PAPER

WILEY bioTROPICA · ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

Long-term recovery of the functional community assembly and carbon pools in an African tropical forest succession

Marijn Bauters[1,2,3] 🄳 | Oscar Vercleyen[1] | Bernard Vanlauwe[4] | Johan Six[5] | Bernard Bonyoma[6] | Henri Badjoko[6] | Wannes Hubau[7] | Alison Hoyt[8,9] | Mathieu Boudin[10] | Hans Verbeeck[2] | Pascal Boeckx[1]

[1]Isotope Bioscience Laboratory—ISOFYS, Department of Green Chemistry and Technology, Faculty of Bioscience Engineering, Ghent University, Gent, Belgium

[2]Computational and Applied Vegetation Ecology—CAVElab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Gent, Belgium

[3]Meise Botanic Garden, Domein Bouchout, Meise, Belgium

[4]Consultative Group on International Agricultural Research—CGIAR, International Institute of Tropical Agriculture–IITA, Nairobi, Kenya

[5]Sustainable Agroecosystems Group, Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland

[6]Institut National pour l'Etude et la Recherche Agronomique—INERA, Yangambi, Democratic Republic of Congo

[7]Service of Wood Biology, Royal Museum for Central Africa, Tervuren, Belgium

[8]Max Planck Institute for Biogeochemistry, Jena, Germany

[9]Lawrence Berkeley National Laboratory, Berkeley, California

[10]Royal Institute for Cultural Heritage, Brussels, Belgium

Correspondence
Marijn Bauters, Isotope Bioscience Laboratory—ISOFYS, Department of Green Chemistry and Technology, Faculty of Bioscience Engineering, Ghent University, Gent, Belgium.
Email: Marijn.Bauters@UGent.be

Abstract

On the African continent, the population is expected to expand fourfold in the next century, which will increasingly impact the global carbon cycle and biodiversity conservation. Therefore, it is of vital importance to understand how carbon stocks and community assembly recover after slash-and-burn events in tropical second growth forests. We inventoried a chronosequence of 15 1-ha plots in lowland tropical forest of the central Congo Basin and evaluated changes in aboveground and soil organic carbon stocks and in tree species diversity, functional composition, and community-weighted functional traits with succession. We aimed to track long-term recovery trajectories of species and carbon stocks in secondary forests, comparing 5 to 200 + year old secondary forest with reference primary forest. Along the successional gradient, the functional composition followed a trajectory from resource acquisition to resource conservation, except for nitrogen-related leaf traits. Despite a fast, initial recovery of species diversity and functional composition, there were still important structural and carbon stock differences between old growth secondary and pristine forest, which suggests that a full recovery of secondary forests might take much longer than currently shown. As such, the aboveground carbon stocks of 200 + year old forest were only 57% of those in the pristine reference forest, which suggests a slow recovery of aboveground carbon stocks, although more research is needed to confirm this observation. The results of this study highlight the need for more in-depth studies on forest recovery in Central Africa, to gain insight into the processes that control biodiversity and carbon stock recovery.

Abstract in French is available with online material.

KEYWORDS
carbon stocks, Central Africa, Congo basin, functional assembly, long-term recovery, secondary succession, tropical forest

1 | INTRODUCTION

Tropical forests provide crucial ecosystem services on both a global scale and a local scale. These services include the mitigation of climate change through their role as carbon sinks (Beer et al., 2010; Pan et al., 2011), acting as safeguards of unique species and exceptionally biodiverse communities (Gardner et al., 2012; Slik et al., 2015), and directly supporting the livelihoods of millions of people (Chomitz, Buys, de Luca, Thomas & Wertz-Kanounnikoff, 2007). However, increasing anthropogenic pressure is leading to accelerated land-use change (FAO, 2016) In the case of subsistence shifting cultivation, deforestation is followed by natural regeneration, which further promotes a tropical forest biome that is dominated by secondary-growth forests (Hansen et al., 2013; Keenan et al., 2015). Therefore, a better understanding of the rate at which these secondary forests recover their carbon stocks and community assembly will benefit both research on the global carbon cycle and biodiversity conservation.

As direct estimates of long-term forest recovery rates in stands monitored over time are largely unavailable, current knowledge on carbon accrual and diversity recovery during secondary succession relies heavily on space-for-time studies of forest chronosequences (Chazdon, 2008; Rozendaal & Chazdon, 2015). These chronosequence studies—primarily conducted in the Neotropics—have shown that recovery rates vary dramatically with climatic factors (Anderson, Allen, Gillooly & Brown, 2006; Becknell, Kissing Kucek & Powers, 2012; Poorter et al., 2016), soil fertility (Becknell & Powers, 2014; Moran et al., 2000), and the duration and intensity of land use prior to abandonment (Gehring, Denich & Vlek, 2005; Jakovac, Peña-Claros, Kuyper & Bongers, 2015). Meta-analyses from the Neotropics have shown that forests in South America seem to be quite resilient to disturbance. After a few decades of regrowth, they seem to attain levels of aboveground carbon (AGC; Becknell et al., 2012; Martin, Newton & Bullock, 2013; Poorter et al., 2016), soil organic carbon (SOC; Marin-Spiotta et al., 2007; Marín-Spiotta & Sharma, 2013; Martin et al., 2013), tree species richness (Chazdon, 2008; Chazdon et al., 2009; Guariguata & Ostertag, 2001; Peña-Claros, 2003), and functional composition (Chazdon, 2008; Dent, Dewalt & Denslow, 2013) close to those from old growth forests. Because of these decadal recovery rates, most studies have classified forests > 100 years as old growth forest. However, little is actually known about longer term forest succession. Here, we investigate the trajectories in vegetation and carbon stocks in old growth secondary forests, decades to centuries post-disturbance.

In addition to the scarcity of data on long-term forest recovery, field studies on the African continent are limited, despite the fact that it contains the second largest contiguous block of tropical forest. Hence, to complement the large existing body of work in Neotropical forests, more studies are needed on forest regrowth in Africa because (a) important differences between African and Amazonian forests exist in forest structure, carbon storage, and species diversity (Banin et al., 2012; Lewis et al., 2013; Parmentier

et al., 2007; Slik et al., 2015, 2017), (b) differences exist in exogenous nutrient inputs (Bauters et al., 2018), and (c) the projected global population growth for the next century is expected to be dominated by population growth in Africa, with an estimated fourfold increase in population on the continent (Gerland et al., 2014). The latter is likely to exert a continued and increasing anthropogenic pressure on sub-Saharan tropical forest ecosystems, highlighting the need to prioritize field studies on Central African forest recovery.

In this study, we explored two research questions for Central African forests: (a) How fast can both aboveground and soil carbon stocks recover in secondary forest trajectories and approach old growth forest carbon stocks, (b) how fast does species diversity and functional assembly of secondary forest trajectories recover to old growth forest composition? We focused on the long-term recovery of carbon stocks and vegetation composition, to extend our understanding beyond the initial first two decades after disturbance, which have been much more well-studied. To do so, we set up and characterized 15 new permanent monitoring 1-ha plots in lowland tropical forest in the central Congo Basin, along a space-for-time forest chronosequence ranging from 5 to 200+ years after disturbance, and including also primary forest as a reference. At these sites, we assessed aboveground and soil organic carbon stocks, along with the functional assembly of the tree community.

