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Author for correspondence:
Jonas Depecker,
Email: jonas.depecker@kuleuven.be

The association between rainforest disturbance and recovery, tree community composition, and community traits in the Yangambi area in the Democratic Republic of the Congo

Jonas Depecker[1,2,7], Justin A. Asimonyio[3], Ronald Miteho[6], Yves Hatangi[2,6], Jean-Léon Kambale[3], Lauren Verleysen[1,4], Piet Stoffelen[2], Steven B. Janssens[2,5,7], Benoit Dhed'a[6], Filip Vandelook[2,7] and Olivier Honnay[1,7]

[1]Division of Ecology, Evolution, and Biodiversity Conservation, KU Leuven, Leuven, Belgium; [2]Meise Botanic Garden, Nieuwelaan 38, 1860 Meise, Belgium; [3]Centre de Surveillance de la Biodiversité et Université de Kisangani, Kisangani, DR Congo; [4]Plant Sciences Unit, Flanders Research Institute for Agriculture, Fisheries and Food, Carittasstraat 39, 9090 Melle, Belgium; [5]Division of Molecular Biotechnology of Plants and Micro-organisms, KU Leuven, Leuven, Belgium; [6]Université de Kisangani, Kisangani, DR Congo and [7]KU Leuven Plant Institute, Leuven, Belgium

Abstract

Despite their key role in biodiversity conservation, forests in the Congo Basin are increasingly threatened by human activities, but it remains challenging to assess the impact of forest degradation under a more or less intact canopy. Likewise, forest recovery following agricultural abandonment remains poorly understood in the Congo Basin. Here, we surveyed 125 vegetation quadrats across 25 forest inventory plots in the Yangambi area. We aimed to find associations between both selective logging and forest recovery, and a range of forest community and tree community trait characteristics, as compared to reference undisturbed old-growth forest. We found that plots in undisturbed old-growth forest harboured both more tree individuals and tree species with a higher wood density as compared to plots in disturbed old-growth forest. In addition, their tree community composition was significantly different, whereas species diversity recovered since relatively recent agricultural abandonment (< 60 years), community composition and forest structure remained significantly different from the plots in undisturbed old-growth forest. Our study provides some insights into the rate of forest recovery in the Congo basin after agricultural abandonment and highlights the need of proper conservation of the remaining relatively undisturbed old-growth forests. Finally, we stress the need for more extensive vegetation surveys in the Congo Basin to further unravel the effects of anthropogenic disturbance.

Introduction

The African continent is home to the world's second largest area of tropical forests which are, together with earth's subtropical forests, by far the most floral-rich biomes on earth (Kier *et al.* 2005, Malhi *et al.* 2013). The African tropical forests appear to be less biodiverse than their Asian and American counterparts (Kier *et al.* 2005, Parmentier *et al.* 2007, Slik *et al.* 2015). Nevertheless, Sosef *et al.* (2017) recorded 22,577 plant species in tropical African forests, of which 30% are endemic, and concluded that much botanical exploration still remains to be done. The forests of the Congo Basin, which account for 89% of the African tropical forests, are also extremely important as carbon sinks, removing up to six times more carbon than the forests in the Amazon region (Harris *et al.* 2021, Malhi *et al.* 2013). Furthermore, the African carbon sink has been stable for the past three decades until 2015, while the Amazonian carbon sink has been declining since the 1990s (Hubau *et al.* 2020).

Despite their key role in biodiversity conservation and carbon sequestration, forests in tropical Africa are increasingly threatened by human activities (Tyukavina *et al.* 2018). Between 1990 and 2000, the annual net loss of forests in Africa corresponded to 3.3 million ha yr^{-1}, increasing to 3.4 million ha yr^{-1} between 2000 and 2010, and further to 3.9 million ha yr^{-1} between 2010 and 2020 (FAO & UNEP 2020). Africa is currently the only region where annual forest change rates are still increasing (FAO & UNEP 2020). The deforestation on the African continent is mainly caused by small-scale subsistence agriculture (Curtis *et al.* 2018, Jayathilake *et al.* 2021, Tegegne *et al.* 2016, Tyukavina *et al.* 2018), driven by very low agricultural yields (Carrasco *et al.* 2017, West *et al.* 2010), and a rapidly growing human population (Gerland *et al.* 2014).

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Although deforestation is a very conspicuous and severe threat to biodiversity, degradation of tropical forests may even be more detrimental, based on the large spatial scales at which it occurs (Barlow *et al.* 2016). Forest degradation refers to within-forest disturbance and mainly includes selective logging, removal of understorey vegetation, and overexploitation of specific species (Sasaki & Putz 2009, Chaturvedi *et al.* 2012, Tyukavina *et al.* 2018). In tropical Africa, forest degradation is primarily driven by selective logging, mainly for the small-scale production of charcoal which is still the most commonly used energy source in many Central African countries (Hosonuma *et al.* 2012, Jayathilake *et al.* 2021, Tyukavina *et al.* 2018). The degradation rate of forests in the Congo Basin has been estimated to be 317,000 ha yr^{-1} between 2000 and 2005 (Ernst *et al.* 2013). Lambin *et al.* (2003) estimated that the annual rate of human-mediated forest degradation in Africa corresponds to approximately 50% of its annual rate of deforestation. This would imply that 1.95 million ha of African forest has been degraded between 2010 and 2020. However, Shapiro *et al.* (2021) recently reported that this assumption may drastically underestimate the actual rate. Using a forest condition index, they estimated that between 2000 and 2016, over 23 million ha of forest has been degraded in the Congo Basin alone.

Although remote-sensing techniques are constantly improving, it remains challenging to monitor the extent and impact of forest degradation due to the interference with the often untouched canopy in degraded forests (Matricardi *et al.* 2020, Peres *et al.* 2006). Evaluation of the extent and impact of forest degradation must therefore largely rely on vegetation surveys on the ground (Heym *et al.* 2021). Impacts of forest degradation on biodiversity have been frequently studied in the Neotropics (e.g. Carreño-Rocabado *et al.* 2012, Mirabel *et al.* 2020), Asia (e.g. Baboo *et al.* 2017, Millet *et al.* 2010), and other parts of Africa (e.g. Bobo *et al.* 2006, Oyugi *et al.* 2008), but similar studies are rare in the Congo Basin (but see Hall *et al.* 2003, Ifo *et al.* 2016), and almost lacking in the Democratic Republic of Congo (DR Congo) (but see Makana & Thomas 2006). Yet, as DR Congo harbours almost 60% of the African tropical forests (Malhi *et al.* 2013), it is essential to comprehend how plant community composition is affected by forest disturbance.

While conservation of existing tropical forests should still be the priority, the restoration of deforested land and degraded forests can aid in the recovery of tropical biodiversity and the recovery of ecosystem services (Brudvig 2011, FAO & UNEP 2020). Between 2000 and 2019, 0.7 million ha of forest has been actively or passively restored in Sub-Saharan Africa (FAO & UNEP 2020). By 2030, the African Forest Landscape Restoration Initiative (AFR100) aims to increase the land surface under restoration to 100 million ha. DR Congo has committed to restore 8 million ha (AFR100 2021). Because of the high variability in restoration outcomes, more research is crucial to clear the path for restoration (Chazdon 2008). Again, studies on the biodiversity consequences of tropical forest recovery are more commonly found in the Neotropics (e.g. Letcher & Chazdon 2009, Oberleitner *et al.* 2021) and tropical Asia (e.g. Hayward *et al.* 2021, Mahayani *et al.* 2020), but are rare in the Congo Basin (but see Bauters *et al.* 2019, Makelele *et al.* 2021).

In this study, we established a set of forest inventory plots in the Yangambi region in DR Congo and aimed to find associations between both anthropogenic disturbance through selective logging and forest recovery on the one side, and a range of forest and tree community characteristics on the other side, as compared to reference undisturbed old-growth forest. Based on 125 sampling quadrats across 25 forest inventory plots, we specifically quantified differences among (i) disturbed old-growth forest, (ii) regrowth forest, and (iii) undisturbed old-growth forest in terms of tree species diversity, community traits, community composition, forest structure, and canopy cover. We hypothesise that (i) selective logging results in the decreasing abundance of some specific tree species and in shifts in community composition, without having a profound effect on the overall tree species diversity, (ii) that selective logging results in a lower community-weighted mean wood density and in lower crown closure, and (iii) that forest recovery following agricultural abandonment will be fast for secondary tree species, with low wood density, but slower for primary forest tree species, with higher wood density, implying that the overall tree species diversity will have recovered, but that the community composition will be different from undisturbed old-growth forest.

