure

Stem density was lower in *G. dewevrei* forest compared to mixed forest ($p < 0.001$); however, no significant difference in average plot basal area was found between the two forest types (Fig. 2). *Gilbertiodendron dewevrei* forest also has less variability in stem number and basal area than mixed terre firme forest (Bartlett test, $p < 0.01$ and $p < 0.001$ for stem number and BA respectively). AGB was higher in *G. dewevrei* forest than mixed terre firme forest, although this difference was not statistically significant (464.6 Mg ha^{-1} and 427.0 Mg ha^{-1} respectively, $p = 0.365$). The same results were found in the sensitivity analysis using equal plot numbers between the two forest types (significantly lower number of stems in *G. dewevrei* forest: $p < 0.001$, and no significant difference between BA or AGB between the two forest types: $p > 0.05$). Different sized *G. dewevrei* plots showed no significant difference in structural attributes, verifying that plot size is not adding a signal into this analysis (Supplementary material 1).

Stem diameter distributions in *G. dewevrei* forest plots were comparable to mixed terre firme forest plots, following the classic reverse J-shaped pattern. The density plot (Fig. 2C) indicates however that there are fewer smaller trees ($< 20 \text{ cm}$) and a greater number of larger trees ($> 70 \text{ cm dbh}$) in *G. dewevrei* forest than the mixed forest stands. Figure 3 shows examples of the visual differences in forest structure of *G. dewevrei* and mixed terre firme forest.



Figure 3. Photographs of forest types in the Nouabalé-Ndoki National Park, Republic of Congo, to illustrate structural differences. **A.** Monodominant *Gilbertiodendron dewevrei* forest. Photograph taken by David J. Harris. **B.** Mixed species terre firme forest. Photograph taken by Ellen Heimpel.

Tree species richness, diversity, and equitability

Species richness, Shannon-Wiener Diversity (H') and estimated abundance evenness (EH') were all lower in *G. dewevrei* plots than in mixed terre firme forest plots (Fig. 4). Mean species richness of *G. dewevrei* plots was 8.4 ± 0.6 per 20 trees, compared to 15.2 ± 0.2 in mixed terre firme plots ($p < 0.001$). Species diversity (Shannon-Wiener - H') in *G. dewevrei* forest was 5.5 ± 0.5 per 20 trees compared to 13.8 ± 0.3 in mixed terre firme forest ($p < 0.001$). Shannon Equitability was also significantly lower in *G. dewevrei* forest (0.620 ± 0.020 per 20 trees compared to 0.902 ± 0.006 , $p < 0.001$). The same trends were seen for species richness and Shannon-Wiener Diversity when *G. dewevrei* stems were removed from the analysis. Shannon equitability however was higher in *G. dewevrei* forest than mixed terre firme forest after the removal of *G. dewevrei* stems (0.938 ± 0.009 in *G. dewevrei* forest compared to 0.902 ± 0.006 in mixed, $p < 0.01$).

Tree species composition

There was a clear difference in the species composition of *G. dewevrei* plots compared to mixed terre firme plots. An ANOSIM analysis comparing species composition in the two forest types found a significant difference (0.663, $p < 0.001$), highlighting that the variation between the two forest groups is bigger than within-group variation. This difference persisted when *G. dewevrei* stems were removed from the analysis (0.406, $p < 0.001$). The control analysis run only on the mixed forest plots, found no difference (-0.00153, standard error = 0.0025). Plot composition formed two distinct groups in both the DCA (Fig. 5A),

and the NMDS (Fig. 5B), with *G. dewevrei* plots clustering together, separated from the mixed terre firme forest. The two ordinations align, indicating that there are two clear groups. The indicator species analysis identified seven indicator species for *G. dewevrei* forest (Table 1). Twenty-one species were identified as indicator species for mixed forest (Supplementary material 2).

Identification of *Gilbertiodendron dewevrei* associated species using a dataset of herbarium specimens

The herbarium dataset consisted of 3,557 specimens, all identified to species level. These spanned 72 families, 253 genera, and 397 species of vascular plants. Of these, 383 specimens were collected in *G. dewevrei* forest belonging to 44 families, 109 genera, and 163 species.

The χ^2 analysis and post-hoc Pearson's calculation of the herbarium specimen dataset identified 52 species of vascular plant that are significantly associated with *G. dewevrei* forest (Table 2). These cover 20 families of vascular plant, 38 genera, and include 15 trees, 19 shrubs, 14 herbs, 2 climbers, 1 hemiepiphyte, and 1 hemiparasite.

DISCUSSION

We compared monodominant *Gilbertiodendron dewevrei* forest in the Sangha Trinational with adjacent mixed terre firme forest in terms of structure, species diversity and composition of vascular plants, asking whether *G. dewevrei*

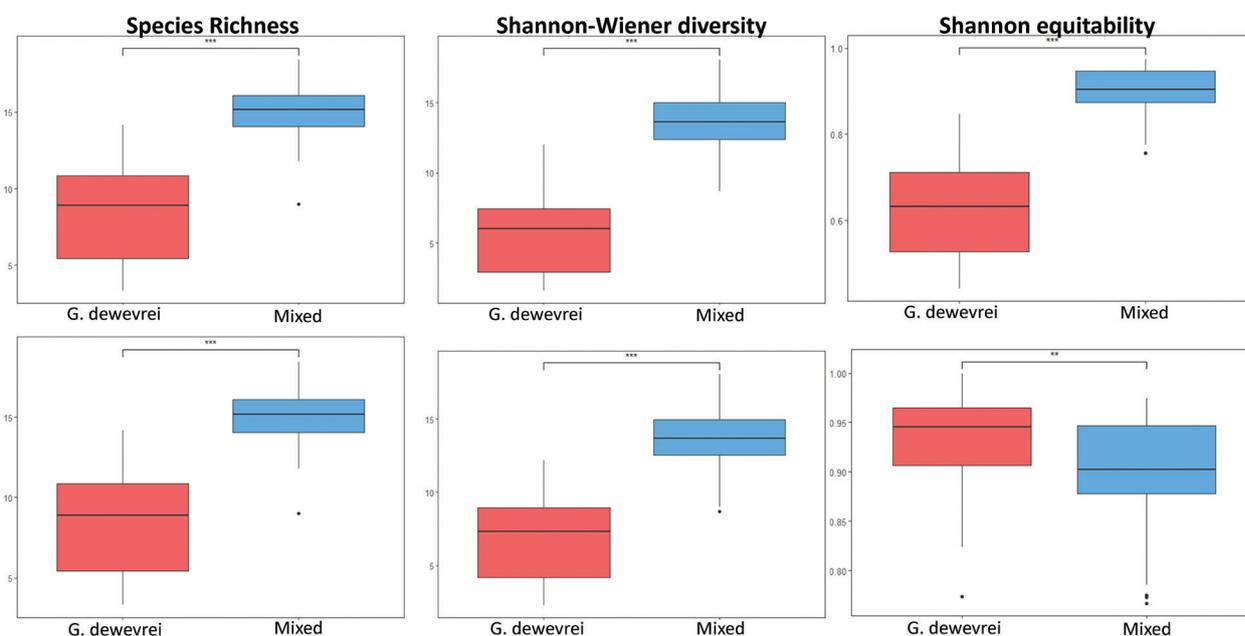


Figure 4. Variation in species richness, diversity, and equitability in *Gilbertiodendron dewevrei* forest and mixed terre firme forest. Top row of panels shows analyses including *G. dewevrei* stems; lower row of panels shows analyses excluding stems of *G. dewevrei*. Boxes bound the first and third quartiles respectively, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the first and third quartiles respectively. Stars indicate Welch two-sample t-test significance levels (***) $p < 0.001$, ** $p < 0.01$).

Table 1. *Gilbertiodendron dewevrei* forest specialists identified from indicator species analysis of plot data collected in the Sangha Trinational.

| Species | Family | Indicator species value | |
|---|------------------------------------|-------------------------|---------|
| | | Indicator value | p value |
| <i>Gilbertiodendron dewevrei</i> (De Wild.) J.Léonard | Fabaceae (subfamily: Detarioideae) | 0.811 | < 0.001 |
| <i>Isolona hexaloba</i> (Pierre) Engl. & Diels | Annonaceae | 0.474 | < 0.001 |
| <i>Tessmannia africana</i> Harms | Fabaceae (subfamily: Detarioideae) | 0.330 | < 0.05 |
| <i>Manilkara mabokeensis</i> Aubrév. | Sapotaceae | 0.267 | < 0.05 |
| <i>Anonidium mannii</i> (Oliv.) Engl. & Diels | Annonaceae | 0.248 | < 0.05 |
| <i>Uvariastrum germainii</i> Boutique | Annonaceae | 0.238 | < 0.05 |
| <i>Drypetes cinnabarina</i> Pax & K.Hoffm. | Putranjivaceae | 0.237 | < 0.05 |