2 | MATERIAL AND METHODS

2.1 | Study site

This study is based on data collected during two field campaigns between November 2015 and September 2016 in the Maringa-Lopori-Wamba forest landscape (1°51′50″N – 0°26′28″N; 19°41′5″E – 23°32′43″E; 350–400 m a.s.l.) in the Tshuapa province in the Democratic Republic of the Congo (DRC). Vegetation at the study site is classified as semi-deciduous rain forest and is characterized by two dominant climax forest types: mixed lowland tropical forest and *Gilbertiodendron* dominated forest, where > 60% of the basal area consists of one species, *Gilbertiodendron dewevrei*. Climate falls within the Af-type (tropical rain forest climate) following the Köppen–Geiger classification. Soils in the region are typical deeply weathered and nutrient-poor Ferralsols, with very limited elevation differences and gentle slopes, and dominated by a sandy texture. Here, we established square permanent sample plots of one hectare in triplicate along five different stages of forest development based on expert judgment of local foresters: recently abandoned farmland dominated by *Musanga cecropioides* and *Macaranga species* (Young; 5–25 years), second growth young forest (SYoung; 25–30 years), second growth old forest (SOld; approx. 150–300 years), and two old growth forest types, old growth mixed forest (Old-Mix; 1700 years) and old growth *Gilbertiodendron* dominated forest (Old-Gil; no age estimation). The latter category was added because this is a known climax stadium of succession in Central Africa (Maley et al., 2018), which provides us with an extra control to compare the structure,

carbon stocks, and diversity of old growth mixed forest with. Hence, our setup consisted of three succession stages at different stages of recovery post-disturbance and two climax forest types as a reference. Although we do not have explicit information on the prior land-use for the selected secondary plots, the context and location make it highly likely that shifting cultivation by slash-and-burn forest clearing is the primary human disturbance. There is no large-scale agriculture in the region, and the site is very remote; by motorbike, it takes two long days on a small dirt-track through the forest to reach the nearest city.

2.2 | Field inventories, sampling, and analysis

We inventoried the 15 1-ha plots following an international standardized protocol for tropical forest inventories (RAINFOR; Malhi et al., 2002). In each plot, the diameter of all live stems with a diameter larger than 10 cm was measured at 1.3 m height and the trees were identified to species level. In addition, the tree heights of approximately 20% of all trees in each plot were measured, with measurements distributed across the observed diameter classes (Nikon Forestry Pro, Nikon, Japan). The height of broken living trees was measured separately. The community-weighted mean values of leaf functional traits were determined in the plots by selecting the most abundant tree species (i.e., the species that, together, make up minimum 70% of the standing basal area per plot). For the selected species of all plots, mature leaves of a minimum of three individuals per species were sampled by tree climbers. For most of the individuals, we sampled fully sunlit leaves, but this was not always practically feasible for the climbers, in which case we sampled partly shaded leaves under the top canopy. Leaf areas were determined by either photographing leaves on white paper with a reference scale or drawing leaf contours and scanning the drawings in the evening of the sampling day. Both pictures and scans were processed using free ImageJ software (Schneider, Rasband & Eliceiri, 2012). Leaves were subsequently sun-dried in the field and oven-dried overnight at 60°C and ground within three weeks of sampling. Specific leaf area (SLA) was calculated by dividing the leaf areas of all sampled leaves per individual by the total dry mass of the sample.

Composite soil samples and soil samples for bulk density measurement were collected at respectively 10 and five places within each plot at five depth increments (0–10, 10–20, 20–30, 30–50, and 50–100 cm) in September 2016. Both sample sets were subdivided into two sets which were (a) oven-dried at 60°C for 48 hr, and subsequently homogenized (composite samples for analysis), or (b) weighed after further drying at 105°C until stable weight was attained (bulk density). Soil subsamples from five profiles were analyzed for Δ^{14}C-SOC on a MICADAS ^{14}C AMS system (Ionplus AG, Dietikon, Switzerland) to assess potential changes in the mean age of soil carbon and rates of soil carbon cycling along the successional gradient. Samples were combusted and graphitized following Steinhof, Altenburg and Machts (2017) prior to analysis. Data are reported as radiocarbon concentrations, rather than calibrated dates. These are not appropriate to open systems such as soils, which include a mix

of carbon fixed from the atmosphere at different times. Leaf and plot-level composite soil samples were analyzed for total carbon and nitrogen content and on nitrogen stable isotope ratio δ^{15}N using an elemental analyzer (automated nitrogen carbon analyzer; ANCA-SL, SerCon, UK), interfaced with an isotope ratios mass spectrometer (IRMS; 20–22, SerCon, UK).

2.3 | Assignment of successional stage: charcoal dating and interviews

We used a combination of two dating techniques to date the 15 experimental plots and to give an approximation of the time since agricultural abandonment for every plot. Young, SYoung, and SOld plots were dated by interviewing the landowners and several older-aged inhabitants of the villages Ingungu and Mbotolongo. Old-Mix plots were selected based on the expert judgment of the botanists of INERA, but additional radiocarbon dating of charcoal pieces found in the uppermost soil layer was used to validate the time since the most recent slash-and-burn event. We searched for charcoal pieces in the composite soil samples from each plot. The charcoal pieces found in the composite topsoil sample are assumed to originate from wood that burnt during the last fire event at the forest site. Subsequently, charcoal pieces were dated with an accelerator mass spectrometer (MICADAS, ETH, Switzerland) at KIKIRPA in Belgium. Radiocarbon age determinations of wood charcoal are commonly used to date past forest fire events (Hubau, van den Bulcke, van Acker & Beeckman, 2015). All residues were pre-treated with the acid-alkali-acid (AAA) method. ^{14}C determinations were measured on the AMS at the Royal Institute for Cultural Heritage, Brussels (Lab code RICH-; Boudin, van Strydonck, van den Brande, Synal & Wacker, 2016). All samples were transformed into graphite using the automatic graphitization device AGE (Wacker, Němec & Bourquin, 2010). Calibrated radiocarbon ages were determined using OxCal version 4.2 (Bronk Ramsey, 2009) and the IntCal13 calibration curve date (Reimer et al., 2013) to correct for variation in atmospheric radiocarbon concentrations over time.

2.4 | Data analysis

For each plot, we used best fitting diameter-height relationships out of 16 published relationships according to the Akaike information criterion (Supporting Information Table S1, Brown, Gillespie & Lugo, 1989; Huang, Titus & Wiens, 1992; Banin et al., 2012; da Silva Scaranello et al., 2012; Feldpausch et al., 2012) and subsequently a pan-tropical tree allometric relationship including height, diameter at breast height (DBH) and wood density (WD; Chave et al., 2014) in order to estimate AGB. For the conversion to AGC, we assumed a wood carbon content of 50% (Chave et al., 2005). Due to logistical constraints, it was not possible to measure the WD of all tree stems on site. Therefore, the WDs collected for research in the Yangambi Man and Biosphere Reserve and the DRYAD WD database (Chave et al., 2009) were used to attribute WD values to the trees. If no species-level data were available in either database, we

used genus-level average WD from both databases to assign WD to the respective individual. We defined stem number as the sum of all living trees with a diameter larger than 10 cm at 1.3 m height within each plot. Maximum tree height was calculated as the average of the three highest trees in each plot.