Methods

Study site and set up

Vegetation sampling was conducted in the Yangambi region, in the Tshopo province in North-Eastern DR Congo, approximately 100 km west of Kisangani between November 2020 and January 2021. In Yangambi, the climate is characterised by two drier seasons (December–March & June–July) and two rainy seasons (April–May & August–November) (van Vliet *et al.* 2018). The general landscape type in this area is typical for the Congo Basin and is characterised by a mosaic of land tenures: the Yangambi Man and Biosphere Reserve created in 1979; the Ngazi Forest Reserve; a logging concession; and customary land. To date, there is no official management plan (van Vliet *et al.* 2018). Prior to the Congolese independence in 1960, Yangambi housed a research station of INEAC (Institut National pour l'Etude Agronomique du Congo Belge), with multiple pastures for research and breeding activities. However, in 1962 the INEAC changed into INERA (Institut National des Etudes et Recherches Agronomiques) in 1962. Since then, the research activities at Yangambi started to diminish (Vanden Abeele *et al.* 2021), and as a result, many agricultural fields were abandoned, allowing forest to recover on these lands.

We established 25 forest inventory plots of 125 m × 125 m (1.56 ha), covering an area of ca. 50 by 20 km, just North of the Congo River (Figure 1). Plots were assigned to three different forest categories by georeferencing (WGS84) them onto historical land-use maps, which were issued by Evrard (1954). Plots located on historical agricultural land from INERA were classified as regrowth forest (R). Although we could not exactly date the start of the forest recovery, our best estimate based on local sources is that the agricultural land was abandoned somewhere between 40 and 60 years ago. Plots located in historically old-growth forest areas but where we observed indications of considerable small-scale selective logging through the presence of tree stumps and other remnants of logging such as parts of trees or active logging were considered as disturbed old-growth forest (DO). These areas were typically located near regrowth forest and close to places with relatively higher population density. The remaining plots that were located in areas with historical old-growth forests, and where no signs of selective logging were present, were categorised as undisturbed old-growth forest (UO). The current UO and DO forests have previously been classified by Evrard (1954) as heterogenous forests with primitive character. These old vegetation maps have been shown to be very reliable (Vancutsem *et al.* 2009), and we may therefore assume there were no pre-existing differences between both forest categories.

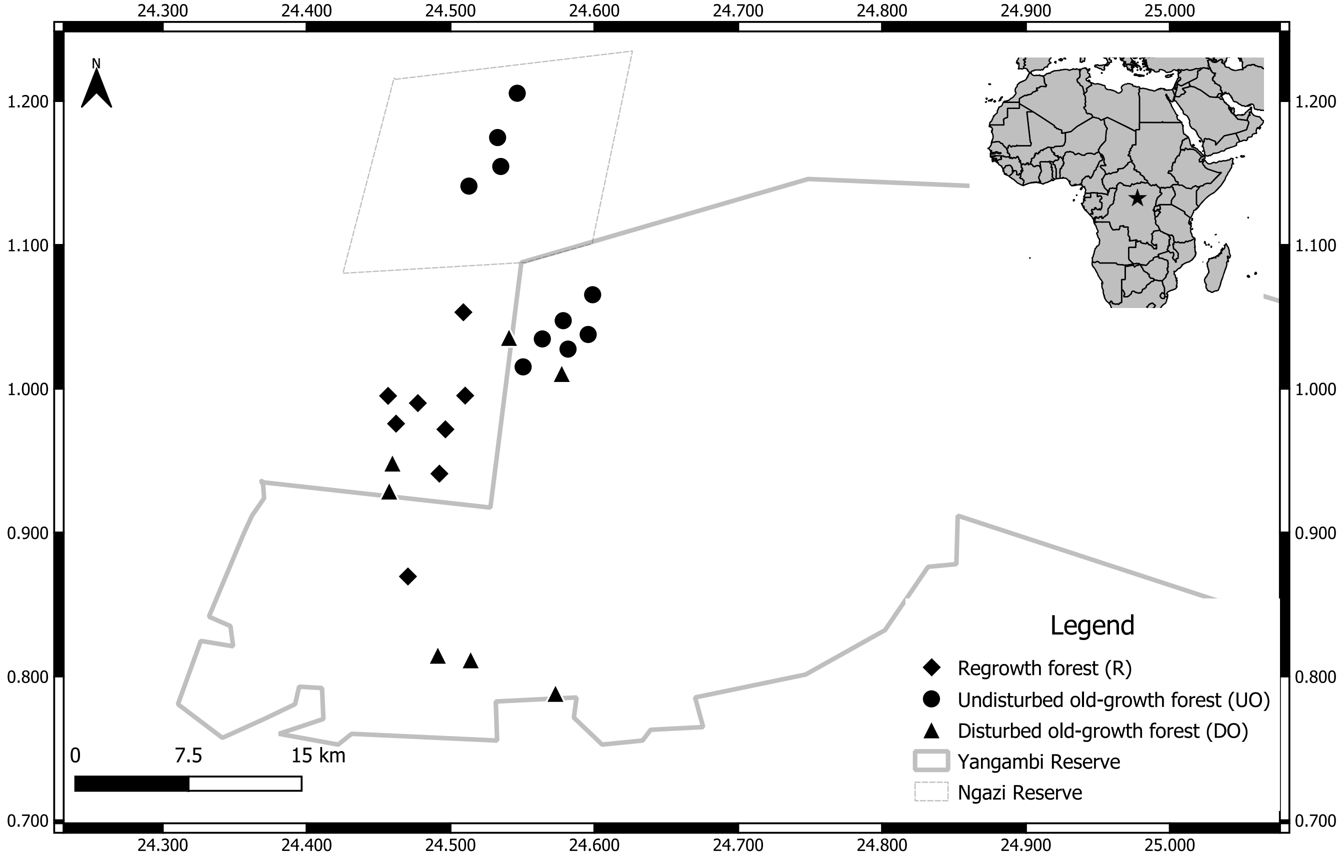

Figure 1. Location of the 25 forest inventory plots across the three forest categories in the Yangambi region (DR Congo).

Vegetation survey and plant trait quantification

Five quadrats (25 m × 25 m) were randomly established in each forest inventory plot, resulting in a total of 125 sampling quadrats. In each quadrat, the abundance and diameter at breast height (DBH) of all woody species with a DBH ≥ 5 cm were measured. The quadrats were geolocated (Garmin GPSMAP 64 series), and crown closure (%) was quantified from four readings in the cardinal directions with a model A convex spherical densiometer.

The specific leaf area (SLA) of all taxa identified at species level was assessed based on dry herbarium specimens from the Meise Botanic Garden herbarium following Pérez-Harguindeguy *et al.* (2013). Perez *et al.* (2020) provided evidence that the SLA can reliably be estimated from herbarium-based measurements. Leaf area was assessed using leaf disks (4.9 cm^2), to minimise damage to herbarium specimens, or otherwise by a whole leaf scan using ImageJ (Rueden *et al.* 2017). The obtained disks and whole leaves were weighted afterwards. Five replicates were used per species. In addition to the SLA, the wood density (WD) of 141 species was compiled from the literature (Table S1) (RMCA 2021, Carsan *et al.* 2012, Harja *et al.* 2021).

Data analyses

Statistical analyses were performed using R software (R Core Team 2020). The data of the five quadrats were summed into one value per plot. For each plot, the number of trees, species richness (Hill's N_0), species diversity (Hill's N_1 or the exponential of the Shannon entropy), and evenness (Hill's N_1/log(Hill's N_0)) were then calculated. These numbers were then standardised for sample completeness, as sample sizes differed between plots. Sample completeness represents the proportion of the total number of individuals in a unit that belongs to the species in the sample, contrary to sample size standardisation which allows less biased comparisons (Chao & Jost 2012). Extrapolation of the estimates was done to twice the reference sample size per plot, following Chao & Jost (2012). Calculations were based on the collected species abundance data with 9999 bootstraps using the *iNEXT* function of the iNEXT package (Hsieh *et al.* 2016). Subsequently, the different variables and the crown closure were tested for differences between the three forest categories using Kruskal-Wallis rank sum tests and pairwise Wilcoxon rank sum tests with correction for multiple testing, as the assumptions for parametric testing were not met.