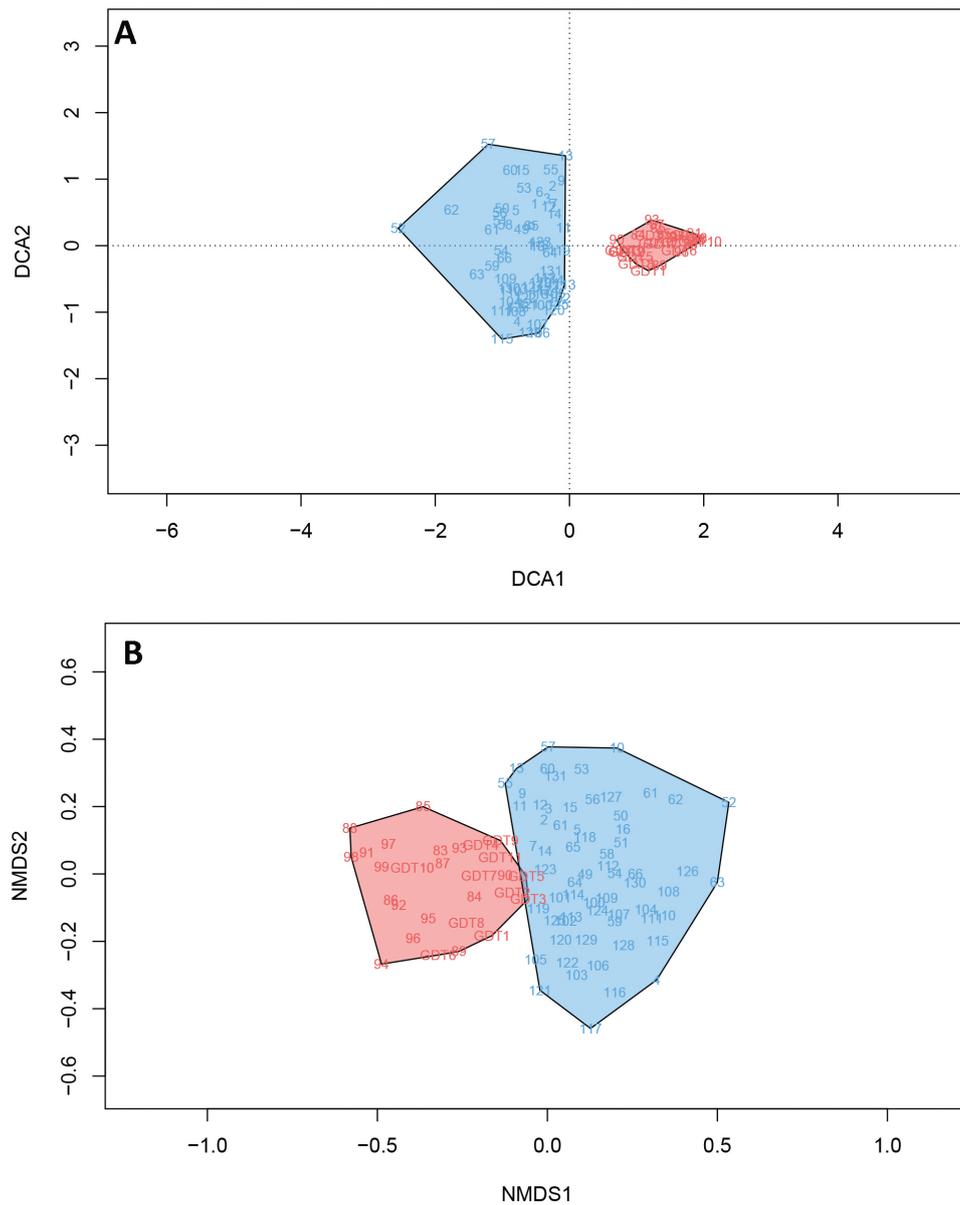


Figure 5. Detrended Correspondence Analysis (DCA) (A) and Non-metric Multidimensional Scaling (NMDS) (B) of plots in the Sangha Trinational, showing the variation in tree species composition between forest types. Red plots are *Gilbertiodendron dewevrei* forest and blue plots are mixed terre firme forest. In the DCA, 89.48% of the variance was explained by axis 1 and 2 (57.0% and 31.98% respectively). The NMDS was run with four dimensions and the stress value was 0.176.

Table 2. Fifty-two *Gilbertiodendron dewevrei* associates identified from χ^2 analysis of herbarium specimens collected in the Sangha Trinational. Table displays p values of χ^2 tests on observed vs expected frequencies in *G. dewevrei* forest, and the associated residuals (Pearson standardized), as well as the percentage of specimens collected in *G. dewevrei* forest and the growth form of each species. Species are listed in descending order of Pearson Residual, with a higher Residual indicating a greater degree of departure between expected and observed numbers in *G. dewevrei* forest.

| Species | Family | p value | Residual | Percentage in <i>G. dewevrei</i> forest | Growth form |
|---|--|----------|----------|---|-----------------|
| <i>Helixanthera subalata</i> (De Wild.) Wiens & Polhill | Loranthaceae | < 0.0001 | 7.9 | 90.0 | hemiparasite |
| <i>Microcos pinnatifida</i> (Mast.) Burret | Malvaceae | < 0.0001 | 7.44 | 81.8 | tree (or shrub) |
| <i>Diospyros ferrea</i> (Willd.) Bakh. | Ebenaceae | < 0.0001 | 6.91 | 80.0 | tree |
| <i>Psychotria cyanopharynx</i> K.Schum. | Rubiaceae | < 0.0001 | 5.92 | 70.0 | shrub |
| <i>Campylospermum excavatum</i> (Tiegh.) Farron | Ochnaceae | < 0.0001 | 5.55 | 63.6 | shrub |
| <i>Chassalia lutescens</i> O.Lachenaud & D.J.Harris | Rubiaceae | < 0.0001 | 5.55 | 63.6 | shrub |
| <i>Psychotria nodiflora</i> O.Lachenaud & D.J.Harris | Rubiaceae | < 0.0001 | 5.3 | 66.7 | shrub |
| <i>Daniellia pynaertii</i> De Wild. | Fabaceae (subfamily: Detarioideae) | < 0.0001 | 4.89 | 80.0 | tree |
| <i>Marantochloa monophylla</i> (K.Schum.) D'Orey | Marantaceae | < 0.0001 | 4.89 | 80.0 | herb |
| <i>Leptactina pynaertii</i> De Wild. | Rubiaceae | < 0.0001 | 4.76 | 47.1 | shrub |
| <i>Leptaulus congolanus</i> (Baill.) Loeb.-Callen & Villiers | Cardiopteridaceae | < 0.0001 | 4.63 | 62.5 | shrub |
| <i>Copaifera mildbraedii</i> Harms | Fabaceae (subfamily: Detarioideae) | < 0.0001 | 4.61 | 54.6 | tree |
| <i>Marantochloa congensis</i> (K.Schum.) J.Léonard & Mullend. | Marantaceae | < 0.0001 | 4.55 | 44.4 | herb |
| <i>Aframomum longiligulatum</i> Koechlin | Zingiberaceae | < 0.0001 | 4.33 | 66.7 | herb |
| <i>Cleistanthus caudatus</i> Pax | Phyllanthaceae | < 0.0001 | 4.26 | 55.6 | tree |
| <i>Belonophora coriacea</i> Hoyle | Rubiaceae | < 0.0001 | 3.94 | 50.0 | shrub |
| <i>Eumachia macrocarpa</i> (Verdc.) Razafim. & C.M.Taylor | Rubiaceae | < 0.0001 | 3.89 | 57.1 | shrub |
| <i>Dicranolepis buchholzii</i> Engl. & Gilg | Thymelaeaceae | < 0.0001 | 3.89 | 57.1 | shrub |
| <i>Calycosiphonia spathicalyx</i> (K.Schum.) Robbr. | Rubiaceae | < 0.001 | 3.66 | 45.5 | shrub |
| <i>Gilbertiodendron dewevrei</i> (De Wild.) J.Léonard | Fabaceae (subfamily: Detarioideae) | < 0.001 | 2.49 | 60.0 | tree |
| <i>Streblus usambarensis</i> (Engl.) C.C.Berg | Moraceae | < 0.001 | 3.49 | 60.0 | shrub |
| <i>Geophila afzelii</i> Hiern | Rubiaceae | < 0.0001 | 3.49 | 60.0 | herb |
| <i>Geophila obvallata</i> (Schumach.) Didr. | Rubiaceae | < 0.0001 | 3.49 | 60.0 | herb |
| <i>Trichostachys microcarpa</i> K.Schum. | Rubiaceae | < 0.001 | 3.49 | 60.0 | shrub |
| <i>Agelaea paradoxa</i> Gilg | Connaraceae | < 0.001 | 3.41 | 41.7 | climber |
| <i>Hymenocoleus hirsutus</i> (Benth.) Robbr. | Rubiaceae | < 0.001 | 3.41 | 41.7 | herb |
| <i>Chytranthus gillettii</i> De Wild. | Sapindaceae | < 0.001 | 3.24 | 35.3 | tree |
| <i>Chytranthus macrobotrys</i> (Gilg) Exell & Mendonça | Sapindaceae | < 0.001 | 3.22 | 44.4 | tree |
| <i>Diospyros pseudomespilus</i> Mildbr. | Ebenaceae | < 0.001 | 3.19 | 38.5 | tree |
| <i>Empogona gossweileri</i> (S.Moore) Tosh & Robbr. | Rubiaceae | < 0.001 | 3.19 | 38.5 | tree |
| <i>Palisota mannii</i> C.B.Clarke | Commelinaceae | < 0.01 | 3.05 | 50.0 | herb |
| <i>Tessmannia africana</i> Harms | Fabaceae (subfamily: Detarioideae) | < 0.01 | 2.81 | 33.3 | tree |
| <i>Commelina capitata</i> Benth. | Commelinaceae | < 0.01 | 2.72 | 36.4 | herb |