To enable comparison of species richness at the plot level, species number was rarefied to the lowest observed number of individual trees in each plot. In addition to rarefied species richness, we calculated both the Shannon and Pielou's evenness indexes, along with the number of unique species per plot. The latter represents the number of species that occurred in the respective plot but were not present in plots from a different successional stage. To analyze functional composition, all trees were grouped into three functional types based on shade tolerance following published work (Hawthorne, 1995): pioneer species (P), non-pioneer light-demanding species (NPLD), and shade bearer species (SB). P species require gaps for establishment, NPLD species can establish in shade but need a gap to grow to their full height, and SB species can be found in shade both as young and older plants (Hawthorne, 1995). Additionally, average tree functional trait values of WD, SLA, mass-based leaf nitrogen content (LNC), ratio of mass-based leaf carbon content (LCC) and LNC (C:N), and δ^{15}N were calculated for every selected species. Subsequently, we calculated community-weighted mean leaf functional trait values per plot using the species composition and the species trait averages, weighting with basal area.

For each depth increment, SOC was determined as the product of mass-based soil organic carbon content, bulk density, and thickness of the increment layer, and extrapolated to the plot surface (1 ha). Subsequently, SOC to a depth of 1 m was quantified for each plot by summing the SOC stocks per depth increment.

2.5 | Statistics

Average plot values and standard deviations were calculated for each successional stage of forest structure variables, soil properties, AGC, SOC, species diversity variables, functional composition, and community-weighted functional traits. We conducted one-way analysis of variance (ANOVA) to compare the successional stages, using the plot-level data, with additional Tukey's honestly significant difference (HSD) post hoc testing. When the underlying assumptions were not met, the data were log-transformed. Kruskal–Wallis and subsequent Dunn's tests were used on the data that did not meet the ANOVA assumptions after transformation. Significance was determined as $p < 0.05$. Successional stages with only one replicate were left out of this analysis. Additionally, we used multivariate analysis to assess species turnover and species' association with successional stage. For this, an exploratory correspondence analysis showed a gradient of roughly four standard deviation units; hence, a unimodal method—detrended correspondence analysis (DCA)—was selected. All analyses were done using the R software (R Development Core Team 2018), using the vegan package for the ordination (Oksanen et al., 2013).

3 | RESULTS

Our chronosequence consisted of three Young plots (5–25 years), three SYoung plots (25–30 years), five SOld plots (approx. 150–300 years), one Old-Mix plot (1700 years), and three Old-Gil plots (no age estimation). Radiocarbon dating of charcoal indicated that two of the three presumed Old-Mix plots were much younger than the third Old-Mix plot and had approximately the same age as the three presumed SOld plots (Supporting Information Table S2). Moreover, the abundance of big trees was significantly lower in these two plots compared with the third Old-Mix plot. Therefore, we reclassified these plots as SOld forest, instead of Old-Mix forest as previously classified by forest experts from INERA. The possible range of ages for plots within the SOld successional stage is relatively wide (Supporting Information Table S2). However, as the highest probability of these dates falls within 1660–1890AD (78.7% probability; 126–356 years prior to sampling) for plot 15 and 1730–1810AD (48.8% probability; 206–286 years prior to sampling) for plot 3, we choose to refer to this successional grouping as "approx. 150–300 years" throughout the paper. For Old-Mix, the dates fall within 230–410AD (95.4%; 1605–1785 years prior to sampling), for which we use "1700 years" throughout the paper. Although we acknowledge that precise age is highly uncertain, and may be much younger (Supporting Information Table S2), we believe there is strong justification for the successional grouping (see Discussion).

Overall, the structure of the forest changed significantly over the succession. Despite an initial decrease in mean tree basal area, plot basal area, and maximum tree height from the Young to the SYoung stage, later successional stages showed a significant increase, with remarkably differing values between SOld and Old-Mix forest. Stem number remained constant over the forest succession, except for the *Gilbertiodendron* forest, where it was significantly lower (Supporting Information Table S3, Figure 1).

For the community assembly, rarefied species richness, Shannon index, and the number of unique species per successional stage significantly increased with succession and converged toward those of Old-Mix forest. Pielou's evenness index did not show any significant differences between the different stages (Figure 2, Supporting Information Table S3). The classification into guilds showed a decrease in the relative share of pioneer species, an increase in shade bearing species, and no significant changes in the non-pioneer light-demanding species, which showed a sustained presence over all the succession stages (Figure 2). Overall, we sampled leaves of a total of 429 individual trees, covering 152 of the 216 tree species that were present in the plots. Additionally, the community-weighted functional traits showed an initial significant increase in WD, and an overall decrease in SLA, but no significant changes in canopy stoichiometry (C:N and canopy LNC; Figure 2). However, no notable differences in the share of pioneer and shade bearing species were found between SOld and Old-Mix, suggesting that functional composition of SOld forest converged toward that of Old-Mix forest. The DCA also shows the species turnover along DCA axis 1 (eigenvalue 0.7, with an axis length of 4.6; Figure 3). Finally, the δ^{15}N isotopic
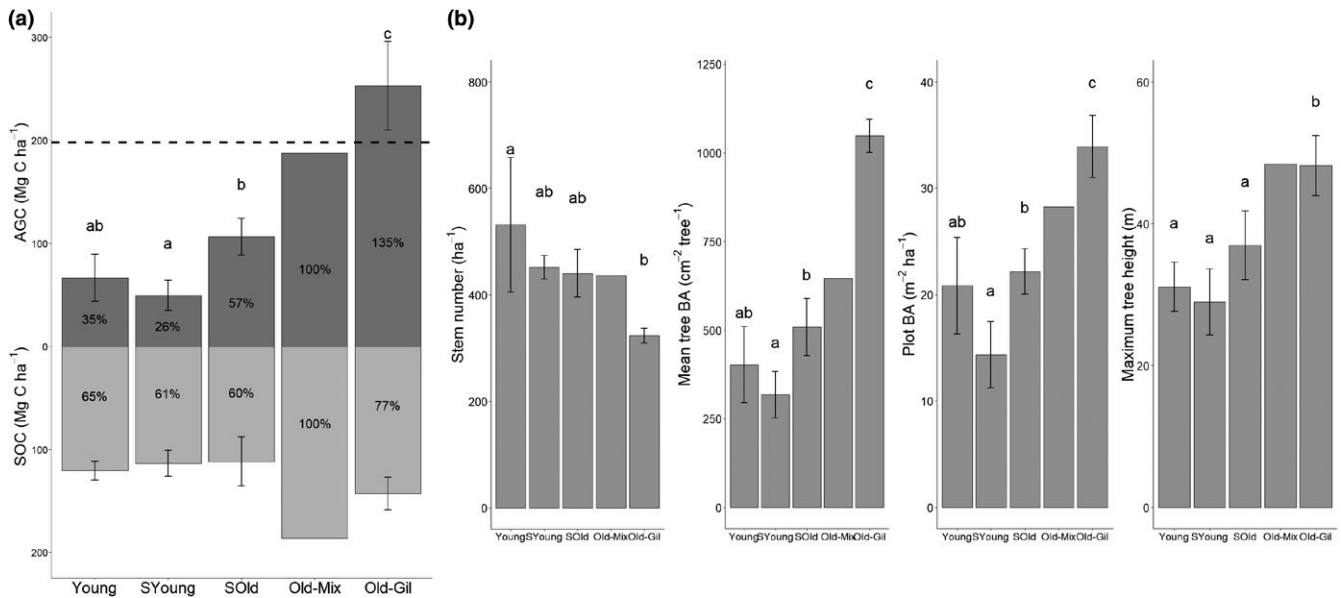
FIGURE 1 (a) Variation of aboveground carbon (AGC) and soil organic carbon (SOC) along the forest succession in the Maringa-Lopori-Wamba landscape. Young: recently abandoned farmland, 5–25 years; SYoung: second growth young forest, 25–30 years; SOld: second growth old forest, approx. 150–300 years; Old-Mix: old growth mixed forest, 1700 years; Old-Gil: old growth *Gilbertiodendron* forest. BA stands for basal area. Error bars represent standard deviations. No standard deviations were calculated for Old forest because of its single plot replicate. Percentages are stock values relative to the value of Old-Mix forest. The dashed horizontal line indicates the regional mean AGC of old growth forests across Central Africa (Lewis et al., 2013). (b) Variation of four forest structure plot variables along the successional stages at our study site. Bars represent mean plot values per successional stage. Error bars represent standard deviations. BA stands for basal area. Error bars represent standard deviations. No standard deviations were calculated for Old-Mix because of its single plot replicate. Significant differences across forest types are indicated by different letters per type ($p < 0.05$)

signature of both the topsoil and the canopy showed no significant differences along the forest succession (Supporting Information Tables S2 and S3).

