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Light-demanding canopy tree species do not indicate past human disturbance in the Yangambi rainforest (Democratic Republic of the Congo)

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Abstract

Key message In a former paper, we investigated whether the presence of light-demanding tree species in the forest canopy of the Yangambi Biosphere Reserve (central Congo basin) might be a result of past human disturbances (Luambua et al., *Ecol Evol* 11:18691–18707, 2021). We focussed on the spatial distribution of the most abundant light demanders, but this approach did not yield conclusive results. In the present study, we focus on all species in the forest and conclude that light demanders are not a transient feature of successional tropical forests but an intrinsic component of old-growth forests in Yangambi.

Context Central African rainforests are characterised by an abundance of light-demanding tree species, which are aggregated in the canopy but underrepresented in the understorey. A popular explanation is that these forests are recovering from slash-and-burn farming activities preceding the relocation of settlements during the colonial era. In a former paper, we showed that the abundance of light-demanding tree species in the Yangambi Biosphere Reserve (central Congo basin) cannot be unambiguously attributed to past human disturbances, using an approach that focused on the spatial distribution of the most abundant light demanders (Luambua et al., *Ecol Evol* 11:18691–18707, 2021).

Aims As the former study was inconclusive, the present study aims to further test the assumptions behind the ‘recovery from human disturbance hypothesis’, by considering all species in the forest of Yangambi. We addressed four specific research questions: (i) do light demanders occur in large ‘pockets’ occupying large areas of forest? (ii) Are light demanders abundant? (iii) Do they exhibit a regeneration deficit? (iv) Is species composition in pockets of light demanders different from the surrounding forests?

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Methods We identified the location and size of pockets of light demanders in several transects cumulating to 50 km. We installed permanent inventory plots within and outside these pockets and calculated the diameter and age distributions of light demanders within each pocket. We assessed whether pockets of light demanders are different from surrounding forests, using plot clustering analysis.

Results Our results showed that light demanders were aggregated, but the pockets were small, scarce, and represent a minor fraction of the total forest area. Furthermore, light demanders were not abundant, even in pockets where they were aggregated. Their age distributions did not show a regeneration deficit. Finally, species composition in pockets of light demanders did not differ substantially from surrounding forests where they were scarce or absent.

Conclusions We conclude that light-demanding canopy species do not indicate past human disturbance in Yangambi and that they are an intrinsic component of old-growth forests rather than a transient feature of successional forests. Our insights show that the large carbon sink observed in mature forests in this region is not driven by successional forest dynamics.

Keywords Central African rainforest, Forest composition, Forest history, Light-demanding canopy species, Recovery from human disturbance hypothesis, Yangambi Biosphere Reserve

1 Introduction

Some central African rainforests are characterised by an abundance of large light-demanding canopy tree species with unimodal diameter and age distributions indicating regeneration deficit (Aubréville 1938; Letouzey 1968; Newbery and Gartlan 1996; Poorter et al. 1996; Van Gemberden et al. 2003; Vlam et al. 2017). A popular explanation for the abundance of these light-demanding species is the one given by the ‘recovery from human disturbance hypothesis’ (Muller-Landau 2009), which is based on the ‘classical succession theory’ (Yamamoto 2000). This theory predicts that light-demanding species should eventually disappear at the end of the forest succession process, leaving only shade-tolerant species when the forest reaches maturity (Yamamoto 2000). This theory claims that the presence, abundance or dominance of light-demanding species indicates a mid-successional state, stemming from earlier (large-scale) disturbances that can allegedly only be explained by human interference (Van Gemberden et al. 2003; Vleminckx et al. 2014; Bourland et al. 2015; Morin-Rivat et al. 2017). An important aspect of this theory is that it assumes that natural disturbance is an unusual event in mature forests (Muller-Dombois and Ellenberg 1974; White 1979). To validate the ‘recovery from human disturbance hypothesis’, a series of conditions need to be met: (i) light-demanding species occur in large ‘pockets’ (corresponding to former farmland) together occupying large areas of forest; (ii) light-demanding species are abundant in the canopy within these pockets; (iii) light-demanding species suffer regeneration deficit; (iv) species composition in the forest containing pockets with light demanders differs significantly from forests outside the pockets; and (v) the light-demanding character of the species is the most important trait explaining their distribution and age patterns.

Most studies that validated the ‘recovery from human disturbance hypothesis’ for African forests were conducted in

West–Central Africa (Cameroon, Gabon and Republic of Congo), where light-demanding species such as *Aucoumea klaineana* Pierre or *Triplochiton scleroxylon* K. Schum. can be locally monodominant (up to 95% of basal area) and are aggregated in large forest pockets (Van Gemberden et al. 2003; Vleminckx et al. 2014; Morin-Rivat et al. 2017; Ligt et al. 2019; Guidosse et al. 2022). Furthermore, the hypothesis seems to be supported in West–Central Africa by an analysis of historical sources, showing that a long tradition of intense slash-and-burn farming activities was abruptly interrupted at the end of the nineteenth century, when colonial regimes moved villages to concentrate them along accessible communication axes. After this reorganization, many forests were abandoned and the (abundant) former farmland patches were left to regenerate throughout the twentieth century (Van Gemberden et al. 2003; Vleminckx et al. 2014; Bourland et al. 2015; Morin-Rivat et al. 2017).

However, conclusions from West–Central Africa have been extrapolated to explain forest dynamics throughout tropical Africa. Specifically, the ‘recovery from human disturbance hypothesis’ has been used to explain the large carbon sink observed throughout African forests (Muller-Landau 2009), questioning the idea that tropical forest carbon sinks might be a direct result of CO₂ fertilisation (Lloyd and Farquhar 1996, 2008; Lewis 2006; Lewis et al. 2009). Assuming that former slash-and-burn patches are abundant and in a mid-successional regeneration state, long-term and large-scale carbon uptake in African forests could be attributed to forest succession dynamics rather than to a response of mature forests to climate change. This debate shows that untangling forest history is an important aspect to fully understand present-day carbon and biodiversity dynamics and the role of African tropical forests in the global climate system. This gap in our knowledge is rapidly gaining importance not only in scientific circles but also in (inter)national

policy on climate change adaptation and mitigation (White et al. 2021).

Therefore, our overall ambition is to test the validity of the ‘recovery from human disturbance hypothesis’ beyond West–Central Africa. Specifically, data supporting the hypothesis for the vast central Congo basin (representing more than half of the Central African rainforest area) remain extremely limited (White et al. 2021). This is why we set up a monitoring experiment in the Yangambi reserve, located in the heart of the Democratic Republic of the Congo (Luambua et al. 2021). In a former study, we showed that the abundance of light demanders in Yangambi cannot be unambiguously attributed to past human disturbances (Luambua et al. 2021). We used a methodological approach that focused on the spatial distribution of the most abundant light demanders, following earlier studies that concentrated on localising and measuring a few light-demanding ‘indicator’ species (Bourland et al. 2015; Morin-Rivat et al. 2017; Vlam et al. 2017). Yet our former study was inconclusive because we tried to draw conclusions on only a subset of species in the forest, ignoring ecological characteristics of the other species (Luambua et al. 2021). Autecology of common species or indicator species is generally used to estimate environmental filtering in species-poor communities, while synecology of functional groups is used for species-rich communities such as tropical forests, especially when applying broad ecological generalisations and extrapolations of results (Liira et al. 2019). Therefore, here we test a few of the assumptions behind the hypothesis by considering all species in the forest of Yangambi.

We investigate four specific research questions, each testing one of the assumptions underlying the ‘recovery from human disturbance hypothesis’: (i) Do light-demanding species occur in large ‘pockets’ together occupying large areas of forest? (ii) Are the light-demanding species abundant compared to other tree functional types? (iii) Do they exhibit the typical regeneration deficit? (iv) Are the forests in which the pockets are located, significantly different from other forests, based on full inventories?

2 Materials and methods

2.1 Study area: the Yangambi Biosphere Reserve

Data for this study were collected in the UNESCO Yangambi Biosphere Reserve in the middle of the central Congo basin. The Yangambi reserve is located in the province of Tshopo in the north-east of the Democratic Republic of Congo (DRC), between 0°49′–0°51′ N and 24°29′–24°35′ E. This region has an Af-type climate according to Köppen’s classification. The average annual rainfall is 1837 mm and the average annual temperature is 25.1 °C (Kasongo Yakusu et al. 2023). The Yangambi reserve has an

area of about 225,000 ha at an average altitude of 430 m. It is managed jointly by the Congolese Man and Biosphere (MAB) Committee of UNESCO and the Institut National pour l’Étude et la Recherche Agronomiques (INERA) (Kipute et al. 2019). Mature forests in Yangambi are semi-deciduous or on the transition between semi-deciduous and evergreen (Réjou-Méchain et al. 2021).