Table 2 (continued). Fifty-two *Gilbertiodendron dewevrei* associates identified from χ^2 analysis of herbarium specimens collected in the Sangha Trinational. Table displays p values of χ^2 tests on observed vs expected frequencies in *G. dewevrei* forest, and the associated residuals (Pearson standardized), as well as the percentage of specimens collected in *G. dewevrei* forest and the growth form of each species. Species are listed in descending order of Pearson Residual, with a higher Residual indicating a greater degree of departure between expected and observed numbers in *G. dewevrei* forest.

| Species | Family | p value | Residual | Percentage in <i>G.dewevrei</i> forest | Growth form |
|--|--|---------|----------|--|-----------------|
| <i>Tessmannia anomala</i> (Micheli) Harms | Fabaceae (subfamily: Detarioideae) | < 0.01 | 2.71 | 42.9 | tree |
| <i>Chassalia chrysoclada</i> (K.Schum.) O.Lachenaud | Rubiaceae | < 0.01 | 2.71 | 42.9 | shrub |
| <i>Campylopermum reticulatum</i> (P.Beauv.) Farron | Ochnaceae | < 0.01 | 2.51 | 33.3 | shrub |
| <i>Aframomum letestuanum</i> Gagnep. | Zingiberaceae | < 0.01 | 2.48 | 29.4 | herb |
| <i>Palisota brachythyrsa</i> Mildbr. | Commelinaceae | < 0.05 | 2.42 | 37.5 | herb |
| <i>Polyspatha paniculata</i> Benth. | Commelinaceae | < 0.01 | 2.42 | 37.5 | herb |
| <i>Scepocarpus thonneri</i> (De Wild. & T.Durand) T.Wells & A.K.Monro | Urticaceae | < 0.05 | 2.42 | 37.5 | climber |
| <i>Irvingia grandifolia</i> (Engl.) Engl. | Irvingiaceae | < 0.05 | 2.32 | 30.8 | tree |
| <i>Stanfieldiella imperforata</i> (C.B.Clarke) Brenan | Commelinaceae | < 0.05 | 2.2 | 26.3 | herb |
| <i>Bertiera iturensis</i> K.Krause | Rubiaceae | < 0.05 | 2.17 | 33.3 | shrub |
| <i>Eumachia gossweileri</i> (Cavaco) Razafim. & C.M.Taylor | Rubiaceae | < 0.05 | 2.17 | 33.3 | shrub |
| <i>Palisota thollonii</i> Hua | Commelinaceae | < 0.05 | 2.09 | 40.0 | herb |
| <i>Warneckea jasminoides</i> (Gilg) Jacq.-Fél. | Melastomataceae | < 0.05 | 2.09 | 40.0 | tree (or shrub) |
| <i>Ficus elasticoides</i> De Wild. | Moraceae | < 0.05 | 2.09 | 40.0 | hemiepiphyte |
| <i>Lasianthus batangensis</i> K.Schum. | Rubiaceae | < 0.05 | 2.09 | 40.0 | shrub |
| <i>Rothmannia lateriflora</i> (K.Schum.) Keay | Rubiaceae | < 0.05 | 2.09 | 40.0 | shrub |
| <i>Aframomum scalare</i> D.J.Harris & Wortley | Zingiberaceae | < 0.05 | 2.09 | 40.0 | herb |
| <i>Isolona hexaloba</i> (Pierre) Engl. & Diels | Annonaceae | < 0.05 | 1.96 | 30.0 | tree |
| <i>Crotonogyne poggei</i> Pax | Euphorbiaceae | < 0.05 | 1.96 | 30.0 | shrub |

forest is sufficiently distinct to merit separate treatment in conservation planning and carbon calculations. Our results show that *G. dewevrei* forest has structural and compositional differences when compared to mixed terre firme forest. Notably, *G. dewevrei* forest has an apparent greater proportion of larger trees than mixed terre firme forest, and contains a distinct composition of vascular plant species. We therefore recommend that *G. dewevrei* be considered as a unique forest type in conservation planning and carbon stock modelling.

Forest structure

The structure of *G. dewevrei* forest differs from mixed species forest in terms of stem number and stem size class distribution, with a significantly lower stem density, and fewer smaller trees but more larger trees (Fig. 2). These structural attributes influence the amount of carbon stored within tropical forests and carbon fluxes into and out of the vegetation (e.g. Durán et al. 2015; Poorter et al. 2015; Balima et al. 2021). We found higher but non-significant AGB in *G. dewevrei* forest than mixed forest in the stands

sampled in the Sangha Trinational (Fig. 2). A significantly higher AGB has been found in *G. dewevrei* forests in other areas. Djuikouo et al. (2010) found higher AGB in *G. dewevrei* forest in the Dja Biosphere Reserve than in mixed terre firme forest, attributing this to variation in the abundance of trees with large diameter between the two forest types. In their study, individuals with diameter > 55 cm accounted for 81.2% of the biomass in *G. dewevrei* forest compared to 59.8% in the mixed forest. Our study also indicated higher amounts of larger trees (≥ 70 cm dbh) in *G. dewevrei* forest in the Sangha Trinational (Fig. 2). Several studies in tropical forests have shown that AGB is strongly correlated with the number of individuals ≥ 70 cm in diameter (Brown et al. 1989; Brown and Lugo 1992; Clark and Clark 2000; Chave et al. 2003). A higher AGB in *G. dewevrei* forest has also been seen in the Ituri forest (eastern DRC), where Makana et al. (2011) noted a 25% higher biomass in *G. dewevrei* forest than mixed forest. Kearsley et al. (2017) found a higher wood density in the community of trees that make up *G. dewevrei* forest than mixed forest (0.66 g/cm³; compared to 0.62 g/cm³, p

< 0.001) in Yangambi, providing another explanation for the higher AGB observed.

AGB was calculated using regional model 12 from Fayolle et al. (2018), which is recommended for estimation of carbon stocks in Congo Basin forests where height data is not available. Fayolle et al. (2018) found comparable site-level RMSE and bias estimates between regional models including and omitting heights. However, tree height is a key component of allometric equations for AGB, as biomass is partially a function of tree volume which is calculated from tree height, trunk basal area, and trunk taper (Chave et al. 2005; Sullivan et al. 2018). Using tree height measurements for all trees is accepted as by far the most accurate method to infer AGB (Feldpausch et al. 2012; Chave et al. 2014; Sullivan et al. 2018). Although comprehensive accurate tree height measurements are rare, a recommended strategy is to construct a stand-specific Height-Diameter (H-D) allometry using a subset of well-measured trees (Réjou-Méchain et al. 2015; Sullivan et al. 2018). H-D relationships are known to be influenced by biogeography and by environmental and compositional variation across small scales, with measurable impacts on AGB (Sullivan et al. 2018). Sullivan et al. (2018) evaluated the performance of different locally derived allometric models constructed with different numbers of trees, finding that allometries derived from just 20 locally measured values could often predict tree height with lower error than regional or climate-based models. Our study had no measured heights, and therefore AGB measures come with significant uncertainties (Réjou-Méchain et al. 2017), and must be interpreted with caution. Obtaining measurements of tree heights in future plots or censuses, even if only for a relatively small subset of trees, would give more accurate measures of AGB within *G. dewevrei* forest in the Sangha Trinational. A further limitation of this study is the small size of most of the forest inventory plots (30 m × 30 m). This is below the recommended size for forest inventory plots, and may explain the lack of significant difference in AGB between the two forest types within our study.

The structural differences between *G. dewevrei* and mixed forest in this study, combined with results from other areas finding higher AGB in *G. dewevrei* forest, suggest that *G. dewevrei* forests may store more carbon than mixed terre firme forests. Separate consideration of *G. dewevrei* forest when designing models of carbon storage across the Congo Basin forest block would therefore produce estimations that are more accurate. In addition, several studies have reported that larger trees show notably higher vulnerability to drought (Nepstad et al. 2007; Rowland et al. 2015; Costa et al. 2022). Thus, the carbon stocks in *G. dewevrei* might be more sensitive to drought under future climate change. This reinforces the need for separate consideration of *G. dewevrei* forest carbon stocks, when considering long-term modelling of carbon across the Congo Basin.