Aboveground carbon increased along the successional gradient, while SOC was relatively uniform, with the exception of the Old-Mix plot. AGC significantly increased after SYoung forest stage, that is, forest of 25–30 years of age (Figure 1). However, second growth forest, with an AGC stock of 106.3 Mg C/ha, never reached a value close to the value of Old-Mix (187.7 Mg C/ha). AGC of SOld forest was estimated to be only 57% of the AGC of Old-Mix. The AGC of the *Gilbertiodendron* forest was highest (135% of the AGC of Old-Mix). In contrast to AGC, no significant differences were found in the SOC stocks over the forest succession (Figure 1). Stocks ranged from 111 to 186 Mg C/ha. Both SOC content and BD were similar at the respective depth increments, across the succession, with exception of the significantly higher BD in the Old-Gil in the 20–30 cm depth layer. BD increased with depth from on average 1,147 to 1,279 kg/m^3, and SOC content decreased with depth from on average 1.9% at 0–10 cm depth to 0.9% at 50–100 cm depth. The highest SOC stock was observed in Old-Mix, primarily due to higher carbon content in the lower soil layers (Figure 1). The SOC of SOld forest was only 60% of that measured in Old-Mix. However, despite this higher carbon content at depth the in Old-Mix compared to other sites, the radiocarbon content of the deep soil was similar across all profiles. At the surface, the Old-Mix had the lowest soil radiocarbon values (from 0 to 20 cm: Figure 4, Supporting Information Table S6). The

$\Delta^{14}C$ decreased in all profiles with depth from an average of 78‰ at 0–10 cm depth to −112‰ at 50–100 cm depth.

4 | DISCUSSION

4.1 | Species composition and diversity along succession: a fast species recovery

An initial fast recovery of composition and diversity was shown in the lack of significant differences between SYoung forest and SOld forest, which suggests that tropical tree species diversity recovered rapidly following agricultural abandonment, and is in line with Neotropical studies (Guariguata & Ostertag, 2001; Martin et al., 2013; Peña-Claros, 2003).

Furthermore, old growth secondary forests and truly pristine forest patches seem to have very similar species composition, based on (a) the number of unique species (Figure 2), (b) the similar functional composition (Figure 2), and (c) the short distance between both clusters in the biplot (Figure 3). The latter was also evidenced by the fact that local experts apparently misjudged the pristine status of two out of three "old growth" plots. This highlights one important outcome of this study that species composition in old growth secondary plots is very close to that of truly pristine forest patches.

In contrast to this work, several studies on tropical forest succession have shown that the proportion of species associated with undisturbed tropical forest found in second growth forest can be low, and
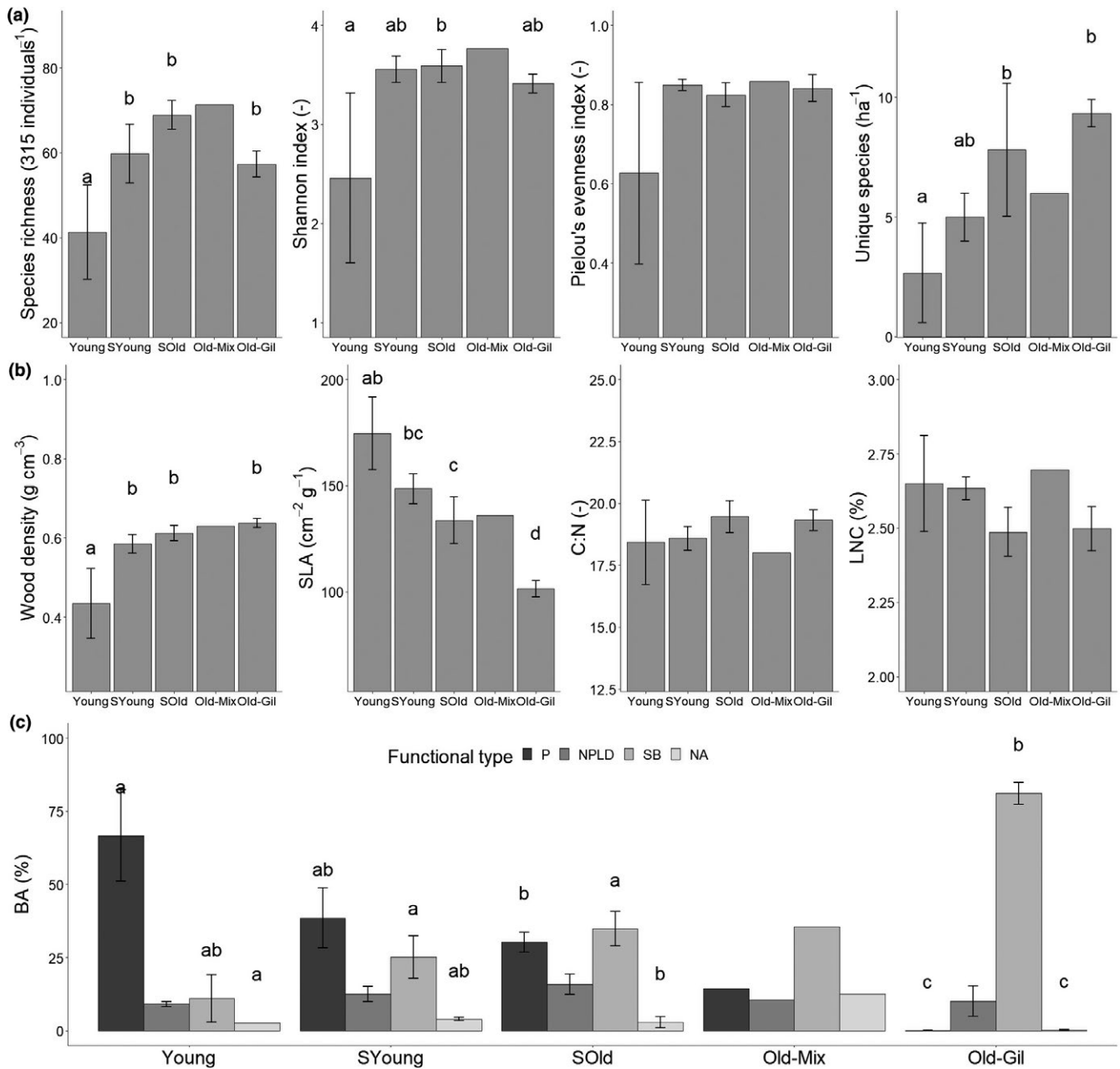
FIGURE 2 (a) Variation of four tree species diversity variables along the forest succession. (b) Variation in community-weighted wood density, specific leaf area (SLA), canopy C:N ratio, and canopy leaf nitrogen content (LNC) along successional stages. (c) Relative share of non-pioneer light-demanding species (NPLD), pioneer species (P), and shade bearer species (SB) for each successional stage. Species for which no functional type was found were assigned with NA. Young: recently abandoned farmland, 5–25 years; SYoung: second growth young forest, 25–30 years; SOld: second growth old forest, approx. 150–300 years; Old-Mix: old growth mixed forest, 1700 years; Old-Gil: old growth *Gilbertiodendron* forest. Relative share is expressed in basal area of functional type relative to total basal area (BA, %). Bars represent mean plot values per successional stage. Error bars represent standard deviations. No standard deviations were calculated for Old-Mix because of its single plot replicate. Significant differences across forest types are indicated by different letters per type ($p < 0.05$). For panel c, the letters indicate between-stage differences in functional types