2.2 Inventory of focal species in Moni river transects

(Luambua et al. 2021)

The forests in the Moni River catchment represent a relevant study area to untangle differences in mature and successional forests and to test the ‘recovery from human disturbance hypothesis’ because they were mapped as a mosaic of mature forest patches (dominated by the shade-tolerant species *Scorodophloeus zenkeri* Harms, *Cynometra hankei* Harms or *Dialium corbisieri* Staner) and mid-successional forest patches (dominated by the light-demanders *Petersianthus macrocarpus* (P. Beauv.) Liben or *Ricinodendron heudelotii* (Baill.) Pierre ex Heckel), with patches of evergreen forests dominated by *Gilbertiodendron dewevrei* (De Wild.) J. Léonard, clearly concentrated along rivers (Fig. 1) (Van Wambeke and Evrard 1954).

We installed eight parallel transects oriented perpendicular to the Moni River (Fig. 2) (Luambua et al. 2021, 2022). Each of these transects is 5 to 8 km long, east–west oriented and separated by ~450 m. Transects were installed by cutting all non-woody vegetation and lianas over a width of 2 m. The transects together cover a total length of ~50 km (Luambua et al. 2021). Along the transects, a focal species inventory was carried out over an area of 25 m on the two sides of the transects’ baseline (so transects are 50 m wide), covering a total area of ~250 ha (Luambua et al. 2021).

The focal species inventory targeted the 32 most common light-demanding species in the Yangambi reserve (Luambua et al. 2021, 2022). The light-demanding character was derived from multiple sources (Hawthorne 1995; Meunier et al. 2015). Four of these species are short-lived pioneers (SLP), 13 are long-lived pioneers (LLP) and 15 are non-pioneer light demanders (NPLD) (Table 1 in the Appendix). SLPs and LLPs are heliophilous species that develop optimally, along their life-span, in bright light conditions, with relative irradiance of at least 30% (Meunier et al. 2015). SLPs display a short lifespan of less than 40 years, while LLPs have a longer lifespan. NPLDs are semi-heliophilous species whose seedlings develop optimally in average light conditions, with relative illumination between 10 and 30% (Meunier et al. 2015).

For comparison, we also targeted *G. dewevrei*, an extremely aggregative shade-tolerant (ST) species, which aggregation in Yangambi is probably (partly) due to a strong preference for proximity to waterways (Fig. 1 and Fig. 2) (Van Wambeke and Evrard 1954; Kearsley et al.

2017b). As such, the distribution pattern of this highly aggregated species served as a reference to evaluate the distribution patterns of the light-demanding species (Luambua et al. 2021). Species groups (SLP, LLP, NPLD, ST) are hereafter referred to as ‘tree functional types,’ following recent literature (Rüger et al. 2018, 2020). A total of 7523 individual trees of these selected focal species with at least 10 cm diameter at breast height (DBH) were identified, measured (DBH) and mapped (X and Y coordinates) along the Moni river transects (834 SLP, 800 LLP, 4694 NPLD, 1195 ST) (Luambua et al. 2021, 2022).

2.3 Identifying the location and estimating the size of pockets of light-demanding trees

In our previous study, the focal species inventory dataset was used to assess spatial patterns of light-demanding trees using the pair correlation function (PCF), Moran's I spatial autocorrelation index and canonical correspondence analysis (CCA) (Luambua et al. 2021). This showed that most focal light-demanding species in the Moni river transects seemed to be randomly distributed in the forest, but the approach did not allow to unambiguously exclude the ‘recovery from human disturbance hypothesis’ for Yangambi (Luambua et al. 2021).

For the present study, we installed permanent full inventory plots within and outside the pockets of light-demanding tree species along the Moni River transects. The first step was to identify the location and estimate the size of these pockets for each tree functional type. We did this using Kernel Density Estimation (KDE), based on tree spatial proximity and producing a spatial distribution map of tree density showing the hotspots for each tree functional type (Serra-Diaz et al. 2016; Negrón-Juárez et al. 2018).

The KDE function counts the number of trees (points) in a region (kernel), around the location where the estimate is made. Density functions are used to weigh nearby trees more heavily than distant trees. To do this, the open-source software SAGA GIS (2.3.2) (Conrad et al. 2015) was employed to produce a spatial distribution raster of tree density using a quartic kernel (Serra-Diaz et al. 2016; Negrón-Juárez et al. 2018; Kovács and Haidu 2022). As input, we used the tree location data (X and Y coordinates along the transect) of the focal species inventory database and the PCF calculated in our previous study (Luambua et al. 2021).

Then, the Raster calculator of the QGIS software version 2.18.28 was used to select all zones with a density greater than or equal to the minimum aggregation density taken from the PCF for each tree functional type. These zones correspond to the aggregates of tree functional types. After this step, the pockets of tree functional types (SLP, LLP, NPLD, ST) were selected by considering only the aggregates with a number of trees greater than the sum of the average number of trees per aggregate and the standard deviation. Finally, the surface area of each pocket and the length of the transects covered by the pockets of each tree functional type were calculated directly using QGIS software.

2.4 Full inventory of ten permanent plots along the Moni river transects and abundance of tree functional types

For the present study, we installed a total of ten full forest inventory plots (each 1 ha) within and outside the pockets localised by the KDE analysis along the Moni river transects (Fig. 2). Specifically, we installed one plot in a pocket of SLP (SLP-01), three plots in pockets of LLP (LLP-01 through -03), two plots in pockets of NPLDs (NPLD-01 and -02), two plots in pockets of the ST species *G. dewevrei* (GIL-01 and -02) and finally two plots were located in a mixed old-growth forest outside the pockets (MIX-01 and -02) (Luambua et al. 2024a).

Plots were installed according to the international standardised inventory protocol for tropical forests (RAINFOR) (Dallmeier 1992; Condit 1998; Phillips et al. 2009; Hubau et al. 2020; ForestPlots.net et al. 2021). All plots are rectangles of one hectare. Each plot has a length of 200 m along the transect and a width of 50 m (25 m either side of the transect). Each plot was divided in sub-plots of 25 m × 25 m, and all trees with DBH ≥ 10 cm were mapped (X and Y coordinates), taxonomically identified at the species level and tagged. On each tree, the point of measurement (POM) of the diameter was marked with paint. For trees with buttresses or any deformations at 1.30 m, the POM was taken about 50 cm above the deformation. For each individual tree in each plot, we defined to which tree functional type it belongs (SLP, LLP, NPLD, ST) using literature sources (Hawthorne 1995; Meunier et al. 2015). The number of individual trees per species and per plot is available in Dryad (<https://doi.org/10.>

(See figure on next page.)

Fig. 1 Forest types in the part of the Yangambi reserve containing the Moni River catchment (Van Wambeke and Evrard 1954). The area of the Moni River transects (Luambua et al. 2021) is indicated as a red box. Detailed structure of the transects is presented in Fig. 2. The inset at the bottom is the legend for the vegetation types relevant for the Moni River catchment area. Forests in this area are composed of mature evergreen forests (patches) dominated by *Gilbertiodendron dewevrei* (M) shown in blue and typically occurring along the rivers; a mosaic of mature semi-deciduous mixed forests (dark green) with abundance of shade-tolerant species such as *Scorodophloeus zenkeri* (o), *Cynometra hancei* (w) or *Dialium corbisieri* (D); and successional forests (light-green patches) with abundance of light-demanding species such as *Petersianthus macrocarpus* and *Ricinodendron heudelotii* (c)