Dissimilarity of the tree community composition across the forest categories was visualised using a non-metric multidimensional scaling (NMDS), based on the Bray-Curtis distance matrix, the most suitable distance for abundance data (Ricotta *et al.* 2017). A two-axis solution provided a stress level (0.13) well below the 0.20 threshold, indicating a good representation in reduced dimensions. The ordination was performed with the *metaMDS* function in the vegan package (Oksanen *et al.* 2020). Subsequently, a Mantel test with 9999 permutations was performed to test the effect of geographic distance on the dissimilarity of the tree community composition using the *mantel* function in the Vegan package (Oksanen *et al.* 2020). In addition to the NMDS, a permutational multivariate analysis of variance with 9999 permutations was performed to test for differences in community composition between the three different forest categories using the *adonis* function in the Vegan package (Oksanen *et al.* 2020). Pairwise comparisons of the different forest groups with 9999 permutations and Bonferroni correction were performed with the *pairwise.adonis.function* in the pairwiseAdonis package (Arbizu 2017). Tree species indicative for each of the three forest categories were identified based on their indicator value (Dufrene & Legendre 1997). This value was calculated using the *multipatt* function in the indicspecies package (De Cáceres & Legendre 2009), with 9999 permutations.

Community-weighted means (CWM) for each plot were calculated for the SLA and the WD, using the number of individuals as weight. The community-weighted means are known to be very responsive to environmental change and highly sensitive to disturbance (Carreño-Rocabado *et al.* 2012). Both variables met the assumptions for parametric testing, and to evaluate differences in community-weighted mean SLA and WD among forest categories, a one-way analysis of variance (ANOVA) was conducted followed by pairwise Tukey post hoc tests.

Forest structure was evaluated using the measured DBHs. Trees were categorised in ten size classes according to their DBH. An interval of 10 cm was used in the first nine classes, starting from 5 cm DBH. The tenth class had a wider interval, aggregating individuals with a DBH over 95 cm. Subsequently, the diameter frequency distribution was compared among the three forest categories with Pearson's chi-squared tests with simulated p-values based on 9999 replicates using the *chisq.test* function in the stats package (R Core Team 2020). The chi-square test was preferred over the frequently used Kolmogorov-Smirnov test, because the former is more flexible than the latter (Mitchell 1971). The diameter frequency distribution comparison was complemented by the calculation of the structural diversity, which is a single measure summarising the diameter distribution (McElhinny *et al.* 2005). Structural diversity was quantified by the first order Hill number which was standardised for sample completeness following the same methodology as outlined above. Calculation and extrapolation of structural diversity was done with the *iNEXT* function with 9999 bootstraps in the iNEXT package, as above. All figures were made using the ggplot2 package (Wickham 2016).

Results

Species richness and diversity

A total of 7375 woody plant individuals (DBH $\geq$ 5 cm) from 211 taxa were recorded across the 25 forest inventory plots. Among the 211 species, 79.15% were identified at species level, 14.22% at genus level, and 6.63% were unidentified species. Crown closure ($\chi^2 = 2.21$, $P > 0.05$) and hill's N_0 ($\chi^2 = 1.98$, $P > 0.05$) were not significantly different among the three forest categories, whereas the tree abundance ($\chi^2 = 10.90$, $P < 0.01$), Hill's N_1 ($\chi^2 = 9.78$, $P < 0.01$) and evenness ($\chi^2 = 10.06$, $P < 0.01$) did differ between the forest categories (Figure 2). Tree abundance was 17.2% lower ($P < 0.05$) in DO forests and 24.3% ($P < 0.05$) lower in R forests, when compared to UO forests. Species diversity and evenness were 33.6% ($P < 0.001$) and 31.9% ($P < 0.001$) higher, respectively, in DO forests as compared to UO forests (Table S2).

Community composition

The NMDS of the 25 forest inventory plots showed a spatial separation of the three forest categories (Figure 3). This was supported by the permutational multivariate analysis of variance which indicated differences between categories ($R^2 = 0.253$; $P < 0.001$). Specifically, community composition significantly differed between DO forests and UO forests ($R^2 = 0.207$; $P < 0.001$), and between R forests and UO forests ($R^2 = 0.267$; $P < 0.001$). The Mantel test between the geographic distance matrix and the Bray-Curtis distance matrix showed a significant but weak correlation ($r = 0.200$; $P < 0.05$). Across the 25 forest inventory plots, 27 out of the 167 at species level identified trees were indicative based on their indicator value (both $P < 0.05$ and indicator value > 0.20). Seventeen indicator species were indicative for UO forest (e.g. *Cola griseiflora*), four for DO forest (e.g. *Leplaea cedrata*), and six for R forest (e.g. *Heisteria parvifolia*) (Table S3).

Specific leaf area and wood density

The community-weighted means for SLA did not differ between forest categories ($F = 1.38$, $P > 0.05$); however, the community-weighted mean WD exhibited a significant difference ($F = 9.03$, $P < 0.01$) (Figure 4). In DO forests, community-weighted mean WD was 5.0 % lower ($P < 0.05$), whereas in R forests it was 6.2 % lower ($P < 0.01$) as compared to UO forests.

Forest structure

The diameter distribution showed that there were more small-sized trees in UO forests than in DO forests ($\chi^2 = 34.51$; $P < 0.001$) and in R forests ($\chi^2 = 61.54$; $P < 0.001$) (Figure 5). These differences between categories were also present for the structural diversity, represented by Hill's N_1, ($\chi^2 = 13.76$; $P < 0.01$), where UO forests differed from DO forests ($P < 0.01$), and from R forests ($P < 0.01$).

Discussion

Understanding how anthropogenic disturbance affects forest structure, tree species richness, and community composition is of major importance for biodiversity conservation in globally underexplored biodiversity hotspots such as the Congo Basin. The goal of our study was to find associations between both anthropogenic disturbance through selective logging and forest recovery on the one side, and a range of forest community and tree community trait characteristics on the other side, as compared to reference undisturbed old-growth forest. Although our three delineated forest categories certainly enveloped some within-variation in terms of time since abandonment (for the regrowth forest plots) and in terms of degree of disturbance (for the disturbed old-growth forest plots), we were able to identify differences in community composition, forest structure, and community traits among forest categories.

Selective logging

As hypothesised, our survey showed that there were clear differences in community composition and forest structure between plots in undisturbed old-growth forest and plots in disturbed old-growth forest. There were no differences in the number of woody species between any forest category; yet contrary to our expectation, species diversity was higher in plots in disturbed old-growth forest. This higher species diversity likely indicates that the species abundance distribution is less skewed in disturbed forests. Indeed, the evenness index showed that the species abundance is more evenly distributed in plots in disturbed forest than in plots in undisturbed old-growth forest. Combined with the observation that plots in disturbed old-growth forests contained significantly less tree individuals, these findings are in line with our hypothesis and might suggest that selective logging, in which exploitable