slowly increases (Derroire et al., 2016; Martin et al., 2013; Peña-Claros, 2003), even to the extent that old growth secondary forests globally might be important for the conservation of a distinct "secondary" species pool (Chazdon et al., 2009). In this study, we found a limited number of unique species in the single hectare plot that was classified as truly old growth forest (six species; Figure 2), which was similar to the average of seven unique species that were present in the 5 1-ha plots of SOld. Overall, this is in accordance with the similar rarefied species richness, Shannon diversity and Pielou's evenness index that both forest types showed (Figure 2), and supports the idea that species composition in the old secondary forests is actually very close to those of truly pristine forests. The *Gilbertiodendron* forest, as an important other climax forest situation in Central Africa, showed marginally lower diversity indices, with yet another set of unique species. This
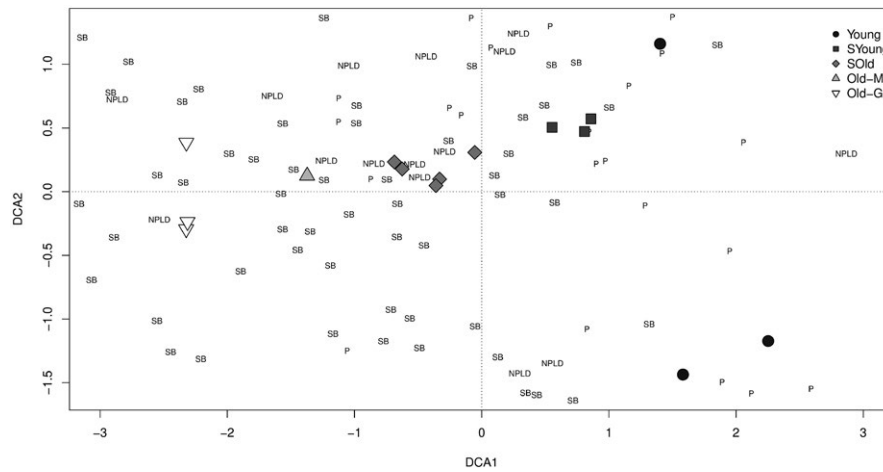
FIGURE 3 Detrended canonical correspondence analysis (DCA) of the species association along the forest succession. Young: recently abandoned farmland, 5–25 years; SYoung: second growth young forest, 25–30 years; SOld: second growth old forest, approx. 150–300 years; Old-Mix: old growth mixed forest, 1700 years; Old-Gil: old growth *Gilbertiodendron* forest. For clarity, the species names were replaced by their respective classes following Hawthorne (1995), being pioneer (P), non-pioneer light-demanding (NPLD), and shade bearer (SB)
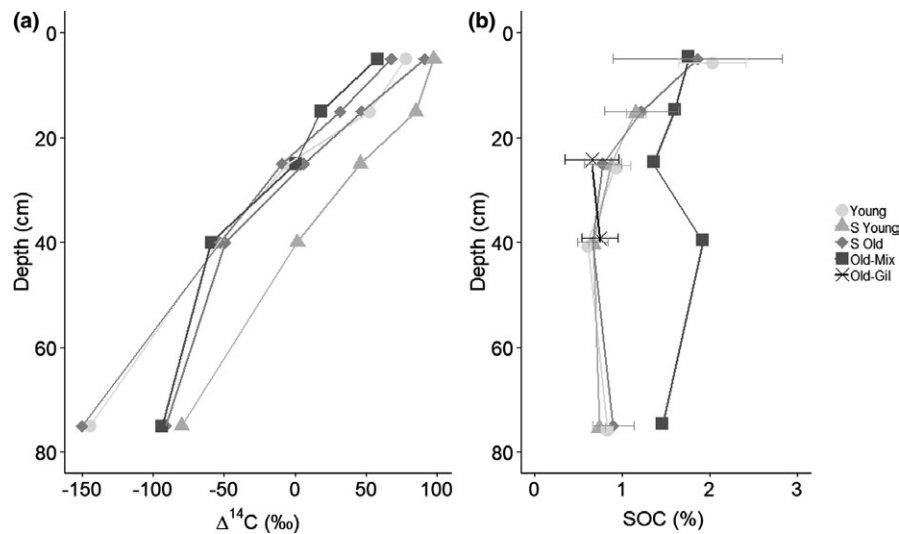

FIGURE 4 (a) Δ^{14}C signature of the soil profiles and (b) Soil organic carbon content depth profiles for the successional stages at our study site with Young: recently abandoned farmland, 5–25 years; SYoung: second growth young forest, 25–30 years; SOld: second growth old forest, approx. 150–300 years; Old-Mix: old growth mixed forest, 1700 years; Old-Gil: old growth *Gilbertiodendron* forest. BA stands for basal area. Error bars represent standard deviations. No standard deviations were calculated for Old-Mix because of its single plot replicate

special climax situation is not yet fully explained (Corrales et al., 2016; Kearsley et al., 2017; Peh, Sonke, Lloyd, Quesada & Lewis, 2011), but it is likely that association with ectomycorrhiza and edaphic factors is at the basis of the monodominance, while N cycling is unlikely to be a determining factor (Bauters, Verbeeck et al., 2019).

4.2 | Functional community assembly: partial shift from resource acquisition to resource conservation

Additionally, we found that functional composition of second growth forest converged to that of pristine forest (Old-Mix), which has also been observed in the Neotropics (Chazdon, 2008; Dent et al., 2013). The successional trends we found for community-weighted tree

functional traits also indicate this fast recovery of functional composition. Moreover, these results confirm that a tree community makes a shift in functional strategies during succession from acquisitive to conservative strategies (Lohbeck et al., 2013; Peñuelas et al., 2013), with species replaced by others to adapt to changing light environments, reflecting a trade-off in plant strategy. Fast growing species with a rapid acquisition of resources thrive in the light-rich environment of early-successional stages, while slow growing species that conserve resources dominate the poor light environment of late-successional stages (Reich, 2014). Hence, during succession leaves run from short-lived, high specific leaf area (SLA) leaves with high assimilation rates to longer-lived, low SLA leaves that supposedly have low assimilation rates (Poorter, Niinemets, Poorter, Wright &

Villar, 2009; Wright et al., 2004) whereas stems run from fast growing, low WD stems to long living, slow growing, and high WD stems (Chave et al., 2009).