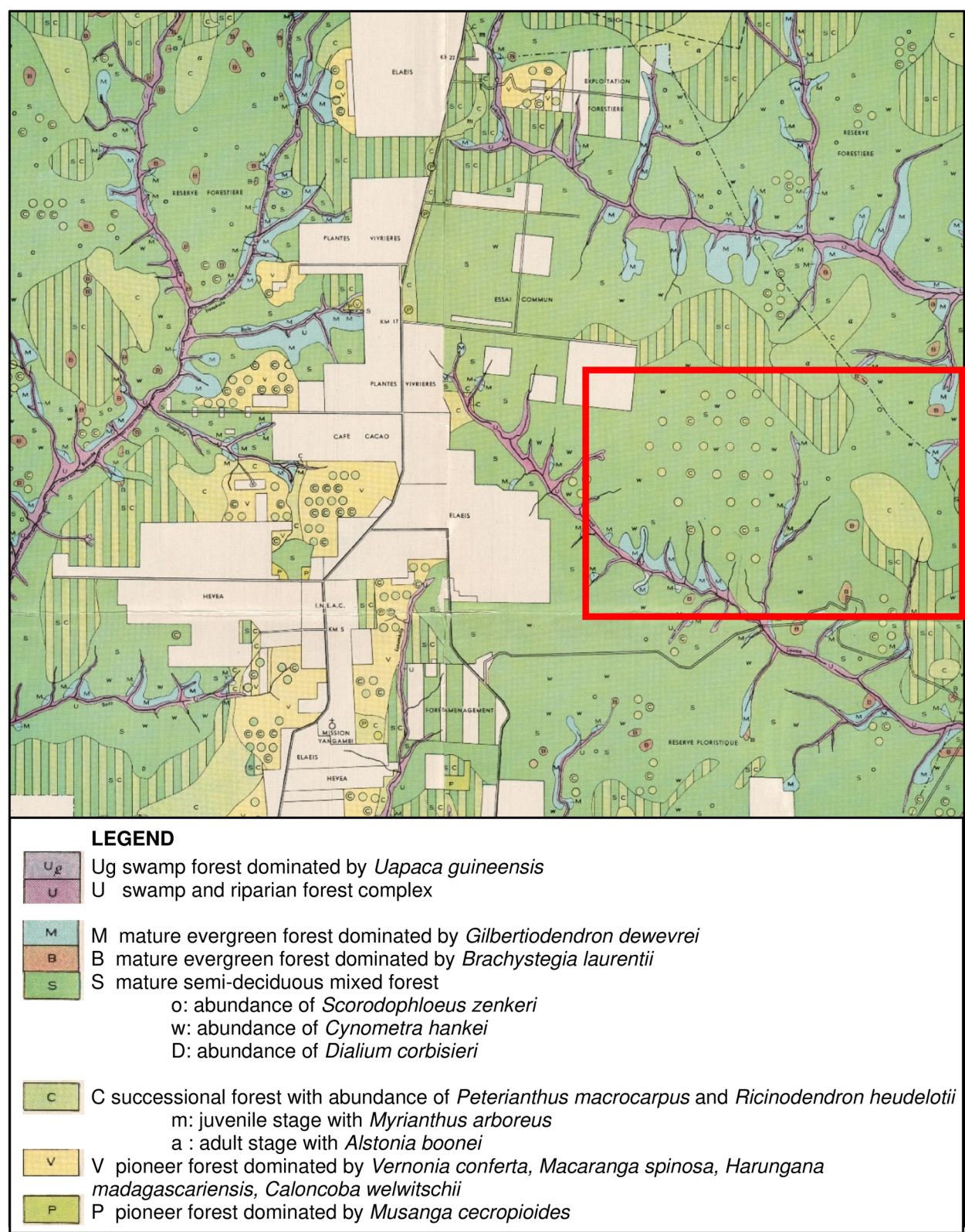


Fig. 1 (See legend on previous page.)

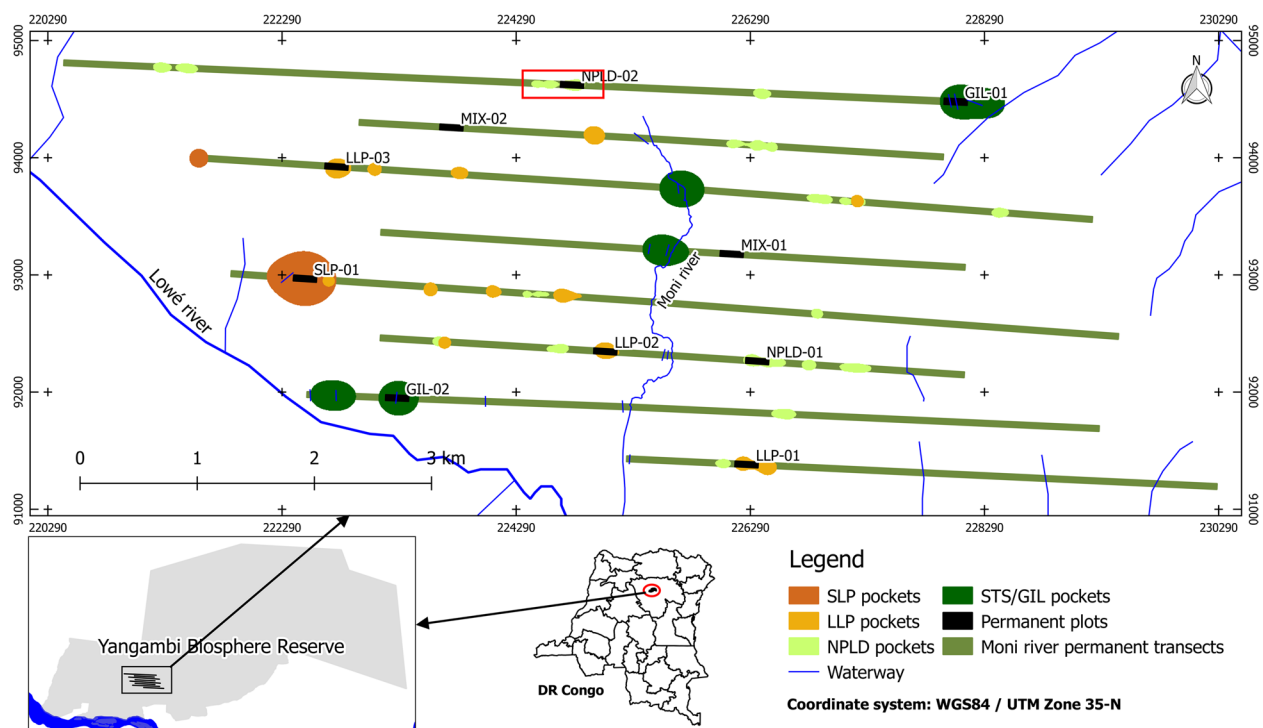


Fig. 2 Moni river transects, pockets of tree functional types and localisation of permanent inventory plots. Green lines represent the transects, black rectangles indicate the position of the ten permanent inventory plots within or outside the pockets. Short-lived pioneer pockets (SLP) are represented in brown, long-lived pioneer pockets (LLP) in yellow, pockets of non-pioneer light demanders (NPLD) in light green, and pockets of the shade tolerant species *Gilbertiodendron dewevrei* (GIL) in dark green. Two plots are located in the mixed old-growth forest (MIX) outside the pockets. The red square indicates the pockets that are represented in detail in Fig. 3

5061/dryad.qv9s4mwpt) (Luambua and Hubau 2024); species are grouped per tree functional type.

We used histograms to determine the abundance of each tree functional type within each plot. Furthermore, we visualised the abundance of tree functional types by mapping out the trees in the permanent inventory plots, using different colours per tree functional type (SLP, LLP, NPLD, ST).

2.5 Tree age distribution of light demanders

We determined tree age distributions of LLPs and NPLDs by counting annual growth rings on wood cores sampled in the pockets of LLPs and NPLDs. We focused on species for which the annual character of tree-ring formation was verified by radiocarbon dating (*Entandrophragma* spp., NPLDs) (Groenendijk et al. 2014) by cross-dating large numbers of individual trees (*Pericopsis elata* (Harms) Meeuwen, LLPs) (De Ridder et al. 2014) or by fire scar (*Albizia* spp., LLPs) (López et al. 2012). From the selected species, we randomly selected trees to obtain a sample that is representative for the diameter distribution of the species. In this way, we compared DBH distribution with age distribution for each tree functional type. Growth ring boundaries were recognised as described by Tarelkin et al. (2016) and Worbes and

Fichtler (2010). Growth-ring boundaries of *P. elata* were generally marked by a thin band of marginal parenchyma but sometimes by a band of flattened fibres. After this thin band of marginal parenchyma or flattened fibres, at the beginning of the adjoining ring, a zone with fewer vessels followed by aliform parenchyma was sometimes observed (De Ridder et al. 2014). *Entandrophragma* spp. tree rings are characterised by patterns of parenchyma and fibre bands (Groenendijk et al. 2014). The boundary was often marked by a continuous band of parenchyma and/or parenchyma bands density variation (Détienne et al. 1998). Regarding *Albizia* spp., ring boundaries were characterised by a narrow marginal parenchyma band (Maingi 2006) or abrupt change in radial fibre diameter, often associated with variation in vessel size.

For each selected individual, at least two bark-to-pith wood cores were extracted per stem using Pressler increment borers of different lengths (70 cm, 50 cm and 30 cm) and 5.15 mm diameter (Norton 1998). The height for extracting the core sample was kept as low as possible in order to have as many rings as possible (Henry and Swan 1974; Fraver et al. 2011; Rosa et al. 2011; UWICER 2017). We generally sampled at a height of 80 cm above ground or 50 cm above buttresses.

The cores were prepared in the Yangambi Wood biology laboratory. They were first polished using a sander (Festool ROTEX RO 150 FEQ) and scanned at 1200 dpi with a high-resolution digital scanner (EPSON Expression 11000XL). Ring widths were measured in two radii per individual using DHXCT2016 software developed at Woodlab-UGent (De Mil et al. 2016). In cases where the pith was absent on the core, the distance between the oldest visible ring and the pith was estimated using the degree of arc in this oldest ring (Hietz 2011; Hubau et al. 2019). The number of missing rings close to the pith was estimated as the ratio of the missing distance to the pith and the average ring width of this sample. The age of the tree was therefore considered to be the number of rings counted from the pith to the bark. We used histograms to visualise age distribution of the two functional types.

2.6 Plot clustering analysis

To determine whether plots within pockets of tree functional types are significantly different from one another, we performed a hierarchical clustering analysis of species composition. To strengthen the clustering analysis, we combined the 10 Moni River plots installed for the purpose of this study (Luambua et al. 2024a), with additional data from 33 plots that were previously installed in mature mixed, mature monodominant or pioneer forest in the vicinity of the Moni River catchment (YGB-05 through -31 and YGM-08 through -12) (Kearsley et al. 2013, 2017b, 2017a). This resulted in a full dataset of 43 plots for clustering analysis (10 Moni River plots, plus 33 additional surrounding plots).