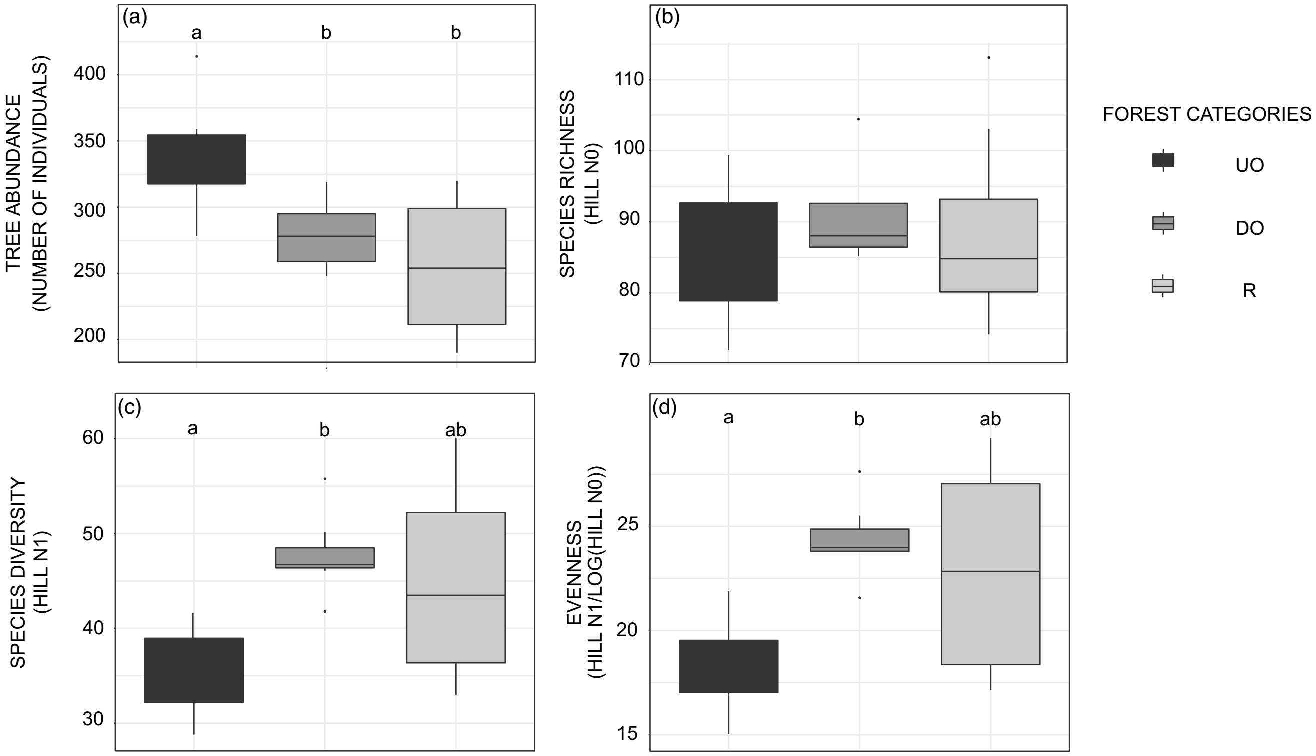

Figure 2. Comparisons between tree abundance and tree species diversity metrics across old-growth undisturbed forest (OU), old-growth disturbed forest (OD), and regrowth forest (R) in the Yangambi region (DR Congo). Hinges represent the 25th, 50th, and 75th percentiles, respectively. Whiskers extend to maximum 1.5 times the interquartile range. Letters code for significant differences between groups. (a) Tree abundance, (b) species richness, (c) species diversity, (d) evenness.

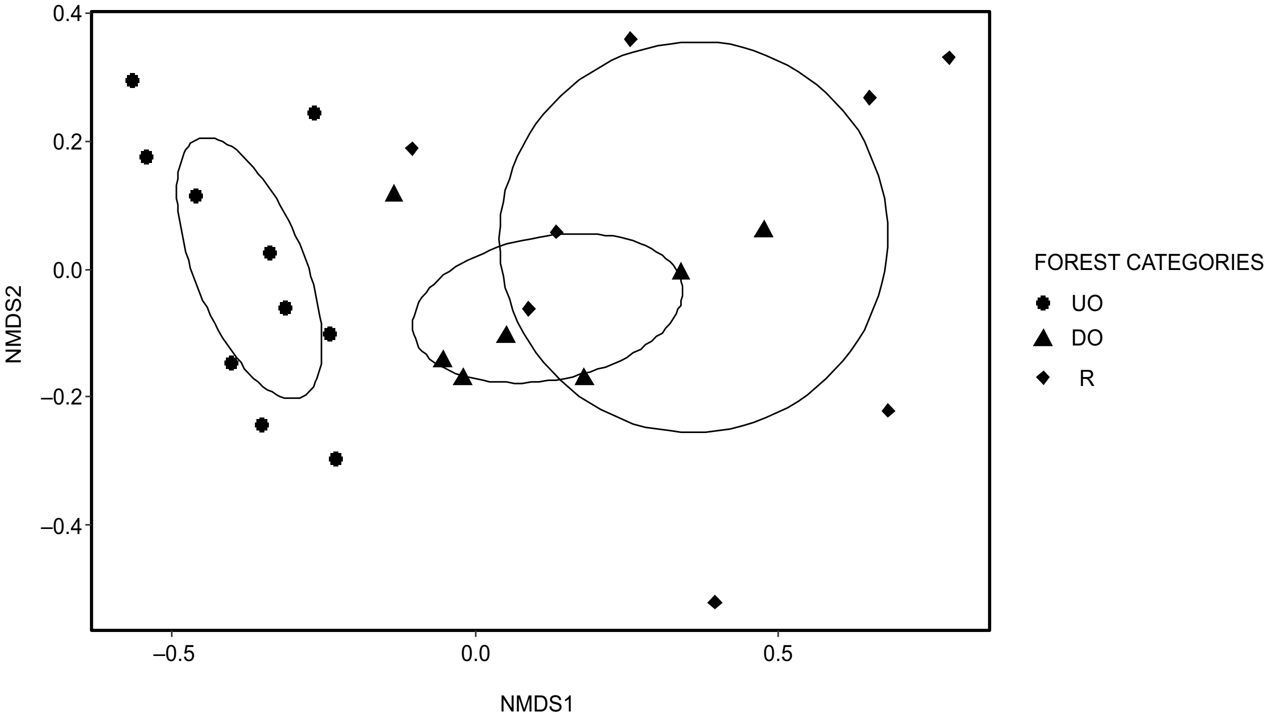

Figure 3. Non-metric multidimensional scaling (NMDS) ordination of 25 forest inventory plots in the Yangambi region (DR Congo) across the three forest categories: undisturbed old-growth forest (UO), disturbed old-growth forest (DO), and regrowth forest (R). Ordination is based on the Bray-Curtis distance matrix calculated from the tree species abundances and represents the woody species (DBH ≥ 5 cm) community composition.

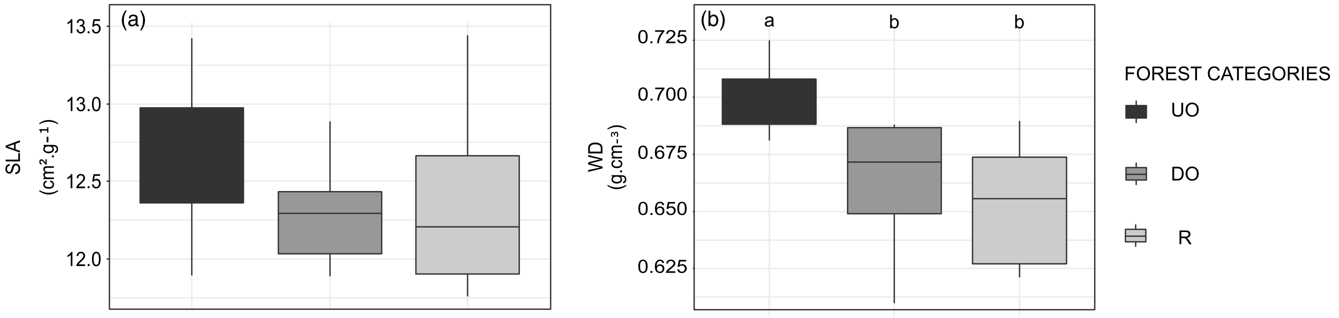

Figure 4. Comparisons between the community-weighted means of specific leaf area (SLA) and wood density (WD) across the three forest categories. Hinges represent the 25th, 50th, and 75th percentiles, respectively. Whiskers extend to maximum 1.5 times the interquartile range. Letters code for significant differences between groups.