However, remarkably, in our study we did not detect any of the expected changes in LNC and leaf C:N ratio across the community-weighted means of the forest succession (Figure 2). This is contrary to the general assumption that succession exerts a shift from resource acquisition to resource conservation strategies, and is what would be expected given the strong correlation between SLA and LNC along the trait continuum (Wright et al., 2004). To date, several studies have documented this apparent decoupling of both traits along forest succession (Becknell & Powers, 2014; Craven, Hall, Berlyn, Ashton & van Breugel, 2015; Whitfeld et al., 2014), which has been attributed to changes in leaf structural attributes (Poorter et al., 2009). Secondly, the availability of N might be exceptionally high at our study site (Bauters et al., 2018). This might further reduce stoichiometric N constraints during forest regeneration, although a study on the abundance and nodulation of N fixers at the same location did identify a clear role of N fixing trees for N input in recovering forests (Bauters, Mapenzi, Kearsley, Vanlauwe & Boeckx, 2016). We conclude from the combination of (a) a lack of shifts in canopy stoichiometry along the succession, (b) the presence of symbiotic N fixing activity in early succession, and (c) a high exogenous N input that Central African forests are able to fully alleviate N limitation during succession. This is also further confirmed by the lack of a strong trend in our foliage and topsoil δ^{15}N (Figure 2, Supporting Information Table S3), which can serve as a proxy for the openness of the N-cycle in natural ecosystems (Craine et al., 2009, 2015). The foliar δ^{15}N signature showed clear increases of up to 3‰ in South American forest successions, indicating an increasingly "leaky" N-cycle (Davidson et al., 2007), while for our forest succession, the differences between extremes did not exceed 1‰ (Supporting Information Table S3).

4.3 | Carbon stocks: fast initial recovery, slow full recovery?

Our dataset suggests that AGC stocks recover very slowly in the central Congo Basin; approx. 150–300 years after agricultural abandonment second growth forest at our study site had AGC that was only 57% of those of our Old-Mix plot. Because this successional stage was represented by only one plot, this result should be treated with caution. However, other Central African studies reported an average AGC value of mature mixed forests, which agreed closely with the stock we found in Old-Mix (Figure 1, Lewis et al., 2013). The higher AGC in Old-Mix is both explained by more large trees with both larger mean tree basal area and maximum tree height (Figure 1). The importance of larger trees for aboveground carbon stocks was also asserted by Bastin et al. (2015) and also in accordance with the second climax forest at our study site, Old-Gil; similar AGC stocks, with on average more large trees (Figure 1). Nevertheless, our results are in stark contrast with the high resilience of carbon stocks of secondary Neotropical forest: Poorter

et al. (2016) showed that AGC of Neotropical second growth forest took a median time of only 66 years to recover to 90% of old growth values, and Martin et al. (2013) found that AGC across the tropics fully recovered at nearly 80 years after disturbance. One important extra point here is that this apparent contrast depends heavily on how we interpret the charcoal datings from the SOld forest. Indeed, the forest might be much younger than indicated by both the charcoal pieces and the interviews, in which case the AGC recovery rate would be closer to those reported for Neotropical forest.

In contrast to AGC, SOC stocks showed relatively little change over the succession gradient, with the exception of the stocks in Old-Mix. Similarly, with the exception of small differences at the surface, soil radiocarbon content did not meaningfully change along the succession gradient, indicating rates of soil C cycling were not impacted by disturbance. Studies across the tropics have found the responses of SOC stocks to deforestation and subsequent forest regeneration vary in both direction and magnitude (Powers, Corre, Twine & Veldkamp, 2011; Powers & Marín-Spiotta, 2017). For example, Marín-Spiotta and Sharma (2013) found that Neotropical second growth forest had SOC stocks similar to nearby undisturbed forest. Cerri et al. (2007) also found small changes in SOC along 11 land-use change chronosequences in the Brazilian Amazon, in both models and measurements. While much work has focused on the changes in surface soils, we provide a valuable dataset to assess deeper changes in SOC and radiocarbon content. Our findings are consistent with Nagy et al. (2018), who also found deep soil C and radiocarbon values were relatively unaffected by land-use change. Although SOC stocks and radiocarbon values were relatively uniform along the succession gradient studied here, SOC stocks in the Old-Mix were much higher, particularly at depth. Because this successional stage was represented by only one plot, the reason for this difference remains unclear. For example, Old-Mix may not have been deforested for reasons linked to the differences in SOC (e.g., more poorly drained area, different soil depth, etc.). Although more data are needed in pristine plots, this dataset suggests that while slash-and-burn events have a huge impact on AGC, the impact on belowground processes is much less pronounced along the chronosequence.

These results suggest that caution is needed when interpreting data from forests classified as old growth. Substantial differences in the carbon stocks of SOld and Old-Mix have the potential to bias datasets across the tropics, especially when assumptions about old growth forest are made as a reference for recovery rates. This might lead to substantial overestimations in the recovery rates of tropical forests. Altogether, we show that the initial recovery of carbon stocks in secondary succession is quite fast across Young to SOld forests. Although our data are inconclusive with respect to Old-Mix, the data suggest that the full recovery to pristine forest carbon stocks might be slower.

Dating of plots in this study must be interpreted with caution. Rather than relying on the exact dates for analysis and interpretation, we prefer to use the charcoal dates as an indicator

and additional evidence for the grouping of plots in successional stages. This uncertainty presents particular challenges for plots in which the age of the last slash-and-burn event is beyond generational memory, since this eliminates the possibility of corroborating interviews. We acknowledge that this method has flaws, as there are significant uncertainties in the radiocarbon dating of charcoal due to high uncertainty in calibrated radiocarbon ages due to variation in atmospheric radiocarbon values during the period of interest for SOld plots (Supporting Information Table S2), uncertainty in the age of the wood itself prior to burning and conversion to charcoal (Gavin, 2001), and possible bias of measurements due to residual SOM adsorbed to the charcoal (Wagner et al., 2018).Thus, care should be taken in interpreting plot ages based on charcoal radiocarbon dates alone. Nevertheless, both the species turnover (Figures 2 and 3) and the structure and carbon stocks (Figure 1) seem to support the classification of our plots into distinct successional classes.

5 | CONCLUSIONS

Overall, we found convincing evidence that the tree species diversity, taxonomic, and functional community assembly of Central African forests recover relatively quickly. However, the two climax forest types and the approx. 200-year-old secondary forest still safeguard a small set of distinct species unique to the respective forest types. Additionally, the recovery of the functional community assembly follows a trajectory from resource acquisition in young forest to resource conservation in climax forest in terms of wood density, specific leaf area, and overall guild classification, except for traits related to nitrogen cycling. Finally, carbon stock recovery seemed to be much slower, with none of the secondary forest types attaining AGC stocks similar to the ones encountered in both climax forest types or those documented in old growth forests across the continent. Altogether, more research on carbon accrual and fluxes in Central African forests is needed to determine whether the apparent slow carbon recovery found in this study holds across the region.

ORCID

Marijn Bauters (iD) https://orcid.org/0000-0003-0978-6639

REFERENCES

Anderson, K. J., Allen, A. P., Gillooly, J. F., & Brown, J. H. (2006). Temperature-dependence of biomass accumulation rates during secondary succession. *Ecology Letters*, *9*, 673–682. https://doi.org/10.1111/j.1461-0248.2006.00914.x

Banin, L., Feldpausch, T. R., Phillips, O. L., Baker, T. R., Lloyd, J., Affum-Baffoe, K., … Lewis, S. L. (2012). What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography*, *21*, 1179–1190. https://doi.org/10.1111/j.1466-8238.2012.00778.x

Bastin, J. F., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., … Bogaert, J. (2015). Seeing Central African forests through their largest trees. *Scientific Reports*, *5*, 1–8.