As species composition can vary within plots, a preliminary subplot-level test revealed a lack of intra-plot heterogeneity. Therefore, full plots were used as sites in the main clustering analysis. As an input to the clustering analysis, we calculated % basal area and % stems for each species, per plot. These metrics best define the relative abundance of species (Baker et al. 2004). We calculated the Bray–Curtis dissimilarity indices between plots and Raup–Crick dissimilarity indices between taxa using the ‘vegdist’ function of the package ‘vegan’ in R (Luambua et al. 2024b). We used the ‘cldiss’ function to visualise an ordered dissimilarity matrix (Borcard et al. 2011).

We then performed hierarchical cluster analysis using Ward’s minimum variance method. We did this for both plot- and taxon-level dissimilarities (‘hclust’ function of the package ‘vegan’). We defined the optimum number of groups based on the Mantel statistic for plot- and taxon-level clustering objects (Borcard et al. 2011). We used the ‘rect.hclust’ function to visualise the retained groups as red rectangles on the cluster dendrogram. We then performed a two-way clustering analysis, ordered by explicit

indexing using both the plot-level and taxon-level clustering objects, using the ‘tabasco’ function of the package ‘vegan’ (Luambua et al. 2024b). The result is a compact community table in the form of a heatmap where rows represent species, and sites represent columns (without duplicates). This community table shows which species occur in which forest types.

We cross-checked the clustering analysis using canonical correspondence analysis (=optionally constrained correspondence analysis) using the ‘cca’ function of the package ‘vegan’. The result is an ordination diagram, where we superimposed polygons (convex hulls) encircling the items in the groups retained by the clustering analysis.

3 Results

3.1 Pockets of tree functional types in the Moni transects

KDE highlighted the tree density hotspot zones for each functional type (Fig. 2). KDE identifies circular hotspots, which is why the pockets extend beyond the transects. A zoom-in on two NPLD pockets shows the repartition of trees along the transect and the outline of the pockets as determined by KDE (Fig. 3). Pocket selection revealed a total of 36 pockets, from which 2 SLP pockets, 12 LLP pockets, 17 NPLD pockets and 5 GIL (*G. dewevrei*) pockets (Fig. 2). SLP and GIL pockets are the largest, with a maximum area of 20.4 ha. LLP pockets are intermediate in size (maximum area of 3.2 ha) and NPLD pockets are generally small (maximum area of 2.5 ha). On average, LLP pockets cover an area of 1.5 ha (range: 0.7–3.2 ha). The relative coverage of the pockets along the transects was 1.3% (SLP), 3.2% (LLP), 4.0% (NPLD) and 3.4% (GIL) (Fig. 1). The remaining 88.1% are covered by mixed old-growth forest.

3.2 Abundance of tree functional types

In our dataset, LLPs were scarce, representing 3.5% of all individuals and 14.6% of the basal area within the group of full inventory plots installed in LLP pockets (Fig. 4). Furthermore, they are more abundant in the highest diameter classes, taking up >40% of the basal area in the DBH classes from 80 cm onwards within these LLP pockets (Fig. 4). LLPs are even scarcer in the mixed old-growth forest outside the pockets (Fig. 4), where they represent only 1% of stems and 2.2% of basal area, and where they also do not dominate the basal area in the larger DBH classes.

NPLDs are slightly more abundant than LLPs, with 17.4% of all individuals and 22.3% of the basal area within the group of full inventory plots containing the NPLD pockets. In mixed forest plots, they represent 5.9% of all individuals and 9.9% of basal area.

In between the light-demanding species (LLPs and NPLDs), even if they form pockets where they are more

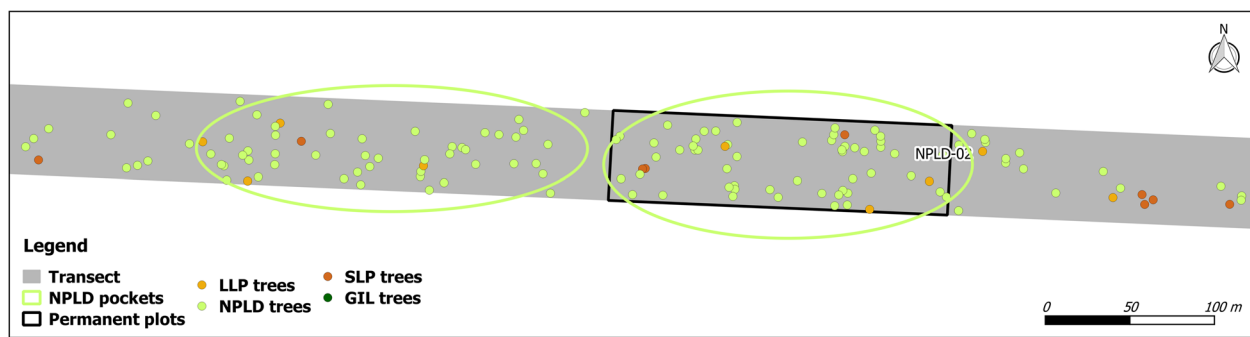


Fig. 3 Detailed representation of the NPLD pockets that were chosen to install plot NPLD-02 (200 m × 50 m plot outline in black). The location of these pockets within the Moni River transects, is shown in Fig. 2

abundant than elsewhere, we find many individuals of shade-tolerant species in all diameter and canopy classes (Fig. 5).

3.3 Tree age distributions of light demanders

Growth-ring boundaries were clearly recognised (Fig. 6) and marked. Tree age distribution of both LLPs and NPLDs show a reverse J-shape, with most individuals in the lowest age class (20–70 years) (Fig. 7). For NPLDs, this compares well with the DBH distribution which is also reverse J-shaped, with most individuals in the lowest diameter class (10–20 cm). However, for LLPs, the age distribution contrasts with DBH distribution which is unimodal, with most individuals in intermediate diameter classes (40–60 cm).

3.4 Plot clustering results

Hierarchical clustering analysis (Fig. 8), canonical correspondence analysis (Fig. 8 inset) and the dissimilarity matrix (Fig. 9 in the Appendix) all show that plots in LLP pockets are similar to plots in NPLD pockets and to mixed old-growth forest (MIX) plots in terms of species composition. In the full dataset of 43 plots, only 3 clusters were identified. One cluster represents a very young pioneer forest, dominated by *Musanga cecropioides* R. Br. ex Tedlie and *Macaranga* spp. A second cluster represents monodominant evergreen forest dominated by *G.*

dewevrei. The third cluster, containing 31 of the 43 plots, includes the SLP, LLP, NPLD and the MIX plots of the Moni transects. Clustering analysis results do not differ whether % basal area (Fig. 8) or % stems (Fig. 10 in the Appendix) is used to express species dominance.

4 Discussion

4.1 Pockets of light demanders are small and do not occupy large areas of forest

The two SLP pockets identified were large (Fig. 2), and the abundance of short-lived pioneer trees indicates recent forest disturbance. The largest was clearly a wind-throw event, while the other one was a farmland (Fig. 2) (Luambua et al. 2021).

In contrast with the SLPs, long-lived pioneers were aggregated in pockets but these pockets were small (0.7–3.2 ha), scarce (12 pockets in 250 ha) and together they occupy only a small area (3.2%) of the total area covered by the transects (Figs. 2 and 3). As such, even if these pockets would represent former farmlands, they do not represent a significant part of the forest in Yangambi and they do not determine the carbon sink of the forest as a whole, as some scholars suggest (Muller-Landau 2009). The small size and scarcity of the LLP pockets in our study site (Fig. 2) might be more compatible with the ‘gap dynamics hypothesis’ than with the ‘recovery from human disturbance hypothesis’. The ‘gap dynamics

(See figure on next page.)

Fig. 4 Abundance of tree functional types (PFT) in the 10 Moni river full inventory plots. Panel **a** includes data from pockets of short-lived pioneers (SLP, $n = 1$ plot). Panel **b** includes data from pockets of long-lived pioneers (LLP, $n = 3$ plots). Panel **c** includes data from pockets of non-pioneer light-demanders (NPLD, $n = 2$ plots). Panel **d** includes data from mixed forest outside pockets (MIX, $n = 2$ plots). Panel **e** includes data from pockets of *Gilbertiodendron dewevrei* (GIL, $n = 2$ plots). Histograms on the left indicate relative stem density (% of all stems in the plots) per DBH (diameter at breast height) class and per tree functional type (dark-green=shade-tolerant (ST), light-green=non-pioneer light demanders (NPLD), yellow=long-lived pioneers (LLP), brown=short-lived pioneers (SLP), grey=unknown). The stacked bar-chart indicates relative stem density per tree functional type, over all DBH classes, highlighting the most abundant species together representing 40% of the stem count. Histograms on the right indicate relative basal area (BA; % of plot basal area) per DBH class and per tree functional type. The stacked bar-chart on the right indicates relative basal area per tree functional type, over all DBH classes, highlighting the most abundant species together representing 40% of the basal area