Species composition

We show that *G. dewevrei* forest has a unique species composition when compared to mixed terre firme forest. This was shown both for tree species, through analysis of plot data, and across all growth forms of vascular plants, using the dataset of herbarium specimens. In the DCA and NMDS analyses, *G. dewevrei* plots consistently clustered together, separate from mixed forest plots (Fig. 5), and this difference was found to be significant by the ANOSIM statistic. This separation persisted when *G. dewevrei* stems were removed from the data, indicating that a distinct tree community is found among *G. dewevrei* within monodominant forest. These findings are contrary to the consensus in the literature that monodominant *G. dewevrei* forest has the same overall species composition as mixed terre firme forest (e.g. Hart et al. 1989; Hart 1990; Djuikouo et al. 2010).

To investigate which species are responsible for the differences between *G. dewevrei* and mixed forest, with a view to assessing their conservation value, we sought to identify which species are observed and collected in *G. dewevrei* forest in higher densities than in mixed forest. Harris (2002) distinguishes “obligate associates” which within this area have only ever been collected in *G. dewevrei* forest, and “facultative associates” which do occur in mixed forest but are much more common in *G. dewevrei* forest. In this study, we used statistical methods to identify species that have been collected in *G. dewevrei* forest more often than expected by chance. We identified 56 species of vascular plant that were significantly associated with *G. dewevrei* forest (52 from the herbarium analysis, and an additional four tree species identified through indicator species analysis of plot data; Tables 1, 2). These species spanned many families of vascular plants and occurred in each major plant life form. In addition, the herbarium dataset used in this study identifies seven species that have only ever been collected within *G. dewevrei* forest in this area (Supplementary material 3). These were excluded from the main analyses, as there are insufficient collections (two to five specimens) to say with certainty that they are associated solely with *G. dewevrei* forest. With more data, we therefore expect the full list of *G. dewevrei* associated species will be greater than 56.

Conservation value

A common misconception of *G. dewevrei* forest is that it does not contain much biodiversity, and therefore it has been considered as low priority for conservation. Our study challenges this by indicating the importance of this forest type to many plant species in the Sangha Trinational, spanning a wide range of plant families and a variety of growth forms. The conservation value of *G. dewevrei* forest has also been highlighted by Cheek et al. (2011), who described monodominant *G. dewevrei* forest within the proposed Mefou National Park near Yaoundé, Cameroon as containing the greatest number of rare

and potential red list plant species within the area, for example *Cola letouzeyana* Nkongmeneck and *Tricalysia amplexicaulis* Robbr. In addition, the ordination and herbarium analyses conducted in this study indicate that *G. dewevrei* forests contain a plant community that is distinct from mixed terre firme forest, and thus, contrary to current management within these National Parks, should be considered separately to mixed forest when designing conservation plans.

The misconception of low biodiversity within *G. dewevrei* forest has also been challenged when looking at other groups. Due to its lower heterogeneity, it is often assumed there are fewer large mammals within *G. dewevrei* forest. However, similar mammal species estimates were found in *G. dewevrei* forests as in mixed species forests based on camera trap monitoring in the Nouabalé-Ndoki National Park (Morgan et al. 2023), suggesting that *G. dewevrei* forest is also important for

megafauna populations in the area. Morgan et al. (2006) also found a higher abundance of chimpanzee nests in *G. dewevrei* forests within the NNNP than in mixed forest. Further, western lowland gorillas in the Ndoki forest exhibit a particular type of foraging behaviour when looking for the deer truffle *Elaphomyces labyrinthinus* Castellano & T.W.Henkel in *G. dewevrei* forest (Abea et al. in review).

Gilbertiodendron dewevrei forest is also important for fungal biodiversity. Ndolo Ebika et al. (2018) list 51 edible fungus species known in northern Republic of Congo, 32 of which are found in *G. dewevrei* forest, and 19 of which have *G. dewevrei* forest listed as their only habitat type. Jumbam et al. (2019), discovered a new species of fungus in *G. dewevrei* forest in the Dja Biosphere Reserve, Cameroon, and Buyck et al. (2020) recently described two new fungal species from *G. dewevrei* forest that are only



Figure 6. Two species identified as *Gilbertiodendron dewevrei* associates from the χ^2 analysis of herbarium specimens collected in the Sangha Trinational. Photographs and herbarium specimens of (A) *Marantochloa monophylla* (Ndolo Ebika 976, E [E00757799]) and (B) *Diospyros ferrea* (Harris 9672, E [E00397397]). Photographs taken by David J. Harris. Specimens collected in *G. dewevrei* forest in the Sangha Department, Republic of Congo.

known from this forest type: *Cantharellus longisporus* and *C. xanthocyaneus*.

In summary, when you look at the whole plant community found within *G. dewevrei* forest, spanning the smallest herbs to the tallest trees, there is a diverse range of species found, and these plants are different to those found within mixed terre firme forest. Therefore, *G. dewevrei* forest is an important ecosystem for plant diversity within the Sangha Trinational, and conservation plans will be more effective if they include both mixed terre firme forest and areas of *G. dewevrei* forest. Other studies have shown that this forest is also important for mammals, and fungi, some of which have so far only been discovered within *G. dewevrei* forest. We predict that these differences in communities between the two forest types will also be observed in other groups.

Utilisation of herbarium specimen data

This study utilised a dataset of herbarium specimens collected in mixed terre firme and monodominant *G. dewevrei* forest in the Sangha Trinational. This allowed us to identify *G. dewevrei* associates across a range of plant lifeforms, beyond just trees that are commonly sampled in plots. For example, *Marantochloa monophylla* (Fig. 6) is an herbaceous plant that was identified as a *G. dewevrei* associate through our analysis of the herbarium specimen data. *Marantochloa monophylla* was collected five times by David J. Harris in the Sangha Trinational. Of these specimens, four (80%) were collected in *G. dewevrei* forest. This highlights how herbarium data can allow us to move away from the purely tree-focused approach for measuring biodiversity that is often present in tropical forest research. Studies of tropical forest ecology are often tree-focused, because of their contribution to carbon sequestration, plant biomass and economic value (Taylor et al. 2023). However, in the tropics the contribution to total plant species richness of co-occurring herbs, epiphytes, and climbers is comparable to that of trees (Spicer et al. 2020). The focus on trees means that non-woody plant growth forms that significantly contribute to biodiversity and forest function are often overlooked in conservation planning (Gentry and Dodson 1987; Schnitzer and Carson 2000; Gilliam 2014; Thrippleton et al. 2016; Landuyt et al. 2019). Plot data for other plant growth forms is rare, due to the time-consuming nature of collecting such data, and the shortage of taxonomists with expertise in non-woody flora. The utilisation of herbarium data for this analysis therefore provides a useful alternate way of identifying species of conservation interest within tropical forests.

Using the herbarium dataset also allowed us to identify rarer tree species that are associated with *G. dewevrei* forest. Out of 52 species of vascular plant identified by the herbarium analysis, 15 were trees. This is in comparison to just six species (in addition to *G. dewevrei*) that were identified through the analysis of plot data. Collectors will preferentially collect rare species, meaning that those

species, not picked up in plots, can be still be identified through herbarium data. For example, *Diospyros ferrea* (Fig. 6) is a relatively rare tree species within this study site, which was not found in the plot inventories. However, 10 specimens were collected in the Sangha Trinational, and eight of these (80%) were collected in *G. dewevrei* forest. Herbarium data is an underutilised source of information for this type of research (Harris et al. 2021; Heberling 2022), and our study helps demonstrate how using herbarium data can provide additional data from that of plot inventories.

By increasing collections within the Sangha Trinational, we would likely identify more *G. dewevrei* associates. Garrett (2017) looked at the same dataset of herbarium specimens, finding that collecting sampling completeness of vascular plants of this area had not been reached, particularly for shrubs, herbaceous plants and climbing plants, and that the expected species richness is still greater than the observed species richness. This suggests there are more *G. dewevrei* associates to be identified, especially in the shrub, climber, herbaceous, (hemi-) epiphytic, and (hemi-) parasitic groups. Our analysis was also limited by the small number of collections for many species. The final dataset of herbarium specimens, containing only species with at least five collections, came to 397 species, while the original dataset with all species (including those with less than five collections) contained 1,172 species collected in the Sangha Trinational. Increasing collections of species with few specimens through general collecting of herbarium specimens would allow more associated species to be identified.

Avenues of future research

A number of factors may influence why the species identified in this study are found associated with *G. dewevrei* forest. These include light requirement (Peh et al. 2014), ectomycorrhizal associations, seed mass (Peh et al. 2014), and water use efficiency (Kearsley et al. 2017). An investigation of how these factors contribute to the ability of *G. dewevrei* associates to establish in this forest type, and conversely the exclusion of the mixed forest specialists, would provide further insights into *G. dewevrei* forest. Comparing the functional traits of associated species to *G. dewevrei* may also help to explain how it achieves its monodominance. Other avenues of research include testing whether our findings apply to *G. dewevrei* forest in other parts of its range. Similar datasets could be used to test whether the same species are associated with *G. dewevrei* in these regions, or whether the plant community is different. In addition, it would be interesting to compare *G. dewevrei* forest neighbouring waterways, and those in dry upland areas, both of which are found in the Sangha Trinational (Letouzey 1983; Hall et al. 2020), to see if similar species are found in both.