Bauters, M., Drake, T. W., Verbeeck, H., Bodé, S., Hervé-Fernandez, P., Zito, P., … Boeckx, P. (2018). High fire-derived nitrogen deposition on central African forests. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 549–554. https://doi.org/10.1073/pnas.1714597115

Bauters, M., Mapenzi, N., Kearsley, E., Vanlauwe, B., & Boeckx, P. (2016). Facultative nitrogen fixation by legumes in the central Congo basin is downregulated during late successional stages. *Biotropica*, *48*, 281–284. https://doi.org/10.1111/btp.12312

Bauters, M., Verbeeck, H., Rütting, T., Barthel, M., Bazirake Mujinya, B., Bamba, F., … Boeckx, P. (2019). Contrasting nitrogen fluxes in African tropical forests of the Congo Basin. *Ecological Monographs*, *89*, e01342. https://doi.org/10.1002/ecm.1342

Bauters, M., Vercleyen, O., Vanlauwe, B., Six, J., Bonyoma, B., Badjoko, H., … Boeckx, P. (2019). Data from: Long-term recovery of the functional community assembly and carbon pools in an African tropical forest succession. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.00000

Becknell, J. M., Kissing Kucek, L., & Powers, J. S. (2012). Aboveground biomass in mature and secondary seasonally dry tropical forests: A literature review and global synthesis. *Forest Ecology and Management*, *276*, 88–95. https://doi.org/10.1016/j.foreco.2012.03.033

Becknell, J. M., & Powers, J. S. (2014). Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. *Canadian Journal of Forest Research*, *44*, 604–613. https://doi.org/10.1139/cjfr-2013-0331

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., … Papale, D. (2010). Terrestrial Gross Carbon dioxide uptake: Global distribution and covariation with Climate. *Science*, *329*, 834–839. https://doi.org/10.1126/science.1184984

Boudin, M., van Strydonck, M., van den Brande, T., Synal, H. A., & Wacker, L. (2016). RICH – A new AMS facility at the Royal Institute for Cultural Heritage, Brussels, Belgium. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions With Materials and Atoms*, *361*, 120–123.

Bronk Ramsey, C. (2009). Bayesian analysis of radiocarbon dates. *Radiocarbon*, *51*, 337–360. https://doi.org/10.1017/S0033822200033865

Brown, S., Gillespie, A. J. R., & Lugo, A. E. (1989). Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science*, *35*, 881–902.

Cerri, C. E. P., Easter, M., Paustian, K., Killian, K., Coleman, K., Bernoux, M., ... Cerri, C. C. (2007). Simulating SOC changes in 11 land-use change chronosequences from the Brazilian Amazon with RothC and Century models. *Agriculture, Ecosystems & Environment*, 122, 46–57. https://doi.org/10.1016/j.agee.2007.01.007

Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., ... Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87–99. https://doi.org/10.1007/s00442-005-0100-x

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20, 3177–3190. https://doi.org/10.1111/gcb.12629

Chazdon, R. L. (2008). Beyond deforestation: Restoring degraded lands. *Science*, 1458, 1458–1460. https://doi.org/10.1126/science.1155365

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., ... Miller, S. E. (2009). The potential for species conservation in tropical secondary forests. *Conservation Biology*, 23, 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x

Chomitz, K. M., Buys, P., de Luca, G., Thomas, T. S., & Wertz-Kanounnikoff, S. (2007). *At Loggerheads? Agricultural expansion, poverty reduction, and environment in the tropical forests*. Washington, DC: The World Bank.

Corrales, A., Mangan, S. A., Turner, B. L., Dalling, J. W., Corrales, A., Mangan, S. A., ... Dalling, J. W. (2016). An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. *Ecology Letters*, 19, 383–392. https://doi.org/10.1111/ele.12570

Craine, J. M., Brookshire, E. N. J., Cramer, M. D., Hasselquist, N. J., Koba, K., Marin-Spiotta, E., & Wang, L. (2015). Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant and Soil*, 396, 1–26. https://doi.org/10.1007/s11104-015-2542-1

Craine, J. M., Elmore, A. J., Aidar, M. P. M., Bustamante, M., Dawson, T. E., Hobbie, E. A., ... Pardo, L. H. (2009). Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist*, 183, 980–992. https://doi.org/10.1111/j.1469-8137.2009.02917.x

Craven, D., Hall, J. S., Berlyn, G. P., Ashton, M. S., & van Breugel, M. (2015). Changing gears during succession: Shifting functional strategies in young tropical secondary forests. *Oecologia*, 179, 293–305. https://doi.org/10.1007/s00442-015-3339-x

da Silva Scaranello, M. A., Alves, L. F., Vieira, S. A., de Camargo, P. B., Joly, C. A., Martinelli, L. A., ... de Camargo, P. B. (2012). Height-diameter relationships of tropical Atlantic moist forest trees in southeastern. *Science in Agriculture*, 69, 26–37.

Davidson, E. A., de Carvalho, C. J. R., Figueira, A. M., Ishida, F. Y., Ometto, J. P. H. B., Nardoto, G. B., ... Martinelli, L. A. (2007). Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature*, 447, 995–998. https://doi.org/10.1038/nature05900

Dent, D. H., Dewalt, S. J., & Denslow, J. S. (2013). Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. *Journal of Vegetation Science*, 24, 530–542. https://doi.org/10.1111/j.1654-1103.2012.01482.x

Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D. K., Lebrija-Trejos, E., ... Healey, J. R. (2016). Resilience of tropical dry forests – A meta-analysis of changes in species diversity and composition during secondary succession. *Oikos*, 125, 1386–1397. https://doi.org/10.1111/oik.03229

FAO, (2016). State of the World's Forests. Forests and agriculture: land-use challenges and opportunities. Rome.

Feldpausch, T. R., Lloyd, J., Lewis, S. L., Brienen, R. J. W., Gloor, M., Monteagudo Mendoza, A., ... Phillips, O. L. (2012). Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, 9, 3381–3403. https://doi.org/10.5194/bg-9-3381-2012

Gardner, T. A., Burgess, N. D., Aguilar-Amuchastegui, N., Barlow, J., Berenguer, E., Clements, T., ... Vieira, I. C. G. (2012). A framework for integrating biodiversity concerns into national REDD+ programmes. *Biological Conservation*, 154, 61–71. https://doi.org/10.1016/j.biocon.2011.11.018

Gavin, D. G. (2001). Estimation of inbuilt age in radiocarbon ages of soil charcoal for fire history studies. *Radiocarbon*, 43, 27–44. https://doi.org/10.1017/S003382220003160X

Gehring, C., Denich, M., & Vlek, P. L. G. (2005). Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. *Journal of Tropical Ecology*, 21, 519–527. https://doi.org/10.1017/S0266467405002543

Gerland, P., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B. K., ... Buettner, T. (2014). World population stabilization unlikely this century. *Science*, 346, 234–237. https://doi.org/10.1126/science.1257469

Guariguata, M. R., & Ostertag, R. (2001). Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management*, 148, 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–854. https://doi.org/10.1126/science.1244693

Hawthorne, W. D. D. (1995). Ecological profiles of Ghanaian forest trees. Tropical Forest Paper No. 29, 345.