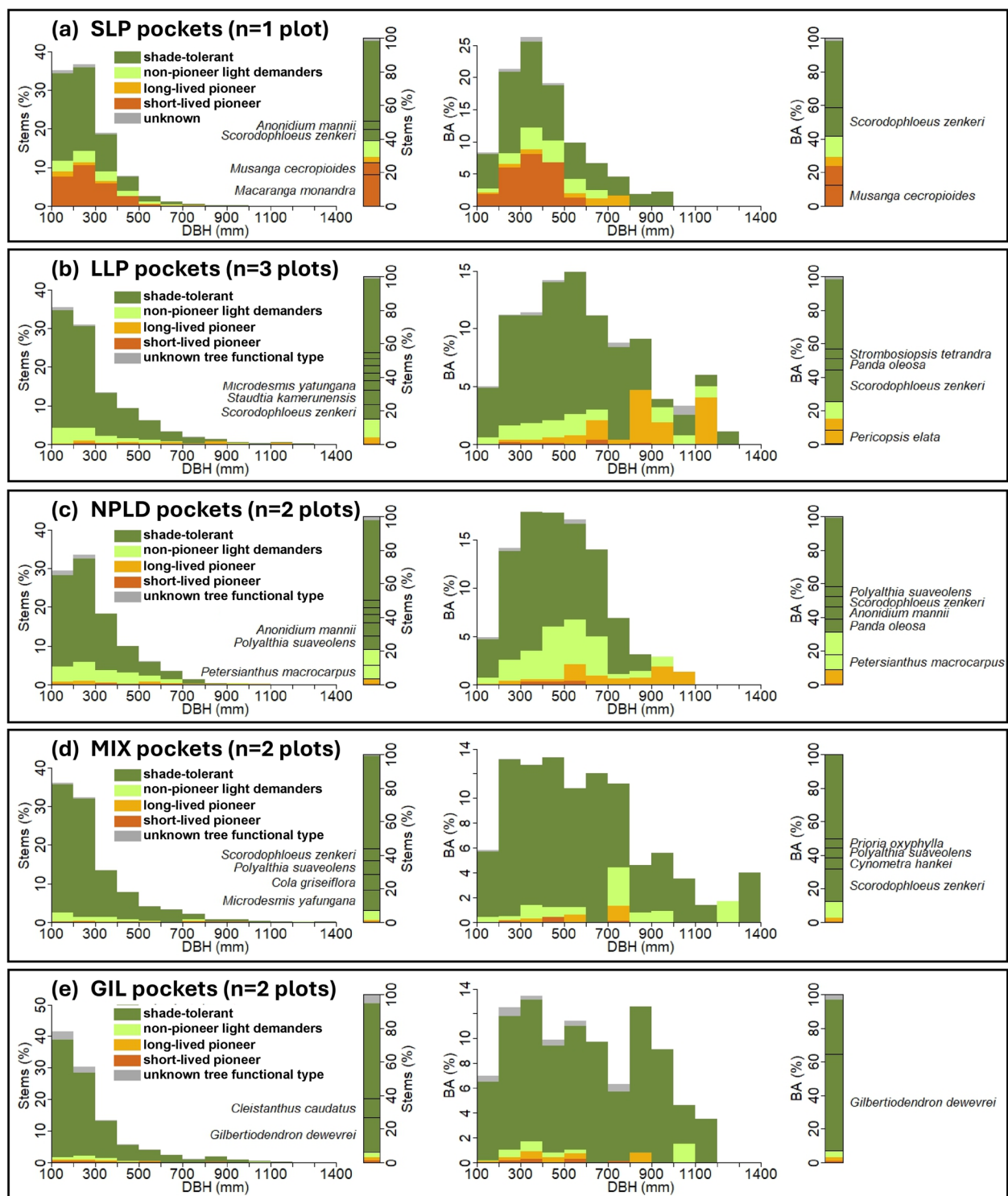


Fig. 4 (See legend on previous page.)

hypothesis' predicts that LLPs, which cannot establish and grow in closed conditions, can be maintained in mature forests because they regenerate in gaps formed by (minor) natural disturbances (Brokaw 1985). This theory

is based on the fact that trees in mature forests can die of natural causes, either individually or as part of multiple event with one or several 'killer' trees (Esquivel-Muelbert et al. 2020), leaving small gaps. These gaps are then

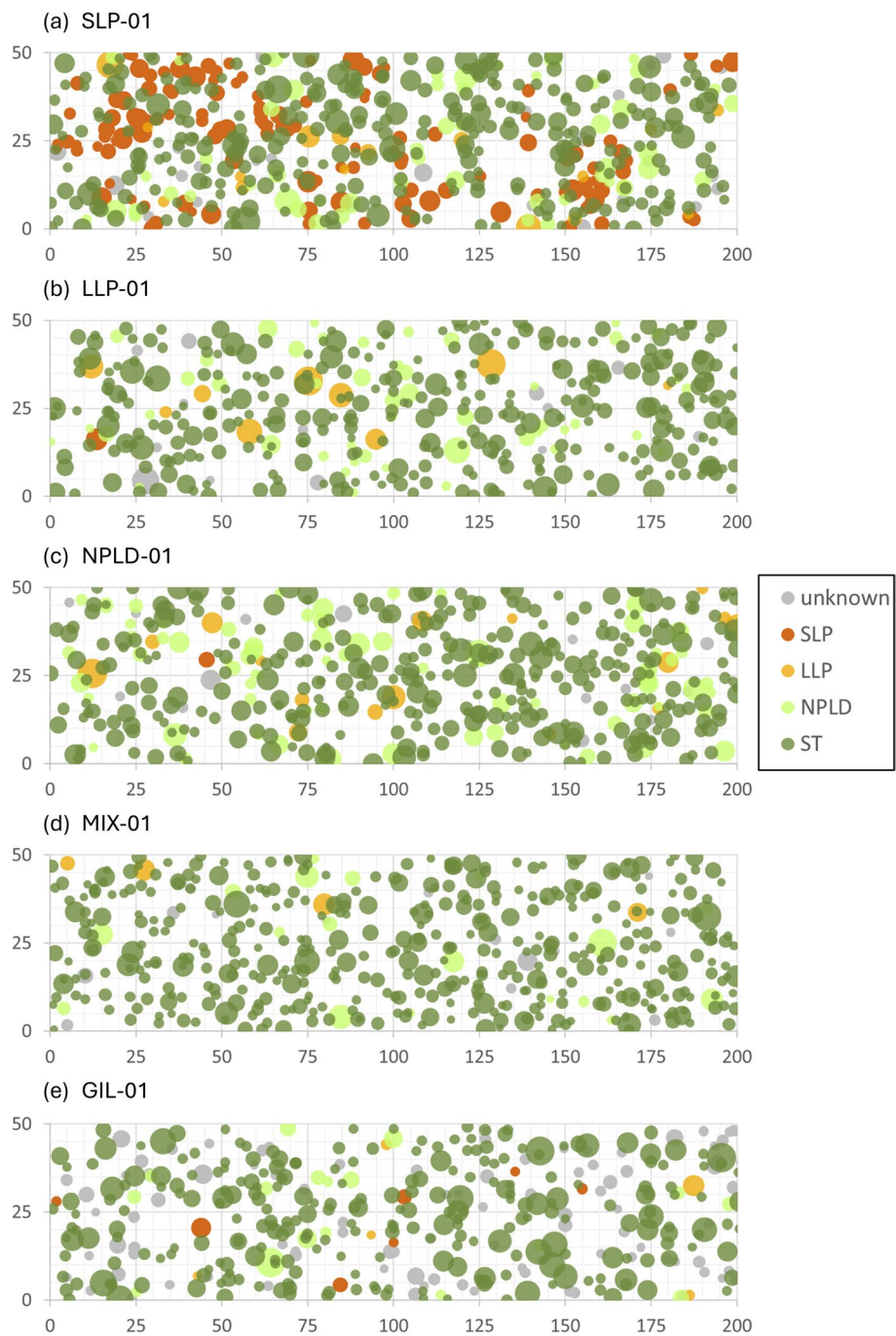


Fig. 5 Distribution of trees belonging to each tree functional type (SLP, LLP, NPLD, ST) in five permanent inventory plots. Panel **a** represents plot SLP-01 which is located in a pocket of short-lived pioneers. Panel **b** shows plot LLP-01 which is located in a pocket of long-lived pioneers. Panel **c** shows plot NPLD-01 which is located in a pocket of non-pioneer light demanders. Panel **d** shows plot MIX-01 which is located in mixed mature forest outside the pocket. Panel **e** shows plot GIL-01 which is located in a pocket of *Gilbertiodendron dewevrei*. Dot size corresponds to tree diameter; colours of tree functional types correspond to Fig. 1

occupied by pioneer trees (Watt 1947; Whitmore 1978; Brokaw 1985). Multiple studies of gap size and frequency in the Amazon confirmed that natural disturbances and formation of gaps are not unusual events in mature

forests but crucial natural processes shaping forest structure and composition (Asner et al. 2013; Espírito-Santo et al. 2014). Most gaps are very small (<0.1 ha) but together account for 98.6% of carbon losses in tropical