In order for *G. dewevrei* forest to be incorporated separately within conservation planning and carbon stock modelling, it is important to have an accurate map

of where *G. dewevrei* forest occurs, and quantifications of the proportion of vegetation that is made up of this forest type. A priority is therefore to map out the locations of *G. dewevrei* forest across the Congo Basin. In terms of management within the national parks and surrounding areas, it would also be useful to consider the impact of road and human settlements in and near *G. dewevrei* forest.

CONCLUSION

Monodominant *Gilbertiodendron dewevrei* forests represent a unique forest type in the Sangha Trinational. *Gilbertiodendron dewevrei* forest has a distinct structure, species richness, diversity, and equitability, and species composition compared to adjacent mixed terre firme forest. Species associated with *G. dewevrei* monodominant forests occur across all growth forms of vascular plant, with at least 56 species significantly associated with *G. dewevrei* forest. The differences in species composition between the two forest types indicate that *G. dewevrei* should be considered separately in conservation planning. In addition, the structural differences between *G. dewevrei* and mixed terre firme forest highlight that it should be considered separately when modelling carbon stocks and fluxes, in order to produce accurate models for the Congo Basin. In particular, the higher number of larger trees in *G. dewevrei* forest could indicate that more carbon is stored in these ecosystems, and thus they should be considered for protection from deforestation and degradation. A key priority is to identify the extent of the Congo Basin forest block that is covered by this forest type, and to map out the locations where it occurs. In summary, we recommend that *G. dewevrei* forest within the Sangha Trinational should be considered as a distinct vegetation type in conservation planning, and in carbon calculations.

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REFERENCES

- Abea G, Ndolo Ebika S, Sanz C, Teberd P, Ebombi F, Brogan S, de Haan M, Stephens C, Morgan D (in review) Long-term observations in the Ndoki Forest resolve enduring questions about truffle foraging by Western Lowland Gorillas. *Primates*.
- Balima LH, Kouamé FN, Bayen P, Ganamé M, Nacoulma BMI, Thiombiano A, Soro D (2021) Influence of climate and forest attributes on aboveground carbon storage in Burkina Faso, West Africa. *Environmental Challenges* 4: 100123. <https://doi.org/10.1016/j.envc.2021.100123>
- Barbier N, Libalah M, Katembo J, Ploton P, Droissart V, Texier N, Kamdem N, Viennois G, Pélissier R, Couteron P, Bosela F, Sonké B (2017) Pistes pour l'étude de la distribution des peuplements de *Gilbertiodendron dewevrei* comme signature des impacts climatiques ou anthropiques anciens. In: de Saulieu G (Ed.) *Pour Une écologie Historique en Afrique Centrale*. AUF-IRD, Bondy, 157–170.
- Blake S, Fay JM (1997) Seed production by *Gilbertiodendron dewevrei* in the Nouabalé-Ndoki National Park, Congo, and its implications for large mammals. *Journal of Tropical Ecology* 13: 885–891. <https://doi.org/10.1017/S0266467400011056>
- Borcard D, Gillet F, Legendre P (2011) *Numerical Ecology with R*. Springer New York, New York, 1–306. <https://doi.org/10.1007/978-1-4419-7976-6>
- Brooks TM, Mittermeier RA, Da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL (2006) Global biodiversity conservation priorities. *Science* 313: 58–61. <https://doi.org/10.1126/science.1127609>
- Brown S, Lugo AE (1992) Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia*. Caracas 17: 8–18.
- Brown S, Gillespie AJR, Lugo AE (1989) Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science* 35: 881–902.
- Buyck B, Ndolo Ebika ST, De Kesel A, Hofstetter V (2020) Tropical African *Cantharellus* Adans.: Fr. (Hydnaceae, Cantharellales) with lilac-purplish tinges revisited. *Cryptogamie, Mycologie* 41: 161–177. <https://doi.org/10.5252/cryptogamie-mycologie2020v41a10>
- Cardoso AW, Oliveras I, Abernethy KA, Jeffery KJ, Glover S, Lehmann D, Edzang Ndong J, White LJT, Bond WJ, Malhi Y (2021) A distinct ecotonal tree community exists at central African forest–savanna transitions. *Journal of Ecology* 109: 1170–1183. <https://doi.org/10.1111/1365-2745.13549>
- Chave J, Condit R, Lao S, Caspersen JP, Foster RB, Hubbell SP (2003) Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *Journal of Ecology* 91: 240–252. <https://doi.org/10.1046/j.1365-2745.2003.00757.x>

- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, Lescure J-P, Nelson BW, Ogawa H, Puig H, Riéra B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99. <https://doi.org/10.1007/s00442-005-0100-x>
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC, Henry M, Martínez-Yrizar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Péllissier R, Ploton P, Ryan CM, Saldarriaga JG, Vieilledent G (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20: 3177–3190. <https://doi.org/10.1111/gcb.12629>
- Cheek M, Harvey Y, Onana J-M (2011) The plants of Mefou proposed national park, Yaoundé, Cameroon. A conservation checklist. Kew Publishing, Royal Botanic Gardens, Kew, 1–252.
- Clark DB, Clark DA (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* 137: 185–198. [https://doi.org/10.1016/S0378-1127\(99\)00327-8](https://doi.org/10.1016/S0378-1127(99)00327-8)
- Costa FRC, Schiatti J, Stark SC, Smith MN (2022) The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought? *New Phytologist* 237: 714–733. <https://doi.org/10.1111/nph.17914>
- Cuni-Sanchez A, Sullivan MJP, Platts PJ, Lewis SL, Marchant R, Imani G, Hubau W, Abiem I, Adhikari H, Albrecht T, Altman J, Amani C, Aneseyee AB, Avitabile V, Banin L, Batumike R, Bauters M, Beeckman H, Begne SK, Bennett AC, Bitariho R, Boeckx P, Bogaert J, Bräuning A, Bulonvu F, Burgess ND, 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 MJ, Klein J, Lisingo J, Lovett J, Lung M, Makana J-R, Malhi Y, Marshall A, Martin EH, Mitchard ETA, Morel A, Mukendi JT, Muller T, Nchu F, Nyirambangutse B, Okello J, Peh KS-H, Pellikka P, Phillips OL, Plumptre A, Qie L, Rovero F, Sainge MN, Schmitt CB, Sedlacek O, Ngute ASK, Sheil D, Sheleme D, Simegn TY, Simo-Droissart M, Sonké B, Soromessa T, Sunderland T, Svoboda M, Taedoumg H, Taplin J, Taylor D, Thomas SC, Timberlake J, Tuagben D, Umunay P, Uzabaho E, Verbeeck H, Vleminckx J, Wallin G, Wheeler C, Willcock S, Woods JT, 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>
- Dargie GC, Lewis SL, Lawson IT, Mitchard ETA, Page SE, Bocko YE, Ifo SA (2017) Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature* 542: 86–90. <https://doi.org/10.1038/nature21048>
- De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* 90: 3566–3574. <https://doi.org/10.1890/08-1823.1>
- Djuikouo MNK, Doucet J-L, Nguembo CK, Lewis SL, Sonké B (2010) Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. *African Journal of Ecology* 48: 1053–1063. <https://doi.org/10.1111/j.1365-2028.2010.01212.x>
- Djuikouo MNK, Peh KS-H, Nguembo CK, Doucet J-L, Lewis SL, Sonké B (2014) Stand structure and species co-occurrence in mixed and monodominant Central African tropical forests. *Journal of Tropical Ecology* 30: 447–455. <https://doi.org/10.1017/S0266467414000352>
- Durán SM, Sánchez-Azofeifa GA, Rios RS, Gianoli E (2015) The relative importance of climate, stand variables and liana abundance for carbon storage in tropical forests: Climate, stand variables and lianas control forest carbon. *Global Ecology and Biogeography* 24: 939–949. <https://doi.org/10.1111/geb.12304>
- European Commission (2010) The forests of the Congo basin: state of the forest 2008. Publications Office of the European Union, Luxembourg, 1–416. <https://data.europa.eu/doi/10.2788/32259>
- FAO/UNESCO (1977) Soils map of the world 1:500,000 Volume VI, Africa. UNESCO, Paris, 1–346.
- Fayolle A, Picard N, Doucet J-L, Swaine M, Bayol N, Bénédet F, Gourlet-Fleury S (2014) A new insight in the structure, composition and functioning of central African moist forests. *Forest Ecology and Management* 329: 195–205. <https://doi.org/10.1016/j.foreco.2014.06.014>
- Fayolle A, Ngomanda A, Mbasi M, Barbier N, Bocko Y, Boyemba F, Couteron P, Fonton N, Kamdem N, Katembo J, Kondouale HJ, Loumeto J, Maïdou HM, Mankou G, Mengui T, Mofack GI, Moundounga C, Moundounga Q, Nguimbous L, Nsue Nchama N, Obiang D, Ondo Meyer Asue F, Picard N, Rossi V, Senguela Y-P, Sonké B, Viard L, Yongo OD, Zapfack L, Medjibe VP (2018) A regional allometry for the Congo basin forests based on the largest ever destructive sampling. *Forest Ecology and Management* 430: 228–240. <https://doi.org/10.1016/j.foreco.2018.07.030>
- Feldpausch TR, Lloyd J, Lewis SL, Brienen RJW, Gloor M, Monteagudo Mendoza A, Lopez-Gonzalez G, Banin L, Abu Salim K, Affum-Baffoe K, Alexiades M, Almeida S, Amaral I, Andrade A, Aragão LEOC, Araujo Murakami A, Arets EJMM, Arroyo L, Aymard C. GA, Baker TR, Bánki OS, Berry NJ, Cardozo N, Chave J, Comiskey JA, Alvarez E, De Oliveira A, Di Fiore A, Djagbletey G, Domingues TF, Erwin TL, Fearnside PM, França MB, Freitas MA, Higuchi N, E. Honorio C., Iida Y, Jiménez E, Kassim AR, Killeen TJ, Laurance WF, Lovett JC, Malhi Y, Marimon BS, Marimon-Junior BH, Lenza E, Marshall AR, Mendoza C, Metcalfe DJ, Mitchard ETA, Neill DA, Nelson BW, Nilus R, Nogueira EM, Parada A, Peh KS-H, Pena Cruz A, Peñuela MC, Pitman NCA, Prieto A, Quesada CA, Ramirez F, Ramirez-Angulo H, Reitsma JM, Rudas A, Saiz G, Salomão RP, Schwarz M, Silva N, Silva-Espejo JE, Silveira M, Sonké B, Stropp J, Taedoumg