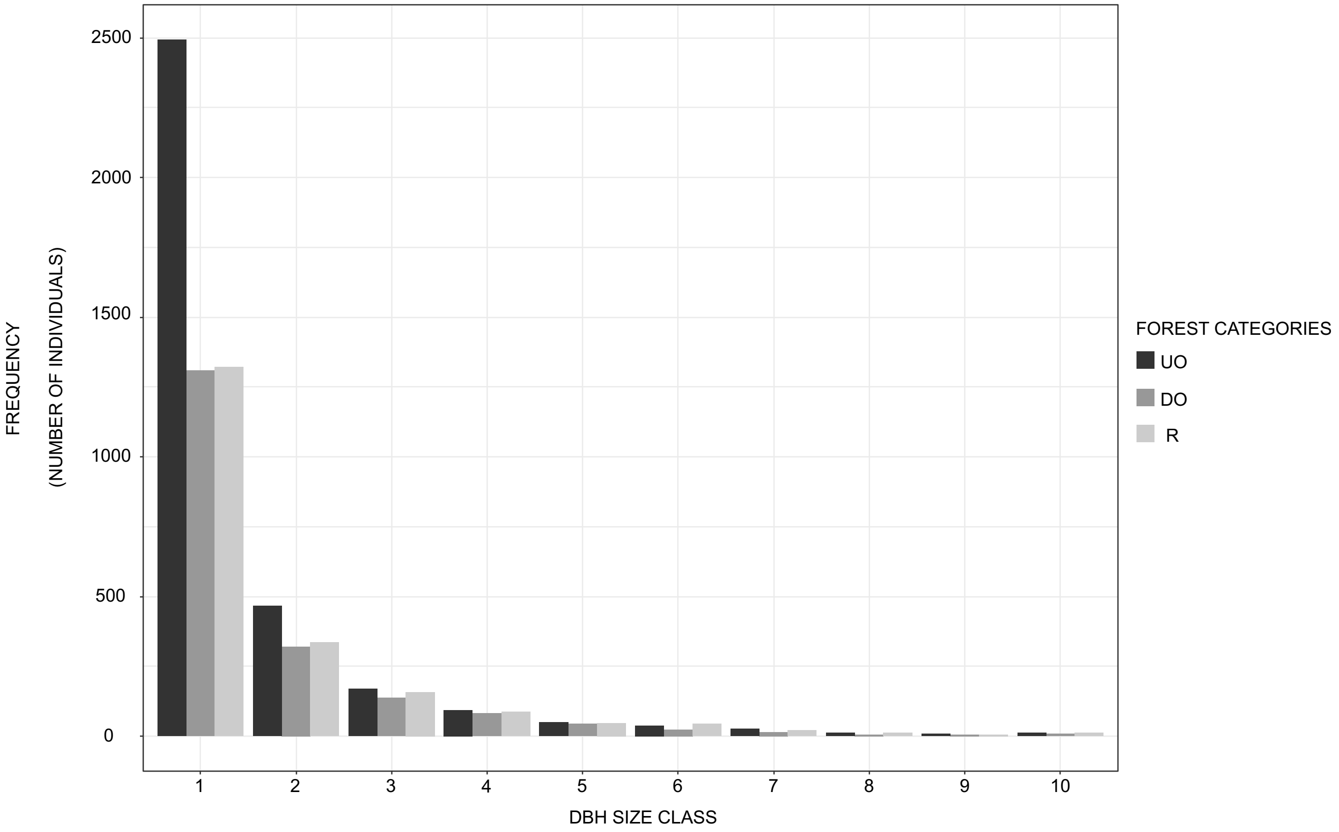

Figure 5. Observed frequencies among the ten DBH size categories compared among the three forest categories. Size classes one to nine have a 10 cm interval, while the tenth has a wider interval, grouping individuals with a DBH of over 95 cm.

species are selectively removed, is closely associated with these patterns. In the Yangambi area, timber is removed by local villagers using, for example, machetes, mainly for construction material and cooking purposes (Depecker pers. obs.). The stems that are removed are usually from species from which the wood is exploitable. We expect that selective logging at first only results in a shift in densities, but that it will ultimately result in the loss of certain species as selective loggers will specifically target species with stems that are exploitable. For example, *Prioria oxyphylla* and *Scorodophloeus zenkeri* were much less abundant in disturbed forests and are used as construction material. Moreover, in DR Congo the latter species is also exploited for its medicinal properties and is used to make charcoal (PROTA 2021). Other species that were highly reduced in numbers were *Dialium pachyphyllum, Greenwayodendron suaveolens*, and *Strombosia pustulata*, which all bear seeds that are dispersed by animals (PROTA 2021, Meunier *et al.* 2015). Animal-dispersed seeded tree species tend to have higher wood densities than abiotic-dispersed seeded tree species (Osuri *et al.* 2016), possibly indicating that loggers specifically target species with high WD, suggesting that species with animal-dispersed seeds are more vulnerable to selective logging. Careful monitoring of tree species is needed to unravel the specific effects of selective logging at the species level.

Plots in disturbed old-growth forest on the other hand still contained many shade-tolerant tree species of which the wood is non-exploitable, such as species of the genus *Cola* which have a low DBH and highly irregular trunks. *Cola acuminata also* produces highly valued nuts with stimulating and medicinal properties

(Meunier *et al.* 2015). Likewise, the abundance of most *Diospyros* spp. is indicative for old-growth forests, of which only *Diospyros crassiflora* is exploited for its wood (Meunier *et al.* 2015).

Although a clear difference was found in community composition between forest categories in our study, the response in terms of species diversity and species richness was more variable. An earlier study on selective logging in the Congo Basin compared disturbed and undisturbed forests in terms of species diversity in two distinct locations (Makana & Thomas 2006). Although a significant influence of disturbance was detected in the first location, similar values for species richness and species diversity were detected in the second location. Furthermore, a clear effect of disturbance, primarily selective logging, on species diversity was detected in tropical forests in the Republic of the Congo (Ifo *et al.* 2016) and India (Baboo *et al.* 2017), but not in a tropical forest in Bolivia (Carreño-Rocabado *et al.* 2012). It is clear that solely assessing the possible impact of anthropogenic disturbance through species diversity can mask its impact and that community composition is a better indicator of the possible impacts of forest degradation (Edwards *et al.* 2014, Imai *et al.* 2014). Indeed, although several studies across different tropical regions have reported varying responses of species diversity to forest disturbance, they all reported significant shifts in the community composition following anthropogenic disturbance (Makana & Thomas 2006, Baboo *et al.* 2017, Carreño-Rocabado *et al.* 2012, Ifo *et al.* 2016)

Because ecosystem functioning is mainly mediated by species' functional traits (Chaturvedi *et al.* 2021, de Bello *et al.* 2021), community-weighted mean functional traits can provide better ecologically information than only using taxonomic data (Katovai *et al.* 2012). We hypothesised that we would find lower community-weighted mean wood density and a lower canopy closure in plots in disturbed old-growth forest, as compared to plots in undisturbed old-growth forest. In terms of canopy closure, we did not find differences between any forest category. Consequently, the light availability in the plots remained unchanged, which presumably clarifies why we observed no significant differences in community-weighted mean specific leaf area between forest categories. It has indeed been established by Carreño-Rocabado *et al.* (2012) that increased light availability can induce changes in community-weighted mean functional traits in tropical forests. Furthermore, although disturbed and undisturbed old-growth forests were characterised by different indicator species assemblages, the majority can still be classified as shade-tolerant, which is commonly associated with low SLA (Poorter 2009). Nonetheless, the absence of differences between forest categories should be interpreted cautiously as SLA is highly responsive to environmental variation, such as sun exposure. In contrast to community-weighted mean SLA, community-weighted mean WD did significantly differ between plots in disturbed and plots in undisturbed old-growth forest. As anticipated, a decrease in community-weighted mean WD was observed in plots in disturbed old-growth forest, which indicates that trees with high WD and of high qualities as construction material have been selectively removed (Saranpää 2003).

The mean diameter distribution in the forests in the Yangambi region has previously been described by the reverse J-shaped model (Fayolle *et al.* 2014). In our study, the reverse J-shape was more pronounced in plots in undisturbed old-growth forests than in plots in disturbed old-growth forests which contained significantly less trees in the first size class, suggesting less regeneration (Gebeyehu *et al.* 2019). Similar results of reduced regeneration in forests were obtained in other tropical forests and were assigned to disturbance (Makana & Thomas 2006, Baboo *et al.* 2017, Hall *et al.* 2003).

Forest recovery following agricultural abandonment

Based on the historical land-use maps, our results indicated that after 40 to 60 years there were no significant differences between plots in regrowth forests and plots in undisturbed old-growth forest in terms of species diversity, which was hypothesised. They only differed in terms of the number of tree individuals and community-weighted mean WD. These findings are in line with other studies in the Congo Basin (Bauters *et al.* 2019, Makelele *et al.* 2021) and in other tropical regions (Letcher & Chazdon 2009, Mahayani *et al.* 2020). In contrast to species diversity, we found that the community composition in plots in regrowth forest was significantly different from those in undisturbed old-growth forest. These findings are in line with what was expected and might suggest that community composition needs more time to converge in similarity to plots in undisturbed old-growth forest. Similar to our results, the community composition of young regrowth forest (25–30 years) differed from old-growth forest in the Maringa-Lopori-Wamba forest landscape in DR Congo, whereas old regrowth forests (150–300 years) were very close to old-growth forests (Bauters *et al.* 2019). Likewise, a recent study in the Yoko forest reserve, at approximately 30 km Southeast of Kisangani, showed that the community composition of 60-year-old regrowth forests was still significantly different from local old-growth forests (Makelele *et al.* 2021). Our results are furthermore in line with studies in the Neotropics (Oberleitner *et al.* 2021, Poorter *et al.* 2021) and tropical Asia (Hayward *et al.* 2021).