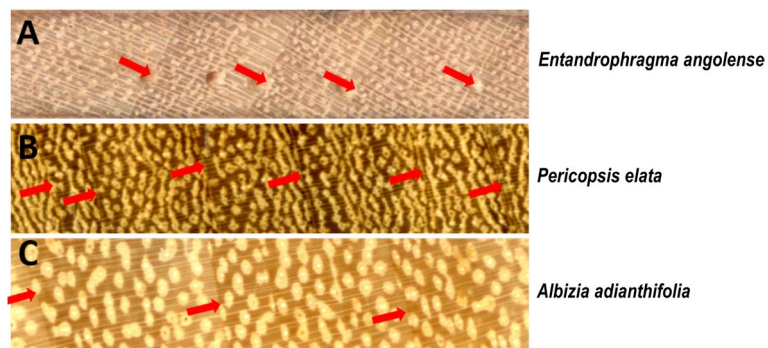


Fig. 6 Annual ring boundaries in the selected species for tree age distribution analysis. The red arrows show the wood structures marking the limits of the growth rings

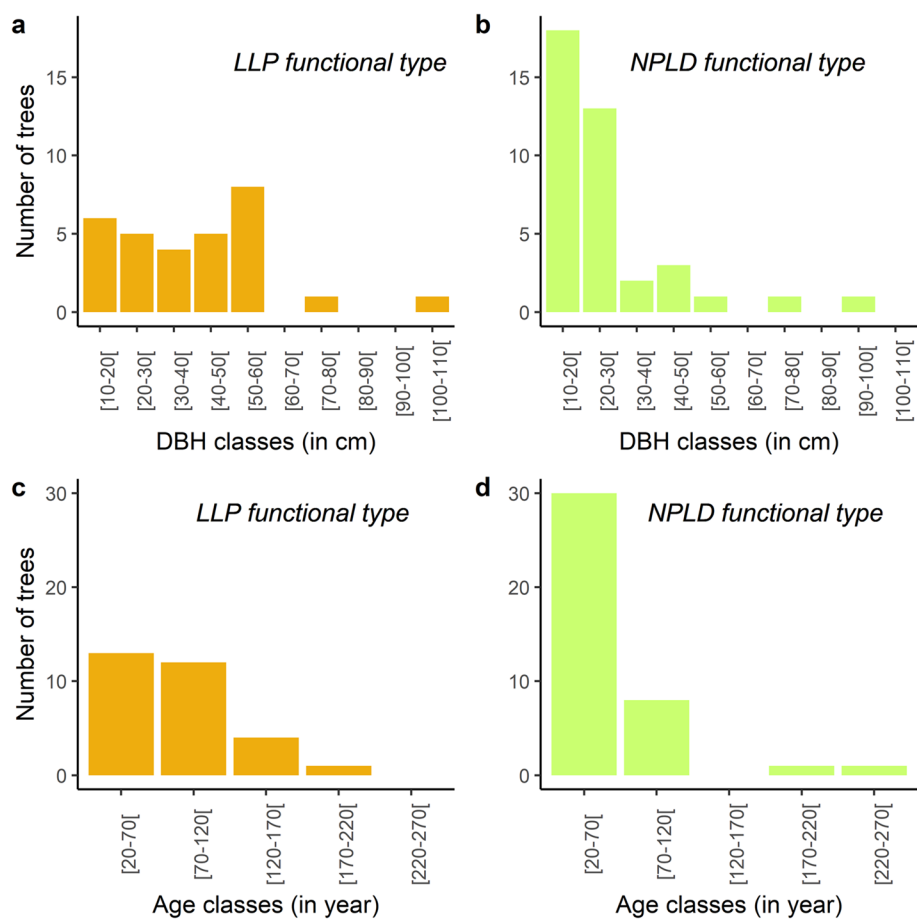


Fig. 7 DBH and tree age distributions of LLPs ($n=30$) and NPLDs ($n=40$) in the Moni river transects, determined from tree rings. Panels **a** and **b** show the diameter class distribution of the number of LLP and NPLD trees respectively. Panels **c** and **d** show the age class distribution of the number of LLP and NPLD trees, respectively

forests (Esp rito-Santo et al. 2014). Intermediate gaps (0.1–5 ha) are scarce and account for only 1.1% of carbon losses (Esp rito-Santo et al. 2014). The ‘pockets’ of light demanders in the Moni transects (Fig. 2) fall within the range of the intermediate gaps, indicating that small gaps are probably not detected by the KDE approach, focusing on just a few indicator species.

4.2 Light-demanding species are not abundant in the pockets

There is a curious discrepancy between the relative scarcity of LLPs and NPLDs observed in our study site (Figs. 4 and 5) versus the alleged ‘abundance’ or even ‘dominance’ of light-demanding species in the forests of Central Africa as described in the literature (Poorter et al. 1996; Van Gernerden et al. 2003; Vleminckx et al. 2014; Bourland et al. 2015; Morin-Rivat et al. 2017). This discrepancy is due to differences in regions and differences among specific forest types. The ‘recovery from human disturbance hypothesis’ stems from research in almost pure monodominant stands of light-demanding species in some places in West–Central Africa, where they indicate large-scale past forest disturbance. Especially the evidence of the anthropogenic origin of the large monodominant stands of *A. klaineana* in Gabon is indisputable (Delègue et al. 2001; Fuhr et al. 2001; Guidosse et al. 2022). These monodominant *A. klaineana* stands emerged through natural regeneration after human populations were decimated and the intense slash-and-burn regime was abandoned following the transatlantic slave trade (Thornton 1983).

As they are often mentioned by scholars advocating the ‘recovery from human disturbance hypothesis’, the history of these *A. klaineana* stands seems to have nourished the now widespread paradigm that the sheer presence of long-lived pioneers is an indicator of past human disturbance (Van Gernerden et al. 2003; Morin-Rivat et al. 2017). However, there is a difference between *A. klaineana* stands, which reach monodominance levels of up to 95% of the stem count (Fuhr et al. 2001; Guidosse et al. 2022), and LLPs in the central Congo Basin, which do not reach more than 3.5% of the stem count in Yangambi (Fig. 4) (Morin-Rivat et al. 2017). Furthermore, there is a difference in human history between the interior of the Congo Basin and the coastal regions of Gabon. The latter might have been more densely populated in the centuries before the transatlantic slave trade and might have suffered more from the transatlantic slave trade due to their proximity to the ports (Thornton 1983). To our knowledge, there is no evidence for the occurrence of truly monodominant

stands of LLP species in the central Congo basin (DRC). Specifically, in our dataset from Yangambi (central DRC), all long-lived pioneers together represent only 2.5% of all stems and only 7.4% of the basal area (Fig. 4).

4.3 Light-demanding species do not exhibit any regeneration deficit

We find that the largest group of light-demanding species, the NPLDs, show characteristics of shade-tolerant species, with clear J-shaped diameter and age distributions indicating no regeneration deficit (Fig. 7) (Vlam et al. 2017). As such, the community structure of NPLDs does not show the signature compatible with the ‘recovery from human disturbance hypothesis’, which accounts for species that combine canopy dominance with regeneration deficit.

However, LLPs in our study site show a DBH distribution that is contrasting with the age distribution (Fig. 7): while there is a deficit of small trees in the DBH distribution, there is no deficit of young trees in the age distribution. This apparent discrepancy can be explained by the fact that the population dynamics of LLPs are not only determined by their light-demanding character and their recruitment rates but also by their fast juvenile growth rates. Analysis of large forest inventory datasets including information on saplings (individuals with DBH < 10 cm) showed that the shape of the size distribution does not correlate with population growth or decline in canopy species (Condit et al. 1998). Other parameters also affect the size distribution. Specifically, juvenile growth was shown to be a strong predictor of size distribution (Condit et al. 1998). The decrease in diameter growth rates with size for LLP species contributes to trees accumulating in the intermediate diameter classes, producing bell-shaped size distributions. This explains why observed low numbers of small LLP individuals in the DBH distribution (Fig. 7) do not correspond with a regeneration deficit in the age distribution. As such, because of interspecific variation in recruitment, mortality and growth rates, the species composition in small diameter classes does not necessarily match that of the future canopy. A small present-day ‘deficit’ of small LLP

(See figure on next page.)