- HE, Tan S, Ter Steege H, Terborgh J, Torello-Raventos M, Van Der Heijden GMF, Vásquez R, Vilanova E, Vos VA, White L, Willcock S, Woell H, Phillips OL (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences* 9: 3381–3403. <https://doi.org/10.5194/bg-9-3381-2012>
- Flores O, Coomes DA (2011) Estimating the wood density of species for carbon stock assessments. *Methods in Ecology and Evolution* 2: 214–220. <https://doi.org/10.1111/j.2041-210X.2010.00068.x>
- Garrett S (2017) Using herbarium specimens to explore species diversity and collecting completeness across plant habit groups in tropical Africa. Master's Thesis, Royal Botanic Garden Edinburgh and University of Edinburgh, UK.
- Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19: 149–156. <https://doi.org/10.2307/2388737>
- Gérard P (1960) Etude écologique de la forêt dense à *Gilbertiodendron dewevrei* dans la région de l'Uele. Institut national pour l'étude agronomique du Congo, Brussels, 1–159.
- Gibbs HK, Brown S, Niles JO, Foley JA (2007) Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters* 2: 045023. <https://doi.org/10.1088/1748-9326/2/4/045023>
- Gilliam F (2014) The herbaceous layer in forests of eastern North America. Oxford University Press, Oxford, 1–508. <https://doi.org/10.1093/acprof:osobl/9780199837656.001.0001>
- Glick HB, Umunay PM, Makana J-R, Thomas SC, Reuning-Scherer JD, Gregoire TG (2021) Developmental dynamics of *Gilbertiodendron dewevrei* (Fabaceae) drive forest structure and biomass in the eastern Congo Basin. *Forests* 12: 738. <https://doi.org/10.3390/f12060738>
- Grantham HS, Shapiro A, Bonfils D, Gond V, Goldman E, Maisels F, Plumptre AJ, Rayden T, Robinson JG, Strindberg S, Stokes E, Tulloch AITT, Watson JEM, Williams L, Rickenbach O (2020) Spatial priorities for conserving the most intact biodiverse forests within Central Africa. *Environmental Research Letters* 15: 0940b5. <https://doi.org/10.1088/1748-9326/ab9fae>
- Hall JS, Harris DJ, Medjibe V, Ashton PMS (2003) The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas. *Forest Ecology and Management* 183: 249–264. [https://doi.org/10.1016/S0378-1127\(03\)00107-5](https://doi.org/10.1016/S0378-1127(03)00107-5)
- Hall JS, Harris DJ, Saltonstall K, Medjibe V de P, Ashton MS, Turner BL (2020) Resource acquisition strategies facilitate *Gilbertiodendron dewevrei* monodominance in African lowland forests. *Journal of Ecology* 108: 433–448. <https://doi.org/10.1111/1365-2745.13278>
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342: 850–853. <https://doi.org/10.1126/science.1244693>
- Harris DJ (2002) The vascular plants of the Dzanga-Sangha Reserve, Central African Republic. *Scripta Botanica Belgica* 23: 1–274.
- Harris DJ, Wortley AH (2008) *Sangha Trees: an Illustrated Identification Manual*. Royal Botanic Garden Edinburgh, Edinburgh, 1–336.
- Harris T, Mulligan M, Brummitt N (2021) Opportunities and challenges for herbaria in studying the spatial variation in plant functional diversity. *Systematics and Biodiversity* 19: 322–332. <https://doi.org/10.1080/14772000.2021.1887394>
- Hart TB (1990) Monospecific dominance in tropical rain forests. *Trends in Ecology & Evolution* 5: 6–11. [https://doi.org/10.1016/0169-5347\(90\)90005-X](https://doi.org/10.1016/0169-5347(90)90005-X)
- Hart TB, Hart JA, Murphy PG (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *The American Naturalist* 133: 613–633. <https://doi.org/10.1086/284941>
- Hart TB, Hart JA, Dechamps R, Fournier M, Ataholo M (1996) Changes in forest composition over the last 4000 years in the Ituri basin, Zaire. In: van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM (Eds) *The Biodiversity of African Plants*. Springer Netherlands, Dordrecht, 545–560. https://doi.org/10.1007/978-94-009-0285-5_70
- Heberling JM (2022) Herbaria as big data sources of plant traits. *International Journal of Plant Sciences* 183: 87–118. <https://doi.org/10.1086/717623>
- Jumbam B, Haelewaters D, Koch RA, Dentinger BTM, Henkel TW, Aime MC (2019) A new and unusual species of *Hericium* (Basidiomycota: Russulales, Hericiaceae) from the Dja Biosphere Reserve, Cameroon. *Mycological Progress* 18: 1253–1262. <https://doi.org/10.1007/s11557-019-01530-1>
- Justice C, Wilkie D, Zhang Q, Brunner J, Donoghue C (2001) Central African forests, carbon and climate change. *Climate Research* 17: 229–246. <https://www.jstor.org/stable/24867358>
- Katembu JM, Libalah MB, Boyemba FB, Dauby G, Barbier N (2020) Multiple stable dominance states in the Congo Basin forests. *Forests* 11: 553. <https://doi.org/10.3390/f11050553>
- Kearsley E, Verbeeck H, Hufkens K, Van de Perre F, Doetterl S, Baert G, Beeckman H, Boeckx P, Huygens D (2017) Functional community structure of African monodominant *Gilbertiodendron dewevrei* forest influenced by local environmental filtering. *Ecology and Evolution* 7: 295–304. <https://doi.org/10.1002/ece3.2589>
- Landuyt D, De Lombaerde E, Perring MP, Hertzog LR, Ampoorter E, Maes SL, De Frenne P, Ma S, Proesmans W, Blondeel H, Sercu BK, Wang B, Wasof S, Verheyen K (2019) The functional role of temperate forest understorey vegetation in a changing world. *Global Change Biology* 25: 3625–3641. <https://doi.org/10.1111/gcb.14756>
- Laporte N (2002) Stratification Forestière des UFA Kabo, Pokola et Loundoungou, Rapport Technique au Wildlife Conservation Society. New York, 1–16.
- Legendre P, Legendre L (2012) *Numerical Ecology*. 3rd Edition. Elsevier, Oxford, 1–1006.
- Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: dissimilarity coefficients and