Despite having a similar community composition as plots in disturbed old-growth forests, plots in regrowth forests were characterised by a different indicator species assemblage, including *Myrianthus arboreus*, a late pioneer species (PROTA 2021). Additionally, *Combretum lokele* and *Dacryodes edulis* were also characteristic for regrowth forests. Both species are commonly found in villages and are indicative for the important anthropogenic influence in these forests (Meunier *et al.* 2015).

The forest structure in the plots in regrowth forests was comparable to plots in disturbed old-growth forest, but significantly different from plots in undisturbed old-growth forest. These differences were not caused by the lower abundance of large-sized trees in regrowth forests, as would be expected because these are slower to recover (Bauters *et al.* 2019, Makelele *et al.* 2021). On the contrary, the observed differences can be explained by the higher frequency of small-sized trees in plots in undisturbed old-growth forests. This possibly implies that the tree regeneration could be hampered. Similar to other studies (Bauters *et al.* 2019, Makelele *et al.* 2021), we suggest that forests in the Yangambi landscape initially recover rapidly to a close canopy forest with shade-tolerant understorey species following agricultural abandonment, but that the recruitment of primary forest species is slow, and that further forest succession may be hampered by ongoing anthropogenic disturbance in these regrowth forests.

Limitations

We acknowledge that our study is not flawless and that there are some limitations that have to be considered. Our plots are to a certain extent spatially clustered, which was not possible to avoid due to the location of the disturbance zone in the Yangambi area. Furthermore, due to reasons of feasibility, it was not possible to incorporate additional control plots to account for potential spatial variability (Davies & Gray 2015). The Mantel test was used to test the effect of geographic distance on the dissimilarity of the tree community composition. It should be noted that the Mantel test showed a significant correlation between geographic distance and dissimilarity of community composition. This distance decay of similarity is commonly reported in tropical forests (Ganivet *et al.* 2020, Liebsch *et al.* 2008, Wittmann *et al.* 2006). Pre-existing spatial variation seems to confound with the main treatment (logging), but the correlation is rather weak. Although we cannot conclude that the observed differences between sites are a direct effect of selective logging per se, we can interpret the results in light of our ecological understanding of the area and its activities (Oksanen 2004, Davies & Gray 2015).

Conclusion

We found that the tree community composition and forest structure were significantly different between forest categories and that the response of species diversity was more variable. Based on our knowledge of the activities in the Yangambi region, our results suggest that these differences in community composition found between UO forest and DO forest can be attributed to selective logging. Our data furthermore suggest that 40 to 60 years after agricultural abandonment, species diversity is able to recover, but community composition and forest structure are not. Given the limitations of our sampling design, we suggest vegetation surveys across larger geographic areas to deal with the spatial clustering of our survey plots within one disturbance category. Based on the known correlation between forest productivity and SLA, and between carbon storage and WD, our results also indicate that disturbed old-growth forest and regrowth forest are as productive as undisturbed old-growth forest but are not able to store as much carbon (Chave *et al.* 2009, Madani *et al.* 2018). Conservation of undisturbed old-growth forests is vital, although also regrowth of forests can play a crucial role in maintaining biodiversity and providing ecosystem services (Crouzeilles *et al.* 2016, Van de Perre *et al.* 2018).

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Data Availability Statement. The data that support the findings of this study will be made openly available in Zenodo

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Conflict of interest. All authors confirm that there is no conflict of interest regarding the publication of this article.

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

References

AFR100 (2021) AFR100 Partners Manual: Principles, Governance, and Core Processes.

Arbizu PM (2017). pairwiseAdonis: Pairwise Multilevel comparison using Adonis. R package version 0.0.1.

Baboo B, Sagar R, Bargali SS and Verma H (2017) Tree species composition, regeneration and diversity of an Indian dry tropical forest protected area. *Tropical Ecology*, **58**, 409–423.

Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Nally RM, Thomson JR, Ferraz SFDB, Louzada J, Oliveira VHF, Parry L, Ribeiro de Castro Solar R, Vieira ICG, Aragão LEOC, Begotti RA, Braga RF, Cardoso TM, Cosme de Oliveira Junior R, Souza Jr CM, Moura NG, Nunes SS, Siqueira JV, Pardini R, Silveira J, Vaz-de-Mello, FZ, Veiga RCS, Venturieri A and Gardner TA (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**, 144–147.

Bauters M, Vercleyen O, Vanlauwe B, Six J, Bonyoma B, Badjoko H, Hubau W, Hoyt A, Boudin M, Verbeeck H and Boeckx P (2019) Long-term recovery of the functional community assembly and carbon pools in an African tropical forest succession. *Biotropica* **51**, 319–329.

Bobo KS, Waltert M, Sainge NM, Njokagbor J, Fermon H and Mühlenberg M (2006) From forest to farmland: species richness patterns of trees and understorey plants along a gradient of forest conversion in Southwestern Cameroon. *Biodiversity and Conservation* **15**, 4097–4117.

Brudvig LA (2011) The restoration of biodiversity: where has research been and where does it need to go? *American Journal of Botany* **98**, 549–558.

Carrasco LR, Webb EL, Symes WS, Koh LP, and Sodhi NS (2017) Global economic trade-offs between wild nature and tropical agriculture. *PLOS Biology* **15**, e2001657.

Carreño-Rocabado G, Peña-Claros M, Bongers F, Alarcón A, Licona J-C and Poorter L (2012) Effects of disturbance intensity on species and functional diversity in a tropical forest. *Journal of Ecology* **100**, 1453–1463.

Carsan S, Orwa C, Harwood C, Kindt R, Stroebel A, Neufeldt H and Jamnadass R (2012) *African Wood Density Database*. Nairobi: World Agroforesty Centre.

Chao A and Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–2547.

Chaturvedi RK, Raghubanshi AS and Singh JS (2012) Effect of grazing and harvesting on diversity, recruitment and carbon accumulation of juvenile trees in tropical dry forests. *Forest Ecology and Management* **284**, 152–162.

Chaturvedi RK, Tripathi A, Raghubanshi AS and Singh JS (2021) Functional traits indicate a continuum of tree drought strategies across a soil water availability gradient in a tropical dry forest. *Forest Ecology and Management* **482**, 118740.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG and Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* **320**, 1458–1460.

Crouzeilles R, Curran M, Ferreira MS, Lindenmayer DB, Grelle CEV and Rey Benayas JM (2016) A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications* **7**, 11666.

Curtis PG, Slay CM, Harris NL, Tyukavina A and Hansen MC (2018) Classifying drivers of global forest loss. *Science* **361**, 1108–1111.

Davies GM and Gray A (2015) Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution* **5**, 5295–5304.

de Bello F, Lavorel S, Hallett LM, Valencia E, Garnier E, Roscher C, Conti L, Galland T, Goberna M, Májeková M, Montesinos-Navarro A, Pausas JG, Verdú M, E-Vojtkó A, Götzenberger L and Lepš JC (2021) Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends in Ecology & Evolution* **36**, 822–836.

De Cáceres M and Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* **90**, 3566–3574.

Dufrene M and Legendre, P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**, 345–366.

Edwards DP, Tobias JA, Sheil D, Meijaard E and Laurance WF (2014) Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution*, **29**, 511–520.

Ernst C, Philippe M, Astrid V, Catherine B, Musampa C and Pierre D (2013) National forest cover change in Congo Basin: deforestation, reforestation, degradation and regeneration for the years 1990, 2000 and 2005. *Global Change Biology* **19**, 1173–1187.

Evrard C (1954) 6. Yangambi. B. Vegetation. In *Carte des sols et de la vegetation du Congo Belge et du Ruanda-Urundi*. L'institu national pour l'etude agronomiqe du Congo Belge (INEAC).

FAO and **UNEP** (2020) The State of the World's Forests 2020. In *Forests, biodiversity and people*. FAO and UNEP.

Fayolle A, Picard N, Doucet JL, Swaine M, Bayol N, Bénédet F and 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.

Ganivet E, Unggang J, Bodos V, Demies M, Ling CY, Sang J and Bloomberg M (2020) Assessing tree species diversity and structure of mixed dipterocarp forest remnants in a fragmented landscape of north-western Borneo, Sarawak, Malaysia. *Ecological Indicators* **112**, 106117.

Gebeyehu G, Soromessa T, Bekele T and Teketay D (2019) Species composition, stand structure, and regeneration status of tree species in dry Afromontane forests of Awi Zone, northwestern Ethiopia. *Ecosystem Health and Sustainability* **5**, 199–215.