Huang, S., Titus, S. J., & Wiens, D. P. (1992). Comparison of nonlinear height-diameter functions for major Alberta tree species. *Canadian Journal of Forest Research*, 22, 1297–1304. https://doi.org/10.1139/x92-172

Hubau, W., van den Bulcke, J., van Acker, J., & Beeckman, H. (2015). Charcoal-inferred Holocene fire and vegetation history linked to drought periods in the Democratic Republic of Congo. *Global Change Biology*, 21, 2296–2308. https://doi.org/10.1111/gcb.12844

Jakovac, C. C., Peña-Claros, M., Kuyper, T. W., & Bongers, F. (2015). Loss of secondary-forest resilience by land-use intensification in the Amazon D. Gibson (Ed). *Journal of Ecology*, 103, 67–77. https://doi.org/10.1111/1365-2745.12298

Kearsley, E., Verbeeck, H., Hufkens, K., van de Perre, F., Doetterl, S., Baert, G., ... Huygens, D. (2017). Functional community structure of African monodominant Gilbertiodendron dewevrei forest influenced by local environmental filtering. *Ecology and Evolution*, 7, 295–304. https://doi.org/10.1002/ece3.2589

Keenan, R. J., Reams, G. A., Achard, F., de Freitas, J. V., Grainger, A., & Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *Forest Ecology and Management*, 352, 9–20. https://doi.org/10.1016/j.foreco.2015.06.014

Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G., van der Heijden, G. M., ... Zemagho, L. (2013). Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368, 20120295. https://doi.org/10.1098/rstb.2012.0295

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martinez-Ramos, M., Meave, J. A., Paz, H., ... Bongers, F. (2013). Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, 94, 1211–1216. https://doi.org/10.1890/12-1850.1

Maley, J., Doumenge, C., Giresse, P., Mahé, G., Philippon, N., Hubau, W., ... Chepstow-Lusty, A. (2018). Late Holocene forest contraction and fragmentation in central Africa. *Quaternary Research*, 89, 43–59. https://doi.org/10.1017/qua.2017.97

Malhi, Y., Phillips, O. L., Lloyd, J., Baker, T., Wright, J., Almeida, S., … Vinceti, B. (2002). An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *Journal of Vegetation Science*, *13*, 439–450. https://doi.org/10.1111/j.1654-1103.2002.tb02068.x

Marin-Spiotta, E., Ostertag, R., Silver, W. L., Marín-Spiotta, E., Ostertag, R., & Silver, W. L. (2007). Long-term patterns in tropical reforestation: Plant community composition and aboveground biomass accumulation. *Ecological Applications*, *17*, 828–839. https://doi.org/10.1890/06-1268

Marín-Spiotta, E., & Sharma, S. (2013). Carbon storage in successional and plantation forest soils: A tropical analysis N. Ramankutty (Ed.). *Global Ecology and Biogeography*, *22*, 105–117. https://doi.org/10.1111/j.1466-8238.2012.00788.x

Martin, P. A., Newton, A. C., & Bullock, J. M. (2013). Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B-Biological Sciences*, *280*, 20132236. https://doi.org/10.1098/rspb.2013.2236

Moran, E. F., Brondizio, E. S., Tucker, J. M., da Silva-Forsberg, M. C., Mccracken, S., & Falesi, I. (2000). Effects of soil fertility and land-use on forest succession in Amazônia. *Forest Ecology and Management*, *139*, 93–108. https://doi.org/10.1016/S0378-1127(99)00337-0

Nagy, R. C., Porder, S., Brando, P., Davidson, E. A., Figueira, A. M. E. S., Neill, C., … Trumbore, S. (2018). Soil Carbon dynamics in soybean cropland and forests in Mato Grosso, Brazil. *Journal of Geophysical Research. Biogeosciences*, *123*, 18–31. https://doi.org/10.1002/2017JG004269

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., … Wagner, H. (2013). Package 'vegan.' R Packag. ver. 2.0–8 254.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., … Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*, 988–993. https://doi.org/10.1126/science.1201609

Parmentier, I., Malhi, Y., Senterre, B., Whittaker, R. J., Alonso, A., Balinga, M. P. B., … 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. https://doi.org/10.1111/j.1365-2745.2007.01273.x

Peh, K. S.-H., Sonke, B., Lloyd, J., Quesada, C. A., & Lewis, S. L. (2011). Soil does not explain monodominance in a Central African tropical forest. *PLoS ONE*, *6*, e16996. https://doi.org/10.1371/journal.pone.0016996

Peña-Claros, M. (2003). Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon1. *Biotropica*, *35*, 450. https://doi.org/10.1111/j.1744-7429.2003.tb00602.x

Peñuelas, J. B., Sardans, J. B., Llusia, J. B., Silva, J. B., Owen, S. M. C., Bala-Ola, B., … Niinemets, Ü. (2013). Foliar chemistry and standing folivory of early and late-successional species in a Bornean rainforest. *Plant Ecology and Diversity*, *6*, 245–256. https://doi.org/10.1080/17550874.2013.768713

Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., … Rozendaal, D. M. (2016). Biomass resilience of Neotropical secondary forests. *Nature*, *530*, 211–214. https://doi.org/10.1038/nature16512

Poorter, H., Niinemets, U., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*, 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Powers, J. S., Corre, M. D., Twine, T. E., & Veldkamp, E. (2011). Geographic bias of field observations of soil carbon stocks with tropical land-use changes precludes spatial extrapolation. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 6318–6322. https://doi.org/10.1073/pnas.1016774108

Powers, J. S., & Marín-Spiotta, E. (2017). Ecosystem processes and biogeochemical cycles during secondary tropical forest succession. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 497–519. https://doi.org/10.1146/annurev-ecolsys-110316-022944

R Development Core Team. (2018). *R: A language and environment for statistical computing*. Retrieved from http://www.r-project.org

Reich, P. B. (2014). The world-wide 'fast – slow' plant economics spectrum : A traits manifesto. *Journal of Ecology*, *102*, 275–301. https://doi.org/10.1111/1365-2745.12211

Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Ramsey, C. B., … van der Plicht, J. (2013). IntCal13 and marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, *55*, 1869–1887. https://doi.org/10.2458/azu_js_rc.55.16947

Rozendaal, D. M. A., & Chazdon, R. L. (2015). Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica. *Ecological Applications*, *25*, 506–516. https://doi.org/10.1890/14-0054.1

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675. https://doi.org/10.1038/nmeth.2089

Slik, J. W., Arroyo-Rodríguez, V., Aiba, S., Alvarez-Loayza, P., Alves, L. F., Ashton, P., … Venticinque, E. M. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, E4628–E4629.

Slik, J. W. F., Franklin, J., Arroyo-Rodríguez, V., Field, R., Aguilar, S., Aguirre, N., … Zang, R. (2017). Phylogenetic classification of the world's tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 1837–1842.

Steinhof, A., Altenburg, M., & Machts, H. (2017). Sample preparation at the Jena 14C Laboratory. *Radiocarbon*, *59*, 815–830. https://doi.org/10.1017/RDC.2017.50

Wacker, L., Němec, M., & Bourquin, J. (2010). A revolutionary graphitisation system: Fully automated, compact and simple. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions With Materials and Atoms*, *268*, 931–934. https://doi.org/10.1016/j.nimb.2009.10.067

Wagner, T. V., Mouter, A. K., Parsons, J. R., Sevink, J., van der Plicht, J., & Jansen, B. (2018). Molecular characterization of charcoal to identify adsorbed SOM and assess the effectiveness of common SOM-removing pretreatments prior to radiocarbon dating. *Quaternary Geochronology*, *45*, 74–84. https://doi.org/10.1016/j.quageo.2017.10.006

Whitfeld, T. J. S., Lasky, J. R., Damas, K., Sosanika, G., Molem, K., & Montgomery, R. A. (2014). Species richness, forest structure, and functional diversity during succession in the New Guinea Lowlands. *Biotropica*, *46*, 538–548. https://doi.org/10.1111/btp.12136

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Gulias, J. (2004). The worldwide leaf economics spectrum. *Nature*, *12*, 821–827. https://doi.org/10.1038/nature02403

SUPPORTING INFORMATION

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