- partitioning. *Ecology Letters* 16: 951–963. <https://doi.org/10.1111/ele.12141>
- Letouzey RG (1968) Étude Phytogéographique du Cameroun. Éditions Paul Lechevalier, Paris, 1–511.
- Letouzey RG (1983) Quelques exemples camerounais de liaison possible entre phénomènes géologiques et végétation. *Bothalia* 14: 739–744.
- Letouzey RG (1985) Notice de la carte phytogéographique du Cameroun au 1:500,000. Institut de la Carte Internationale de Végétation, Toulouse, France, 1–240.
- Lewis SL, Sonké B, Sunderland T, Begne SK, Lopez-Gonzalez G, van der Heijden GMF, Phillips OL, Affum-Baffoe K, Baker TR, Banin L, Bastin J-F, Beeckman H, Boeckx P, Bogaert J, De Cannière C, Chezeaux E, Clark CJ, Collins M, Djagbletey G, Djuikouo MNK, Droissart V, Doucet J-L, Ewango CEN, Fauset S, Feldpausch TR, Foli EG, Gillet J-F, Hamilton AC, Harris DJ, Hart TB, de Haulleville T, Hladik A, Hufkens K, Huygens D, Jeanmart P, Jeffery KJ, Kearsley E, Leal ME, Lloyd J, Lovett JC, Makana J-R, Malhi Y, Marshall AR, Ojo L, Peh KS-H, Pickavance G, Poulsen JR, Reitsma JM, Sheil D, Simo M, Steppe K, Taedoumg HE, Talbot J, Taplin JRD, Taylor D, Thomas SC, Toirambe B, Verbeeck H, Vleminckx J, White LJ, Willcock S, Woell H, Zemagho L (2013) Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 20120295. <https://doi.org/10.1098/rstb.2012.0295>
- Makana JR, Ewango CN, McMahon SM, Thomas SC, Hart TB, Condit R (2011) Demography and biomass change in monodominant and mixed old-growth forest of the Congo. *Journal of Tropical Ecology* 27: 447–461. <https://doi.org/10.1017/S0266467411000265>
- Mittermeier RA, Myers N, Thomsen JB, Da Fonseca GAB, Olivieri S (1998) Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12: 516–520. <https://doi.org/10.1046/j.1523-1739.1998.012003516.x>
- Morgan D, Sanz C, Onononga JR, Strindberg S (2006) Ape abundance and habitat use in the Goulougo Triangle, Republic of Congo. *International Journal of Primatology* 27: 147–179. <https://doi.org/10.1007/s10764-005-9013-0>
- Morgan D, Strindberg S, McElmurray P, Zambarda A, Singono I, Huskisson S, Musgrave S, Ayina CE, Funkhouser J, Hellmuth H, Joshi P, Cassidy R, Sanz C (2023) Extending the conservation impact of great ape research: flagship species sites facilitate biodiversity assessments and land preservation. *Primates*. <https://doi.org/10.1007/s10329-023-01080-x>
- Ndolo Ebika ST, Codjia JEI, Yorou NS, Attibayeba A (2018) Les champignons sauvages comestibles et connaissances endogènes des peuples autochtones Mbènzèlè et Ngombe de la République du Congo. *Journal of Applied Biosciences* 126: 12675. <https://doi.org/10.4314/jab.v126i1.5>
- Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* 88: 2259–2269. <https://doi.org/10.1890/06-1046.1>
- Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Cáceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlenn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022) *vegan: Community Ecology Package*. R package version 2.6-2. <https://CRAN.R-project.org/package=vegan> [accessed 11.12.2023]
- Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D (2011) A large and persistent carbon sink in the world's forests. *Science* 333: 988–993. <https://doi.org/10.1126/science.1201609>
- Panzou GJ Loubota, Bocko YE, Mavoungou AY, Loumeto J-J (2021) Height-diameter allometry in African monodominant forest close to mixed forest. *Journal of Tropical Ecology* 37: 98–107. <https://doi.org/10.1017/S0266467421000183>
- Peh KSH, Lewis SL, Lloyd J (2011) Mechanisms of monodominance in diverse tropical tree-dominated systems. *Journal of Ecology* 99: 891–898. <https://doi.org/10.1111/j.1365-2745.2011.01827.x>
- Peh KSH, Sonké B, Séné O, Djuikouo M-NK, Nguembou CK, Taedoumg H, Begne SK, Lewis SL (2014) Mixed-forest species establishment in a monodominant forest in Central Africa: implications for tropical forest invasibility. *PLoS ONE* 9: e97585. <https://doi.org/10.1371/journal.pone.0097585>
- Poorter L, van der Sande MT, Thompson J, Arets EJMM, Alarcón A, Álvarez-Sánchez J, Ascarrunz N, Balvanera P, Barajas-Guzmán G, Boit A, Bongers F, Carvalho FA, Casanoves F, Cornejo-Tenorio G, Costa FRC, de Castilho CV, Duivenvoorden JF, Dutrieux LP, Enquist BJ, Fernández-Méndez F, Finegan B, Gormley LHL, Healey JR, Hoosbeek MR, Ibarra-Manríquez G, Junqueira AB, Levis C, Licona JC, Lisboa LS, Magnusson WE, Martínez-Ramos M, Martínez-Yrizar A, Martorano LG, Maskell LC, Mazzei L, Meave JA, Mora F, Muñoz R, Nytch C, Pansonato MP, Parr TW, Paz H, Pérez-García EA, Rentería LY, Rodríguez-Velázquez J, Rozendaal DMA, Ruschel AR, Sakschewski B, Salgado-Negret B, Schiatti J, Simões M, Sinclair FL, Souza PF, Souza FC, Stropp J, ter Steege H, Swenson NG, Thonicke K, Toledo M, Uriarte M, van der Hout P, Walker P, Zamora N, Peña-Claros M (2015) Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography* 24: 1314–1328. <https://doi.org/10.1111/geb.12364>
- Raven PH, Gereau RE, Phillipson PB, Chatelain C, Jenkins CN, Ulloa Ulloa C (2020) The distribution of biodiversity richness in the tropics. *Science Advances* 6: eabc6228. <https://doi.org/10.1126/sciadv.abc6228>
- R Core Team (2022) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> [accessed 11.12.2023]
- Réjou-Méchain M, Tymen B, Blanc L, Fauset S, Feldpausch TR, Monteagudo A, Phillips OL, Richard H, Chave J (2015) Using repeated small-footprint LiDAR acquisitions to infer spatial and temporal variations of a high-biomass