Gerland P, Raftery AE, Ševčíková H, Li N, Gu D, Spoorenberg T, Alkema L, Fosdick BK, Chunn J, Lalic N, Bay G, Buettner T, Heilig GH and Wilmoth J (2014) World population stabilization unlikely this century. *Science* **346**, 234–237.

Hall JS, Harris DJ, Medjibe V and 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.

Harja D, Rahayu S and Pambudi S (2021) *Tree Functional Attributes and Ecological Database*. Nairobi: World Agroforestry Centre.

Harris NL, Gibbs DA, Baccini A, Birdsey RA, de Bruin S, Farina M, Fatoyinbo L, Hansen MC, Herold M, Houghton RA, Potapov PV, Suarez DR, Roman-Cuesta RM, Saatchi SS, Slay CM, Turubanova SA and Tyukavina A (2021) Global maps of twenty-first century forest carbon fluxes. *Nature Climate Change* **11**, 234–240.

Hayward RM, Banin LF, Burslem DFRP, Chapman DS, Philipson CD, Cutler MEJ, Reynolds G, Nilus R and Dent DH (2021) Three decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo. *Forest Ecology and Management* **488**, 119036.

Heym M, Uhl E, Moshammer R, Dieler J, Stimm K and Pretzsch H (2021) Utilising forest inventory data for biodiversity assessment. *Ecological Indicators* **121**, 107196.

Hosonuma N, Herold M, De Sy V, De Fries RS, Brockhaus M, Verchot L, Angelsen A and Romijn E (2012) An assessment of deforestation and forest degradation drivers in developing countries. *Environmental Research Letters* **7**, 044009.

Hsieh TC, Ma K H and Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**, 1451–1456.

Hubau W, Lewis SL, Phillips OL, Affum-Baffoe K, Beeckman H, Cuní-Sanchez A, Daniels AK, Ewango CEN, Fauset S, Mukinzi JM, Sheil D, Sonké B, Sullivan MJP, Sunderland TCH, Taedoumg H, Thomas SC, White LJT, Abernethy KA, Adu-Bredu S, Amani CA, Baker TR, Banin LF, Baya F, Begne SK, Bennett AC, Benedet F, Bitariho R, Bocko YE, Boeckx P, Boundja P, Brienen RJW, Brncic T, Chezeaux E, Chuyong GB, Clark CJ, Collins M, Comiskey JA, Coomes DA, Dargie GC, de Haulleville T, Kamdem MND, Doucet J, Esquivel-Muelbert A, Feldpausch TR, Fofanah A, Foli EG, Gilpin M, Gloor E, Gonmadje C, Gourlet-Fleury S, Hall JS, Hamilton AC, Harris DJ, Hart TB, Hockemba MBN, Hladik A, Ifo SA, Jeffery KJ, Jucker T, Yakusu EK, Kearsley E, Kenfack D, Koch A, Leal MA, Levesley A, Lindsell JA, Lisingo J, Lopez-Gonzalez G, Lovett JC, Makana J, Malhi Y, Marshall AR, Martin J, Martin EH, Mbayu FM, Medjibe VP, Mihindou V, Mitchard ETA, Moore S, Munishi PKT, Bengone NN, Ojo L, Ondo FE, Peh KS, Pickavance GC, Poulsen AD, Poulsen JR, Qie L, Reitsma J, Rovero F, Swaine MD, Talbot J, Taplin J, Taylor DM, Thomas DW, Toirambe B, Mukendi JT, Tuagben D, Umunay PM, van der Heijden GMF, Verbeeck H, Vleminckx J, Willcock S, Wöll H, Woods JT and Zemagho L (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature* **579**, 80–87.

Ifo SA, Moutsambote J-M, Koubouana F, Yoka J, Ndzai SF, Bouetou-Kadilamio LNO, Mampouya H, Jourdain C, Bocko Y, Mantota AB, Mbemba M, Mouanga-Sokath D, Odende R, Mondzali LR, Wenina YEM, Ouissika BC and Joel LJ (2016) Tree species diversity, richness, and similarity in intact and degraded forest in the tropical rainforest of the Congo Basin: case of the forest of Likouala in the Republic of Congo. *International Journal of Forestry Research* **2016**, 1–12.

Imai N, Tanaka A, Samejima H, Sugau JB, Pereira JT, Titin J, Kurniawan Y and Kitayama K (2014) Tree community composition as an indicator in biodiversity monitoring of REDD+. *Forest Ecology and Management* **313**, 169–179.

Jayathilake HM, Prescott GW, Carrasco LR, Rao M and Symes WS (2021) Drivers of deforestation and degradation for 28 tropical conservation landscapes. *Ambio* **50**, 215–228.

Katovai E, Burley AL and Mayfield MM (2012) Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands. *Biological Conservation* **145**, 214–224.

Kier G, Mutke J, Dinerstein E, Ricketts TH, Küper W, Kreft H and Barthlott W (2005) Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* **32**, 1107–1116.

Lambin EF, Geist HJ and Lepers E (2003) Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources* **28**, 205–241.

Letcher SG and Chazdon RL (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in Northeastern Costa Rica. *Biotropica* **41**, 608–617.

Liebsch D, Marques MCM and Goldenberg R (2008) How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biological Conservation* **141**, 1717–1725.

Madani N, Kimball JS, Ballantyne AP, Affleck DLR, van Bodegom PM, Reich PB, Kattge J, Sala A, Nazeri M, Jones MO, Zhao M and Running SW (2018) Future global productivity will be affected by plant trait response to climate. *Scientific Reports* **8**, 2870.

Mahayani NPD, Slik FJW, Savini T, Webb EL and Gale GA (2020) Rapid recovery of phylogenetic diversity, community structure and composition of Bornean tropical forest a decade after logging and post-logging silvicultural interventions. *Forest Ecology and Management* **476**, 118467.

Makana JR and Thomas SC (2006) Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo. *Biodiversity and Conservation* **15**, 1375–1397.

Makelele IA, Verheyen K, Boeckx P, Cizungu Ntaboba L, Mujinya Bazirake B, Ewango C and Bauters M (2021) Afrotropical secondary forests exhibit fast diversity and functional recovery, but slow compositional and carbon recovery after shifting cultivation. *Journal of Vegetation Science* **32**, 1–13.

Malhi Y, Adu-Bredu S, Asare RA, Lewis SL and Mayaux P (2013) African rainforests: past, present and future. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120312.

Matricardi EAT, Skole DL, Costa OB, Pedlowski MA, Samek JH and Miguel EP (2020) Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science*, **369**, 1378–1382.

McElhinny C, Gibbons P, Brack C and Bauhus J (2005) Forest and woodland stand structural complexity: its definition and measurement. *Forest Ecology and Management*, **218**, 1–24.

Meunier Q, Doucet J-L and Moumbogou C (2015) *Arbres Utiles du Gabon*. Liège: Les presses agronomiques de Gembloux.

Millet J, Pascal JP and Kiet LC (2010) Effects of disturbance over 60 years on a lowland forest in southern Vietnam. *Journal of Tropical Forest Science* **22**, 237–246.

Mirabel A, Hérault B and Marcon E (2020) Diverging taxonomic and functional trajectories following disturbance in a Neotropical forest. *Science of the Total Environment* **720**, 137397.

Mitchell B (1971) A comparison of Chi-square Smirnov tests. *Area* **3**, 237–241.

Oberleitner F, Egger C, Oberdorfer S, Dullinger S, Wanek W and Hietz P (2021) Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. *Forest Ecology and Management* **479**, 118580.

Oksanen AJ, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Minchin PR, Hara RBO, Simpson GL, Solymos P, Stevens MHH, Szoecs E and Wagner H (2020) Package 'vegan.'

Oksanen L (2004) The devil lies in details: reply to Stuart Hurlbert. *Oikos* **104**, 598–605.

Osuri AM, Ratnam J, Varnam V, Alvarez-Loayza P, Astaiza JH, Bradford M, Fletcher C, Ndoundou-Hockemba M, Jansen PA, Kenfack D, Marshall AR, Ramesh BR, Rovero F and Sankaran M (2016) Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature Communications* **7**, 11351.

Oyugi JO, Brown JS and Whelan CJ (2008) Effects of human disturbance on composition and structure of Brachystegia woodland in Arabuko-Sokoke Forest, Kenya. *African Journal of Ecology* **46**, 374–383.