Fig. 8 Plot clustering results based on species-specific % basal area. **a** presents a heatmap showing the two-way ordered community table indexed using both the plot-level and species-level clustering objects of the 43 full inventory plots in the Yangambi inventory dataset. Rows represent species, columns represent plots (all species and all sites are present, without duplicates). Cell colours within the heatmap (white-yellow-red) represent % basal area of each species within each plot, ranging from 0% (white) to 95% (dark red). Cluster dendrograms represent the plot-level clustering (top) and the species-level clustering (left). The red boxes indicate the retained groups defined by the Mantel statistic, showing three groups of significantly different plots. Most abundant taxa (representing >3% of the basal area) within each of these clusters, are indicated within the heatmap. Plot codes (bottom of the figure) from plots in Moni transects are highlighted with colours, as in Fig. 1. **b** presents the plot-level ordination diagram resulting from the canonical correspondence analysis, with superimposed convex hulls (red polygons) from the clustering analysis (see red boxes in the cluster dendrogram). Moni River plots are indicated within this ordination diagram with their corresponding colours

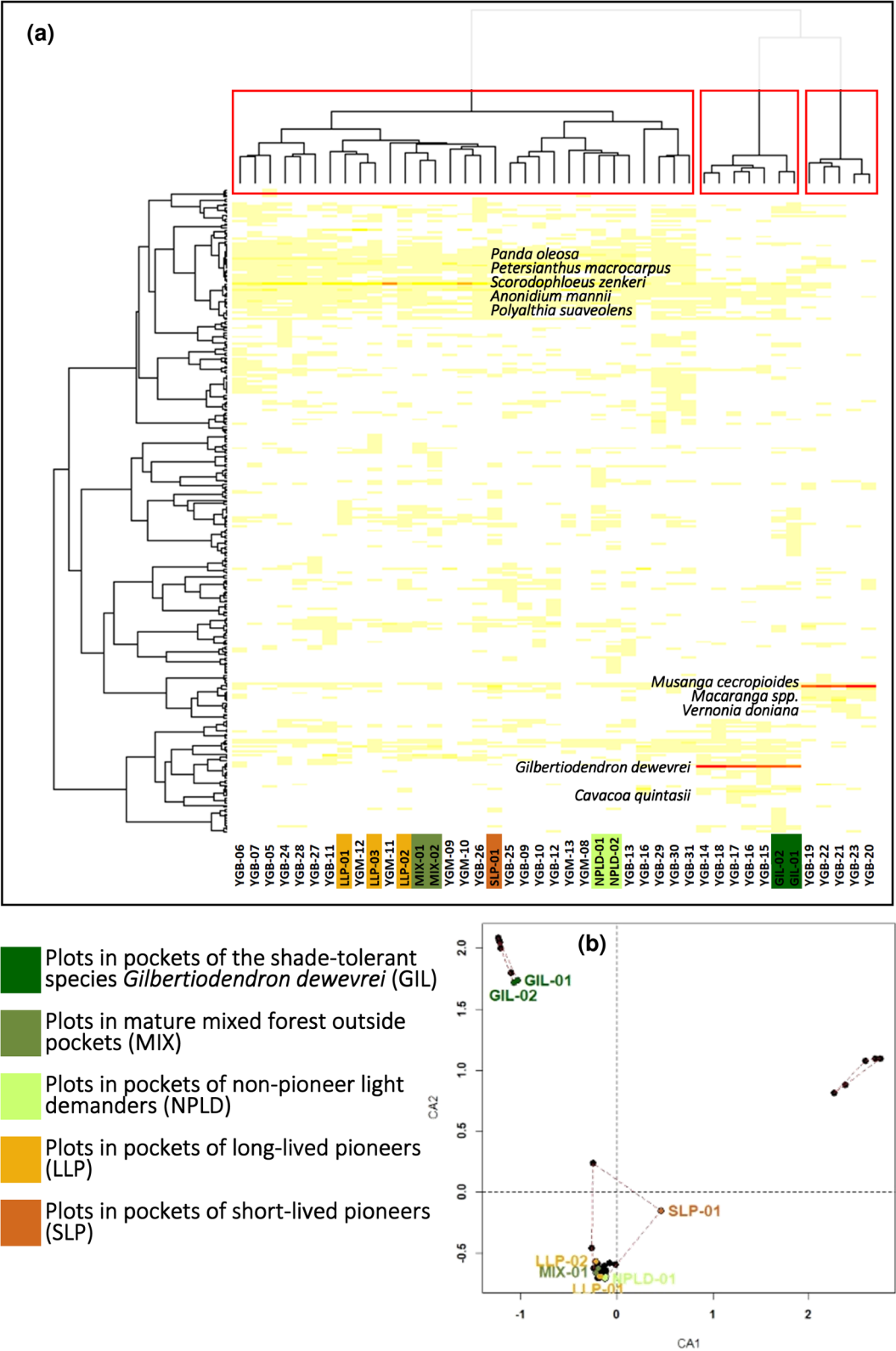


Fig. 8 (See legend on previous page.)

trees will not result in a declining population in the future (Morin-Rivat et al. 2017).

4.4 Pockets of light-demanders do not differ from surrounding forests

Clustering analysis shows that forests in pockets of LLPs were not significantly different from forests where they were less abundant (Fig. 8, Fig. 9 in the Appendix). This apparent contradiction with the KDE analysis (pockets, Fig. 1) confirms that we cannot draw conclusions on the autecology of only a subset of focal species in the forest of Yangambi. Our clustering analysis is an example of synecology, focussing on functional groups, which is more appropriate for species-rich communities such as tropical forests (Liira et al. 2019).

The clustering analysis shows that mixed forests in Yangambi seem to be homogeneous, as most plots were clustered in a single large group. This confirms that LLPs are part of the mature forest. A recent analysis of large forest inventory datasets, combined with state-of-the-art demographic forest modelling, showed that LLPs are indeed an integral component of old-growth forests and do not necessarily disappear or become scarce after a fully completed successional trajectory (Rüger et al. 2018, 2020). On the contrary, they can become progressively more abundant and even dominant over very long timespans (several centuries) after forest regeneration. This is because forest composition is defined by a complex set of species traits that are part of both the “fast–slow” continuum and the “stature–recruitment” continuum.

The “fast–slow” continuum is characterised only by the growth–survival trade-off (Rüger et al. 2018). This trade-off implies that “fast” species are light-demanding, grow quickly, dominate early successional stages, but survive poorly and are no longer abundant in mature forests. In contrast, “slow” species are shade-tolerant, grow slowly, survive well and reach dominance in later successional stages (Yamamoto 2000; Chazdon et al. 2007; Chazdon 2008).

A second major dimension of demographic variation is the “stature–recruitment” continuum, characterised by a trade-off between recruitment performance versus survival and eventual size of mature individuals (Rüger et al. 2018). This “stature–recruitment” continuum distinguishes LLPs which grow fast, live long, reach a large stature, but have low recruitment rates; from short-lived breeders (SLBs) which grow and survive poorly, remain short-statured, but produce large numbers of recruits. Demographic models show that SLBs disappear quickly after forest regeneration, while LLPs remain abundant (Rüger et al. 2020).

A combination of the two demographic continua (fast–slow versus stature–recruitment) explains why LLPs dominate earlier successional stages (they grow fast under full light conditions) and why they can also maintain populations of predominantly large-statured trees in old-growth mature forests (they compensate for their relatively low recruitment by fast juvenile growth, growing quickly to large proportions, persisting as a massive seed source for several centuries). This framework also explains the co-existence and intense mixing of both LLPs and shade-tolerant trees in the canopy of our forest plots (Fig. 5).

4.5 Implications

Our insights have implications on the debate about the drivers of the carbon sink in central African forests, which has been large and stable for more than three decades (Hubau et al. 2020). Scholars supporting the ‘recovery from human disturbance hypothesis’ claim that this sink might be a result of a mid-successional (regenerating) state of these forests, which might thus be accumulating carbon as part of their successional trajectory rather than as a response on changing climatic conditions (Muller-Landau 2009). While several studies already showed the effect of carbon dioxide (CO₂) fertilisation (Keenan et al. 2016; Hubau et al. 2020; Walker et al. 2021; Chen et al. 2022), our analysis adds to the evidence that the Yangambi rainforests are likely not mid-successional but genuine old-growth mature ecosystems characterised by gap dynamics.

Our results also have implications on forest management in African tropical rainforests. Several LLPs are among the most important timber species (e.g. *P. elata*, *T. scleroxylon*, *A. klaineana*). Based on the diameter distributions showing regeneration deficits and on the ‘recovery from human disturbance hypothesis’, it has been suggested that creating large openings in the canopy might be a suitable forest management strategy to maintain populations of these valuable timber species (Morin-Rivat et al. 2017). Our results, together with previously published analysis, show that such practices are not needed in the intact (unlogged) Yangambi rainforest, as the populations of the present LLPs are likely stable as an inherent element of the mature rainforest. On the contrary, populations of LLPs may be very vulnerable to logging because the few large individuals are the seed reservoirs of the population and their sporadic emergence to large sizes often does not make up for the loss through logging (Ohse et al. 2023).

Our study area is representative for a large area of the Congo basin because it is situated in the transition

zone between two widely distributed forest types: evergreen and semi-deciduous forests (Réjou-Méchain et al. 2021). However, more sites within these species-rich forests should be investigated using a holistic approach based on the synecology of functional groups before conclusions can be generalised or extrapolated to the entire Congo basin (Liira et al. 2019). We recommend to further test the ‘recovery from human disturbance hypothesis’ through analysis of full inventory plots, with a special focus on recruitment, growth and mortality of trees within all functional groups (SLP, LLP, NPLD, ST) and all life stages (from young seedlings to old mature trees). We specifically recommend investing in permanent inventory plots following the ForestGEO protocol (Davies et al. 2021). Such plots are large (10 ha or more), include small trees (DBH < 10 cm) in the inventory and are therefore labour-, time- and cost-intensive to install and remeasure. However, data of such plots is key to understand why tree species coexist (Davies et al. 2021).