- neotropical forest. *Remote Sensing of Environment* 169: 93–101. <https://doi.org/10.1016/j.rse.2015.08.001>
- Réjou-Méchain M, Tanguy A, Piponiot C, Chave J, Hérault B (2017) BIOMASS: an R package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution* 8: 1163–1167. <https://doi.org/10.1111/2041-210X.12753>
- Réjou-Méchain M, Mortier F, Bastin J-F, Cornu G, Barbier N, Bayol N, Bénédet F, Bry X, Dauby G, Deblauwe V, Doucet J-L, Doumenge C, Fayolle A, Garcia C, Kibambe Lubamba J-P, Loumeto J-J, Ngomanda A, Ploton P, Sonké B, Trottier C, Vimal R, Yongo O, Péliissier R, Gourlet-Fleury S (2021) Unveiling African rainforest composition and vulnerability to global change. *Nature* 593: 90–94. <https://doi.org/10.1038/s41586-021-03483-6>
- Rowland L, Da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS, Ferreira LV, Malhi Y, Grace J, Mencuccini M, Meir P (2015) Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* 528: 119–122. <https://doi.org/10.1038/nature15539>
- Schnitzer SA, Carson WP (2000) Have we forgotten the forest because of the trees? *Trends in Ecology & Evolution* 15: 375–376. [https://doi.org/10.1016/S0169-5347\(00\)01913-3](https://doi.org/10.1016/S0169-5347(00)01913-3)
- Shannon CE (1948) A mathematical theory of communication. *The Bell System Technical Journal* 27: 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
- Shapiro A, d'Annunzio R, Desclée B, Jungers Q, Kondjo HK, Iyanga JM, Gangyo FI, Nana T, Obame CV, Milandou C, Rambaud P, Sonwa DJ, Mertens B, Tchana E, Khasa D, Bourgoïn C, Ouissika CB, Kipute DD (2023) Small scale agriculture continues to drive deforestation and degradation in fragmented forests in the Congo Basin (2015–2020). *Land Use Policy* 134: 106922. <https://doi.org/10.1016/j.landusepol.2023.106922>
- Slik JWF, Arroyo-Rodríguez V, Aiba S-I, Alvarez-Loayza P, Alves LF, Ashton P, Balvanera P, Bastian ML, Bellingham PJ, Van Den Berg E, Bernacci L, Da Conceição Bispo P, Blanc L, Böhning-Gaese K, Boeckx P, Bongers F, Boyle B, Bradford M, Brearley FQ, Breuer-Ndoundou Hockemba M, Bunyavejchewin S, Calderado Leal Matos D, Castillo-Santiago M, Catharino ELM, Chai S-L, Chen Y, Colwell RK, Chazdon RL, Clark C, Clark DB, Clark DA, Culmsee H, Damas K, Dattaraja HS, Dauby G, Davidar P, DeWalt SJ, Doucet J-L, Duque A, Durigan G, Eichhorn KAO, Eisenlohr PV, Eler E, Ewango C, Farwig N, Feeley KJ, Ferreira L, Field R, De Oliveira Filho AT, Fletcher C, Forshed O, Franco G, Fredriksson G, Gillespie T, Gillet J-F, Amarnath G, Griffith DM, Grogan J, Gunatilleke N, Harris D, Harrison R, Hector A, Homeier J, Imai N, Itoh A, Jansen PA, Joly CA, De Jong BHJ, Kartawinata K, Kearsley E, Kelly DL, Kenfack D, Kessler M, Kitayama K, Kooyman R, Larney E, Laumonier Y, Laurance S, Laurance WF, Lawes MJ, Amaral ILD, Letcher SG, Lindsell J, Lu X, Mansor A, Marjokorpi A, Martin EH, Meilby H, Melo FPL, Metcalfe DJ, Medjibe VP, Metzger JP, Millet J, Mohandass D, Montero JC, De Morisson Valeriano M, Mugerwa B, Nagamasu H, Nilus R, Ochoa-Gaona S, Onrizal, Page N, Parolin P, Parren M, Parthasarathy N, Paudel E, Permana A, Piedade MTF, Pitman NCA, Poorter L, Poulsen AD, Poulsen J, Powers J, Prasad RC, Puyravaud J-P, Razafimahaimodison J-C, Reitsma J, Dos Santos JR, Roberto Spironello W, Romero-Saltos H, Rovero F, Rozak AH, Ruokolainen K, Rutishauser E, Saiter F, Saner P, Santos BA, Santos F, Sarker SK, Satdichanh M, Schmitt CB, Schöngart J, Schulze M, Suganuma MS, Sheil D, Da Silva Pinheiro E, Sist P, Stevart T, Sukumar R, Sun I-F, Sunderland T, Suresh HS, Suzuki E, Tabarelli M, Tang J, Targhetta N, Theilade I, Thomas DW, Tchouto P, Hurtado J, Valencia R, Van Valkenburg JLCH, Van Do T, Vasquez R, Verbeeck H, Adekunle V, Vieira SA, Webb CO, Whitfeld T, Wich SA, Williams J, Wittmann F, Wöll H, Yang X, Adou Yao CY, Yap SL, Yoneda T, Zahawi RA, Zakaria R, Zang R, De Assis RL, Garcia Luize B, Venticinque EM (2015) An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences* 112: 7472–7477. <https://doi.org/10.1073/pnas.1423147112>
- Smith B, Wilson JB (1996) A consumer's guide to evenness indices. *Oikos* 76: 70–82. <https://doi.org/10.2307/3545749>
- Snedecor GW, Cochran WG (1989) *Statistical Methods*. Eighth Edition. Iowa State University Press, Ames, 1–503.
- Spicer ME, Mellor H, Carson WP (2020) Seeing beyond the trees: a comparison of tropical and temperate plant growth forms and their vertical distribution. *Ecology* 101: e02974. <https://doi.org/10.1002/ecy.2974>
- Stévant T, Dauby G, Lowry PP, Blach-Overgaard A, Droissart V, Harris DJ, Mackinder BA, Schatz GE, Sonké B, Sosef MSM, Svenning J-C, Wieringa JJ, Couvreur TLP (2019) A third of the tropical African flora is potentially threatened with extinction. *Science Advances* 5: eaax9444. <https://doi.org/10.1126/sciadv.aax9444>
- Sullivan MJP, Talbot J, Lewis SL, Phillips OL, Qie L, Begne SK, Chave J, Cuni-Sanchez A, Hubau W, Lopez-Gonzalez G, Miles L, Monteagudo-Mendoza A, Sonké B, Sunderland T, ter Steege H, White LJT, Affum-Baffoe K, Aiba S, de Almeida EC, de Oliveira EA, Alvarez-Loayza P, Dávila EÁ, Andrade A, Aragão LEOC, Ashton P, Aymard C. GA, Baker TR, Balinga M, Banin LF, Baraloto C, Bastin J-F, Berry N, Bogaert J, Bonal D, Bongers F, Brienen R, Camargo JLC, Cerón C, Moscoso VC, Chezeaux E, Clark CJ, Pacheco ÁC, Comiskey JA, Valverde FC, Coronado ENH, Dargie G, Davies SJ, De Canniere C, Djuikouo K. MN, Doucet J-L, Erwin TL, Espejo JS, Ewango CEN, Fauset S, Feldpausch TR, Herrera R, Gilpin M, Gloor E, Hall JS, Harris DJ, Hart TB, Kartawinata K, Kho LK, Kitayama K, Laurance SGW, Laurance WF, Leal ME, Lovejoy T, Lovett JC, Lukasu FM, Makana J-R, Malhi Y, Maracahipes L, Marimon BS, Junior BHM, Marshall AR, Morandi PS, Mukendi JT, Mukinzi J, Nilus R, Vargas PN, Camacho NCP, Pardo G, Peña-Claros M, Pétronelli P, Pickavance GC, Poulsen AD, Poulsen JR, Primack RB, Priyadi H, Quesada CA, Reitsma J, Réjou-Méchain M, Restrepo Z, Rutishauser E, Salim KA, Salomão RP, Samsuodin I, Sheil D, Sierra R, Silveira M, Slik JWF, Steel L, Taedoumg H, Tan S, Terborgh JW, Thomas SC, Toledo M, Umunay PM, Gamarra LV, Vieira ICG, Vos VA, Wang O, Willcock S, Zemagho L (2017) Diversity and carbon storage

- across the tropical forest biome. *Scientific Reports* 7: 39102. <https://doi.org/10.1038/srep39102>
- Sullivan MJP, Lewis SL, Hubau W, Qie L, Baker TR, Banin LF, Chave J, Cuni-Sanchez A, Feldpausch TR, Lopez-Gonzalez G, Arets E, Ashton P, Bastin J-F, Berry NJ, Bogaert J, Boot R, Brearley FQ, Brienen R, Burslem DFRP, de Canniere C, Chudomelová M, Dančák M, Ewango C, Hédli R, Lloyd J, Makana J-R, Malhi Y, Marimon BS, Junior BHM, Metali F, Moore S, Nagy L, Vargas PN, Pendry CA, Ramírez-Angulo H, Reitsma J, Rutishauser E, Salim KA, Sonké B, Sukri RS, Sunderland T, Svátek M, Umunay PM, Martinez RV, Vernimmen RRE, Torre EV, Vleminckx J, Vos V, Phillips OL (2018) Field methods for sampling tree height for tropical forest biomass estimation. *Methods in Ecology and Evolution* 9: 1179–1189. <https://doi.org/10.1111/2041-210X.12962>
- Taylor A, Weigelt P, Denelle P, Lirong C, Holger K (2023) The contribution of plant life and growth forms to global gradients of vascular plant diversity. *New Phytologist* 240: 1548–1560. <https://doi.org/10.1111/nph.19011>
- Tegegne YT, Lindner M, Fobissie K, Kanninen M (2016) Evolution of drivers of deforestation and forest degradation in the Congo Basin forests: exploring possible policy options to address forest loss. *Land Use Policy* 51: 312–324. <https://doi.org/10.1016/j.landusepol.2015.11.024>
- Thinkabail PS, Hall J, Lin T, Ashton MS, Harris D, Enclona EA (2003) Detecting floristic structure and pattern across topographic and moisture gradients in a mixed species Central African forest using IKONOS and Landsat-7 ETM+ images. *International Journal of Applied Earth Observation and Geoinformation* 4: 255–270. [https://doi.org/10.1016/S0303-2434\(03\)00006-0](https://doi.org/10.1016/S0303-2434(03)00006-0)
- Thrippleton T, Bugmann H, Kramer-Priewasser K, Snell RS (2016) Herbaceous understorey: an overlooked player in forest landscape dynamics? *Ecosystems* 19: 1240–1254. <https://doi.org/10.1007/s10021-016-9999-5>
- Torti SD, Coley PD, Kursar TA (2001) Causes and consequences of monodominance in tropical lowland forests. *The American Naturalist* 157: 141–153. <https://doi.org/10.1086/318629>
- Tovar C, Harris DJ, Breman E, Brncic T, Willis KJ (2019) Tropical monodominant forest resilience to climate change in Central Africa: a *Gilbertiodendron dewevrei* forest pollen record over the past 2,700 years. *Journal of Vegetation Science* 30: 575–586. <https://doi.org/10.1111/jvs.12746>
- UNESCO (1978) Tropical Forest Ecosystems: A State of Knowledge Report. UNESCO, Paris, 1–683.
- Welch BL (1938) The significance of the difference between two means when the population variances are unequal. *Biometrika* 29: 350–362. <https://doi.org/10.2307/2332010>
- White F (1983) The Vegetation of Africa, a Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. UNESCO, Paris, 1–356.
- White LJT, Masudi EB, Ndongo JD, Matondo R, Soudan-Nonault A, Ngomanda A, Averti IS, Ewango CEN, Sonké B, Lewis SL (2021) Congo Basin rainforest — invest US\$150 million in science. *Nature* 598: 411–414. <https://doi.org/10.1038/d41586-021-02818-7>
- Zanne AE, Lopez-Gonzalez G, Coomes DA (2009) Data from: Towards a worldwide wood economics spectrum [Dataset]. Dryad. <https://doi.org/10.5061/dryad.234>

SUPPLEMENTARY MATERIALS

Supplementary material 1

Structural attributes calculated for *Gilbertiodendron dewevrei* plots of different sizes to verify that plot size is not causing its own signal in the analysis. Light red plots are the 11 100 m × 40 m plots, and dark red plots are the 17 30 m × 30 m plots. Graphs show stem number per ha, basal area per ha, and AGB per ha respectively. Whiskers on box plots represent 1.5 times the interquartile range plus or minus the first and third quartiles respectively. Values found beyond the whiskers are shown individually as points. Stars signify significance with NS indicating a lack of significant difference.

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Supplementary material 2

Mixed terre firme forest specialist species identified from indicator species analysis of plot data collected in the Sangha Trinational.

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Supplementary material 3

Seven species of vascular plants exclusively collected in monodominant *Gilbertiodendron dewevrei* forest in the Sangha Trinational, from a dataset of 5,603 specimens collected through general collecting. Species with only one collection were removed from this list. Table lists family, species, number of specimens collected in *G. dewevrei* forest, and plant lifeform.

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