Parmentier I, Malhi Y, Senterre B, Whittaker RJ, N ATD , Alonso A, Balinga MPB, Bakayoko A, Bongers F, Chatelain C, Comiskey JA, Cortay R, Kandem MD, Doucet J, Gautier L, Hawthorne WD, Issembe YA, Kouamé FN, Kouka LA, Leal ME, Lejoly J, Lewis SL, Nusbaumer L, Parren MPE, Peh KS, Phillips OL, Sheil D, Sonké B, Sosef MSM, Sunderland TCH, Stropp J, Ter Steege H, Swaine MD, Tchouto MGP, Van Gemerden BS, Van Valkenburg JLCH and Wöll H (2007) The odd man out? Might climate explain the lower tree α-diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology* **95**, 1058–1071.

Peres CA, Barlow J and Laurance WF (2006) Detecting anthropogenic disturbance in tropical forests. *Trends in Ecology & Evolution* **21**, 227–229.

Perez TM, Rodriguez J and Heberling JM (2020) Herbarium-based measurements reliably estimate three functional traits. *American Journal of Botany* **107**, 1–8.

(PROTA) Plant Resources of Tropical Africa (2021) PROTA4U.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S and Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167–234.

Poorter L (2009) Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytologist* **181**, 890–900.

Poorter L, Craven D, Jakovac CC, van der Sande MT, Amissah L, Bongers F, Chazdon RL, Farrior CE, Kambach S, Meave JA, Muñoz R, Norden N, Rüger N, van Breugel M, Zambrano AMA, Amani B, Andrade JS, Brancalion PHS, Broadbent EN, de Foresta H, Dent DH, Derroire G, DeWalt SJ, Dupuy JM, Durán, SM, Fantini AC, Finegan B, Hernández-Jaramillo A, Hernández-Stefanoni JL, Hietz P, Junqueira AB, N'dja JK, Letcher SG, Lohbeck M, López-Camacho R, Martínez-Ramos M, Melo FPL, Mora F, Müller SC, N'Guessan AE, Oberleitner F, Ortiz-Malavassi E, Pérez-García EA, Pinho BX, Piotto D, Powers JS, Rodríguez-Buriticá S, Rozendaal DMA, Ruíz J, Tabarelli M, Teixeira HM, Sampaio EVSB, van der Wal H, Villa PM, Fernandes GW, Santos BA, Aguilar-Cano J, de Almeido-Cortez JS, Alvarez-Davila E, Arreola-Villa F, Balvanera P, Becknell JM, Cabral GAL, Castellanos-Castro C, de Jong BHJ, Nieto JE, Espírito-Santo MM, Fandino MC, García H, García-Villalobos D, Hall JS, Idárraga A, Jiménez-Montoya J, Kennard D, Marín-Spiotta E, Mesquita R, Nunes YRF, Ochoa-Gaona S, Peña-Claros M, Pérez-Cárdenas N, Rodríguez-Velázquez J, Villanueva LS, Schwartz NB, Steininger MK, Veloso MDM, Vester HFM, Vieira ICG, Williamson GB, Zanini K and Hérault B (2021) Multidimensional tropical forest recovery. *Science*, **374**, 1370–1376.

R Core Team (2020) *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Ricotta C, Podani J, and **Uv ED** (2017) On some properties of the Bray-Curtis dissimilarity and their ecological meaning. *Ecological Complexity* **31**, 201–205.

(RMCA) Royal Museum for Central Africa (2021) Data derived via DRYAD.

Rueden CT, Schindelin J, Hiner MC, Dezonia BE, Walter AE, Arena ET and Eliceiri KW (2017) ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* **18**, 529.

Saranpää P (2003) *Wood density and growth.* In J. R. Barnett & G. Jeronimidis (Eds.), *Wood Quality and Its Biological Basis.* Hoboken, New Jersey: Wiley-Blackwell Publishing.

Sasaki N and Putz FE (2009) Critical need for new definitions of "forest" and "forest degradation" in global climate change agreements. *Conservation Letters* **2**, 226–232.

Shapiro AC, Grantham HS, Aguilar-Amuchastegui N, Murray NJ, Gond V, Bonfils D and Rickenbach O (2021) Forest condition in the Congo Basin for the assessment of ecosystem conservation status. *Ecological Indicators* **122** 1470–1160.

Slik JWF, Arroyo-Rodríguez V, Aiba SI, Alvarez-Loayza P, Alves LF, Ashton P, Balvanera P, Bastian ML, Bellingham PJ, Van Den Berg E, Bernacci L, Bispo PC, Blanc L, Böhning-Gaese K, Boeckx P, Bongers F, Boyle B, Bradford M, Brearley FQ, Hockemba MB, Bunyavejchewin S, Matos DCL, Castillo-Santiago M, Catharino ELM, Chai S, 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, Duque A, Durigan G, Eichhorn KAO, Eisenlohr PV, Eler E, Ewango C, Farwig N, Feeley KJ, Ferreira L, Field R, Filho ATO, Fletcher C, Forshed O, Franco G, Fredriksson G, Gillespie T, Gillet J, 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, do Amaral IL, Letcher SG, Lindesll J, Lu X, Mansor A, Marjokorpi A, Martin E, Meilby H, Melo FPL, Metcalfe DJ, Medjibe VP, Metzger JP, Millet J, Mohandass D, Montero JC, Valeriano MM, Mugerwa B, Nagamasu H, Nilus R, Ochoa-Gaona S, Onrizal, Page N, Parolin P, Parren P, Parthasaranthy N, Paudel E, Permana A, Piedade MTF, Pitman NCA, Poorter L, Poulsen AD, Poulsen J, Powers J, Prasad RC, Puyravaud J, Razafimahaimodison J, Reitsma J, dos Santos JR, Spironello WR, 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, Pinheiro ES, Sist E, Stevart T, Sukumar R, Sun IF, 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, Yao CYA, Yap SL, Yoneda T, Zahawi RA, Zakaria R, Zang R, de Assis RL, Luize BG and Venticinque EM (2015) An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 7472–7477.

Sosef MSM, Dauby G, Blach-Overgaard A, van der Burgt X, Catarino L, Damen T, Deblauwe V, Dessein S, Dransfield J, Droissart V, Duarte MC, Engledow H, Fadeur G, Figueira R, Gereau RE, Hardy OJ, Harris DJ, de Heij J, Janssens S, Klomberg Y, Ley AC, Mackinder BA, Meerts P, van de Poel JL, Sonké B, Stévart T, Stoffelen P, Svenning J, Sepulchre P, Zaiss R, Wieringa J and Couvreur TLP (2017) Exploring the floristic diversity of tropical Africa. *BMC Biology* **15**, 15.

Tegegne YT, Lindner M, Fobissie K and 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.

Tyukavina A, Hansen MC, Potapov P, Parker D, Okpa C, Stehman SV, Kommareddy I and Turubanova S (2018) Congo Basin forest loss dominated by increasing smallholder clearing. *Science Advances* **4**, eaat2993.

Van de Perre F, Willig MR, Presely SJ, Andemwana FB, Beeckman H, Boeckx P, Cooleman S, de Haan M, De Kesel A, Dessein S, Grootaert P, Huygens D, Jansens SB, Kearsley E, Kabeya PM, Leponce M, Van den Broeck D, Verbeeck H, Würsten B, Leirs H and Verheyen E (2018) *Science advances* 4, eaar6603.

van Vliet N, Muhindo J, Kambale Nyumu J, Mushagalusa O and Nasi R (2018) Mammal depletion processes as evidenced from spatially explicit and temporal local ecological knowledge. *Tropical Conservation Science* **11**, 1–16.

Vancutsem C, Pekel JF, Evrard C, Malaisse F and Defourny P (2009) Mapping and characterizing the vegetation types of the Democratic Republic of Congo using SPOT VEGETATION time series. *International Journal of Applied Earth Observation and Geoinformation* **11**, 62–76.

Vanden Abeele S, Janssens SB, Asimonyio Anio J, Bawin Y, Depecker J, Kambale B, Mwanga Mwanga I, Ebele T, Ntore S, Stoffelen P and Vandelook F (2021) Genetic diversity of wild and cultivated Coffea canephora in northeastern DR Congo and the implications for conservation. *American Journal of Botany* **108**, 2425–2434.

West PC, Gibbs HK, Monfreda C, Wagner J, Barford CC, Carpenter SR and Foley JA (2010) Trading carbon for food: global comparison of carbon stocks vs. crop yields on agricultural land. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 19645–19648.

Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.

Wittmann F, Schongart J, Montero JC, Motzer T, Junk WJ, Piedade MTF, Queiroz HL and Worbes M (2006) Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography* **33**, 1334–1347.