5 Conclusion

We conclude that light-demanding canopy species are no indicators of past human disturbance in the Yangambi rainforest because they do not meet the four conditions tested in this study. Although light demanders seem to be aggregated, the pockets were small, scarce and represent a minor fraction of the total forest area. Furthermore, light-demanding species were not abundant, even not in the pockets where they were aggregated. Their age distributions do not show a regeneration deficit and their unimodal diameter distribution can be explained by fast juvenile growth. Finally, the forests with pockets of light-demanders were not different from forests where they were scarce or absent, confirming that light-demanding species in Yangambi are not a transient feature of successional forests but an intrinsic component of old-growth forests determined by natural gap dynamics. These insights support recently published claims that the large carbon sink observed in Yangambi (Hubau et al. 2020) is not driven by secondary successional forest dynamics but rather by a CO₂ fertilisation effect. Furthermore, we strongly suggest to avoid large-impact forest management decisions based on interpretations of size distributions of a small group of commercial timber species. We recommend that past and future dynamics of tropical forests should be deduced considering all trees in the forest and not from a small group of alleged indicator species.

Appendix

Table 1 Focal species inventory data statistics of the 250ha covered by the Moni transects (Luambua et al. 2021)

Taxa	Stems inventoried	Tree density (stems ha ⁻¹)	DBH min	DBH mean	DBH max	DBH Sd
Short-lived pioneers (SLPs)	834	3.328				
<i>Macaranga monandra</i>	347	1.385	10.0	20.0	74.6	11.3
<i>Macaranga spinosa</i>	36	0.144	10.0	14.7	30.3	4.1
<i>Macaranga zenkeri</i>	9	0.036	10.6	15.2	20.1	4.1
<i>Musanga cecropioides</i>	442	1.764	10.0	30.9	78.7	13.9
Long-lived pioneers (LLPs)	800	3.192				
<i>Albizia adianthifolia</i>	45	0.180	12.4	35.4	86.9	18.4
<i>Albizia ferruginea</i>	12	0.048	22.8	63.7	87.6	18.6
<i>Albizia gum-mifera</i>	25	0.100	10.1	36.4	106.2	21.1
<i>Albizia laurentii</i>	1	0.004	13.9	13.9	13.9	-
<i>Alstonia boonei</i>	78	0.311	23.4	64.1	86.4	12.6
<i>Canarium schweinfurthii</i>	39	0.156	10.3	67.9	137.8	43.9
<i>Ceiba pentandra</i>	1	0.004	18.8	18.8	18.8	-
<i>Erythrophloeum suaveolens</i>	295	1.177	10.3	55.9	125.0	27.2
<i>Milicia excelsa</i>	5	0.020	31.5	64.7	97.6	28.9
<i>Nauclea diderrichii</i>	23	0.092	14.4	64.7	105.7	32.4
<i>Pericopsis elata</i>	162	0.646	12.0	66.0	133.9	28.5
<i>Piptadeniastrum africanum</i>	82	0.327	10.1	45.5	146.1	31.1
<i>Ricinodendron heudelotii</i>	32	0.128	10.0	30.5	86.0	18.3
Non-pioneer lightdemanders (NPLD)	4694	18.729				
<i>Afzelia bella</i>	9	0.036	10.8	22.0	61.0	16.7
<i>Afzelia bipindensis</i>	5	0.020	17.7	28.1	36.0	8.1
<i>Austranella congolensis</i>	24	0.096	10.4	29.0	131.2	31.6
<i>Celtis mildbraedii</i>	350	1.397	10.0	25.9	121.2	21.3
<i>Celtis tessmannii</i>	860	3.431	10.0	26.3	87.6	14.4
<i>Entandrophragma angolense</i>	106	0.423	10.1	34.7	133.4	28.7

Taxa	Stems inventoried	Tree density (stems ha ⁻¹)	DBH min	DBH mean	DBH max	DBH Sd
<i>Entandrophragma candollei</i>	71	0.283	10.0	28.8	166.0	36.4
<i>Entandrophragma cylindricum</i>	46	0.184	11.6	50.1	182.0	48.8
<i>Entandrophragma utile</i>	61	0.243	10.0	25.9	110.0	23.3
<i>Lovoa trichilioides</i>	22	0.088	10.4	28.8	91.3	23.6
<i>Petersianthus macrocarpus</i>	2407	9.604	10.0	27.2	99.1	15.0
<i>Pterocarpus soyauxii</i>	344	1.373	10.0	49.6	120.0	26.7
<i>Pycnanthus angolensis</i>	388	1.548	10.0	16.9	98.7	10.6
<i>Pycnanthus marchalianus</i>	1	0.004	33.7	33.7	33.7	-
Shade tolerant species (ST)	1148	4.581				
<i>Gilbertiodendron dewevrei</i>	1148	4.581	10.0	43.5	144.7	26.2

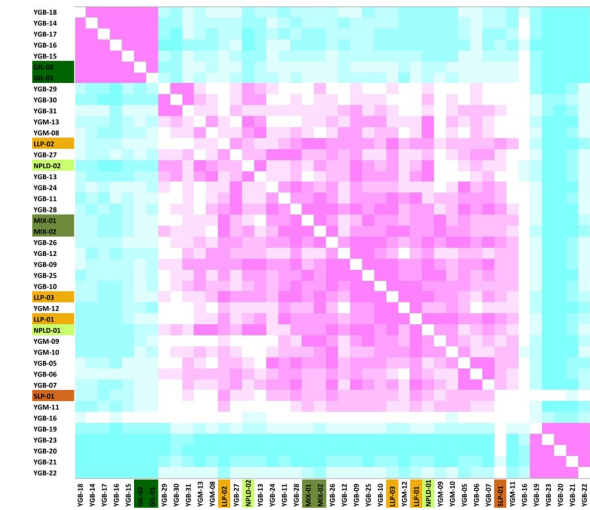


Fig. 9 Ordered Bray–Curtis dissimilarity matrix for the plot-level analysis. The dissimilarity index ranges from 0 (dark blue) to 1 (dark pink). The larger the number, the stronger the similarity. Plot codes from plots in Moni transects are highlighted with colours, as in Fig. 1

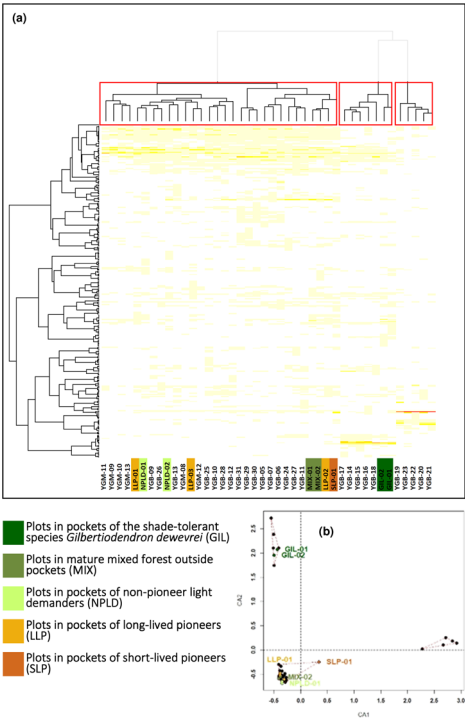


Fig. 10 Plot clustering results based on species-specific % stems. The heatmap (panel **a**) shows the two-way ordered community table indexed using both the plot-level and taxon-level clustering objects of the 43 full inventory plots in the Yangambi inventory dataset. Rows represent species, columns represent plots (all taxa and all sites are present, without duplicates). Cell colours represent % stems of each taxon within each plot, ranging from 0% (white) to 63% (dark red). Cluster dendrograms represent the plot-level clustering (top) and the taxon-level clustering (left). The red boxes indicate the retained groups defined by the Mantel statistic, showing three groups of significantly different plots. Plot codes (bottom of the figure) from plots in Moni transects are highlighted with colours, as in Fig. 1. The panel **b** represents the plot-level ordination diagram resulting from the canonical correspondence analysis, with superimposed convex hulls (red polygons) from the clustering analysis (see red boxes in the cluster dendrogram). Moni River plots are indicated within this ordination diagram with their corresponding colours

Abbreviations

SLP	Short-lived pioneers
LLP	Long-lived pioneers
NPLD	Non-pioneer light demanders
ST	Shade-tolerant
GIL	<i>Gilbertiodendron dewevrei</i>
DBH	Diameter at breast height
PCF	Pair correlation function
KDE	Kernel Density Estimation

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Code availability

The custom R code generated during the current study are available via the link: <https://doi.org/10.5281/zenodo.11636748>.

Authors' contributions

H.B., W.H., C.E., H.N. and N.L. conceived the idea of this study. N.B., A.K., D.M., F.L. and N.L. carried out the fieldwork and collected the data. N.L., H.B., K.V.S., TDM and W.H. analysed the data and drafted the manuscript with the help of C.E., H.N. and O.H. All authors participated in the final draft of the manuscript. All authors read and approved the final manuscript.

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Data availability

Focal species inventory data of the Moni transects that support the findings of this study are available on Dryad: <https://doi.org/10.5061/dryad.qv9s4mwdf>. The dataset of permanent inventory plots is also available on Dryad via the link: <https://doi.org/10.5061/dryad.nk98sf81m>.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no conflict of interest.

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